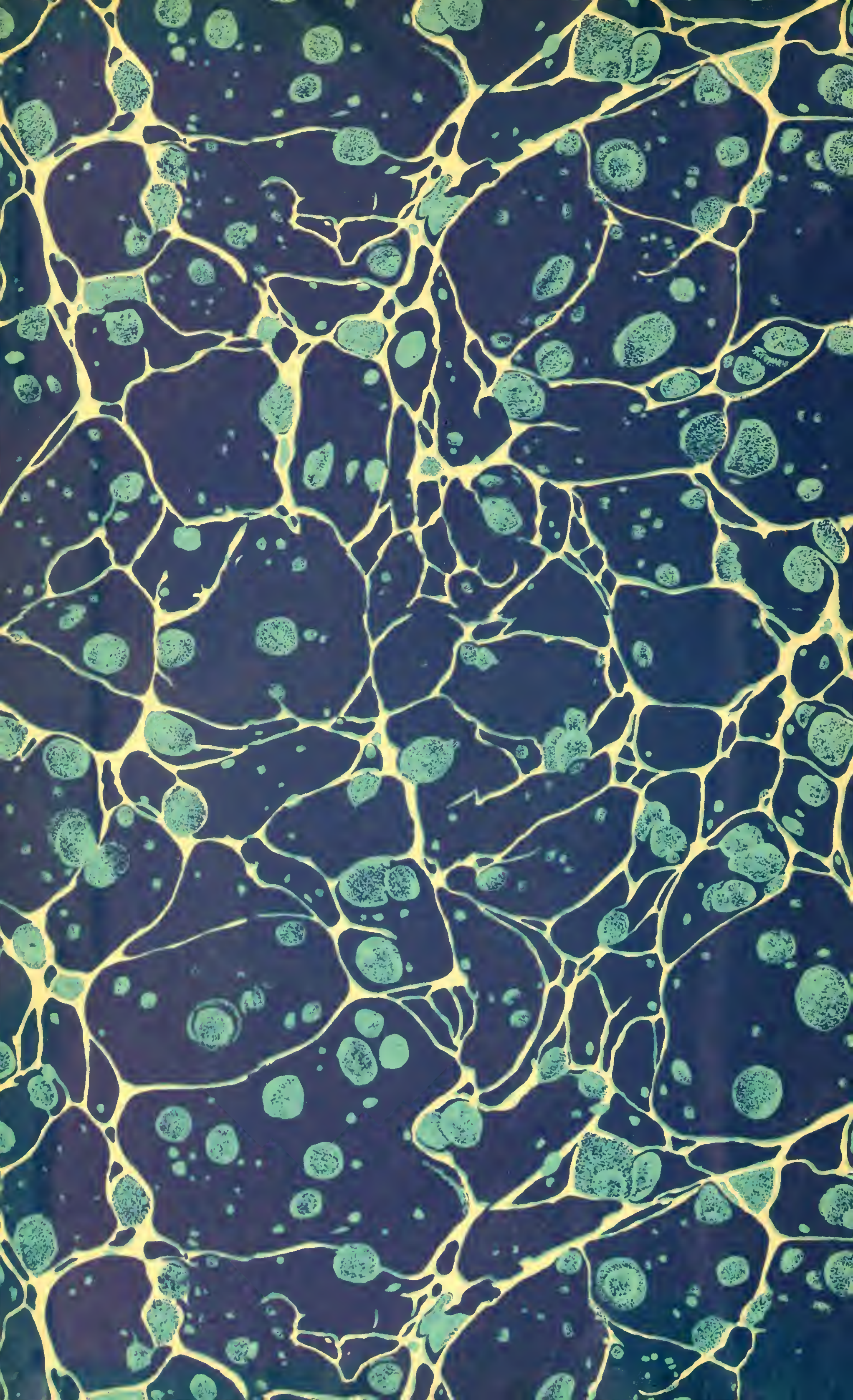

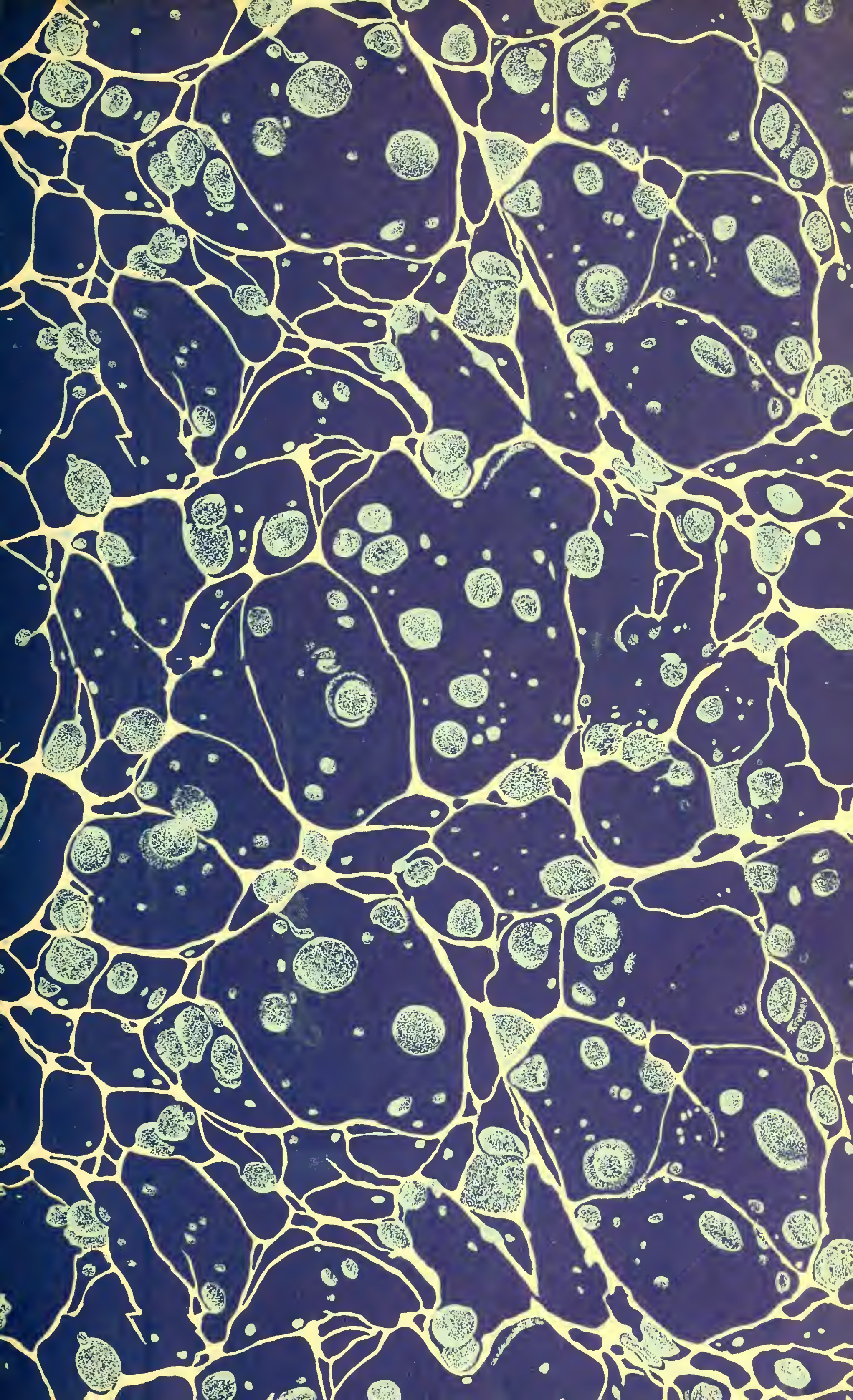

SMITHSONIAN
MISCELLANEOUS COLLECTIONS

VOL. 85

"EVERY MAN IS A VALUABLE MEMBER OF SOCIETY WHO, BY HIS OBSERVATIONS, RESEARCHES, AND EXPERIMENTS, PROCURES KNOWLEDGE FOR MEN"—SMITHSON

(Publication 3175)

CITY OF WASHINGTON
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1933

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C. G. Abbot,
Secretary of the Smithsonian Institution.

CONTENTS

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 85, NUMBER 1

Hodgkins Fund
and
Roebling Fund

WEATHER DOMINATED BY SOLAR CHANGES

BY
C. G. ABBOT

(Publication 3114)

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WEATHER DOMINATED BY SOLAR CHANGES

By C. G. ABBOT

My title suggests a radical change of view regarding weather and weather forecasting. Let us contrast, for a moment, weather and climate. All men realize that it is the sun which furnishes the heat which warms the earth, and that the regular motions of rotation of the earth upon its axis, and of its revolution in its orbit around the sun produce those periodic variations of the solar heating which govern climates. Differences in latitude and of proximity to oceans and to other great terrestrial features introduce alterations from place to place in these periodic changes of solar heating; thereby are produced climatic differences. As regards weather, which consists in departures from regularity in climate, I suppose that practically all meteorologists have been holding hitherto that it depends principally on the complexities of the earth. According to that view, weather represents, as it were, the changing eddies and whirlpools in the Niagara of climate, due to the jutting rocks of local circumstances, and, owing to enormous complexities, is essentially unpredictable for any considerable time in advance.

I shall present evidence to show that weather, on the contrary, is caused chiefly by the frequent interventions of actual changes of the emission of radiation within the sun itself. Local conditions, to be sure, alter the magnitudes and times of the effects of these interventions into terrestrial affairs by the variable sun, but in ways determinable by statistical studies. Hopeful indications will be given that changes of the solar radiation and their weather-consequences may be predictable long in advance.

Figure 1 shows the daily observations of the solar constant of radiation made at Montezuma, Chile, by the Astrophysical Observatory of the Smithsonian Institution since 1924. The values give the intensity of the sun's radiation as it would be found by an observer in free space situated at the earth's mean distance from the sun. As far as possible, they are independent of any effects of the varying trans-

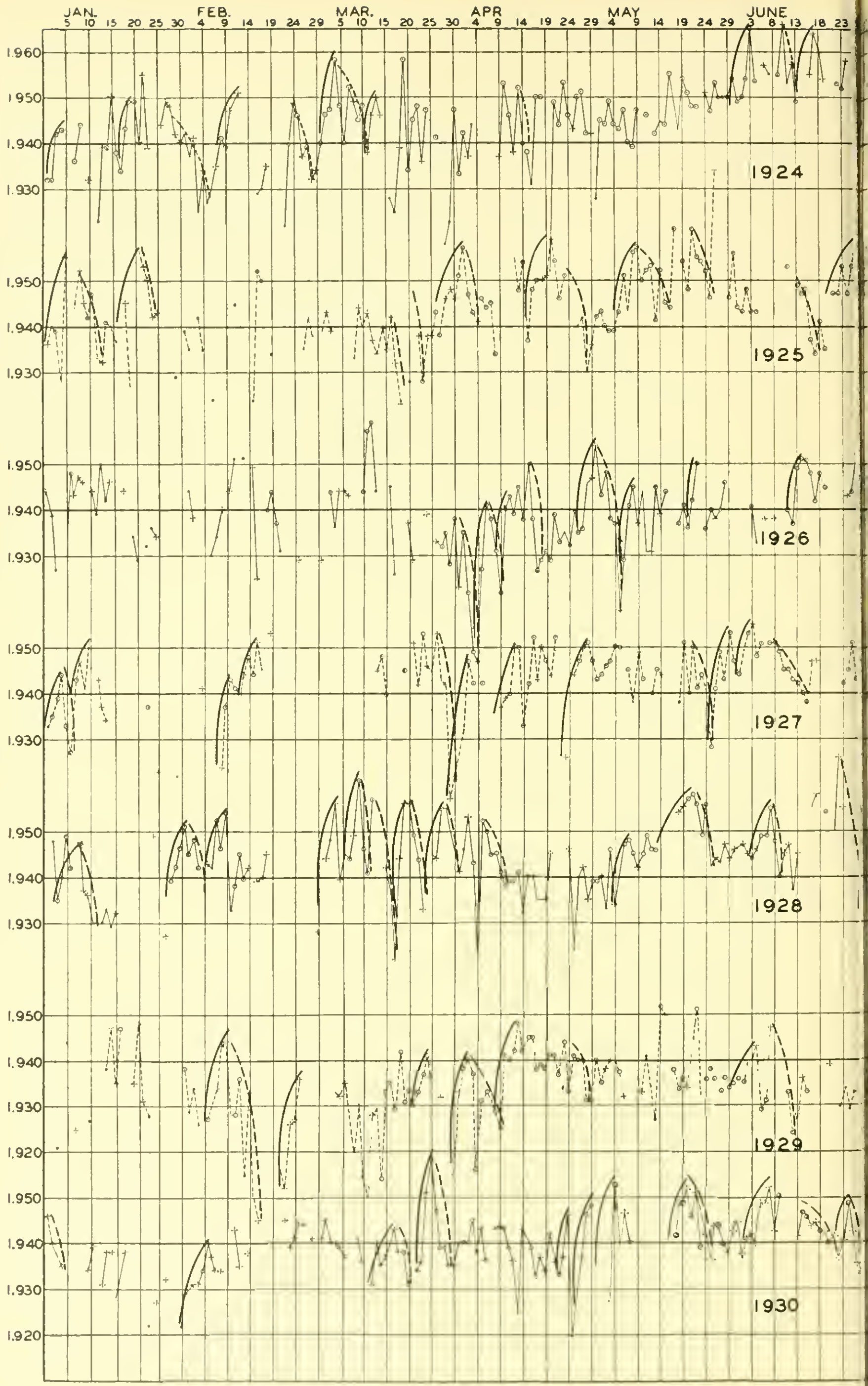
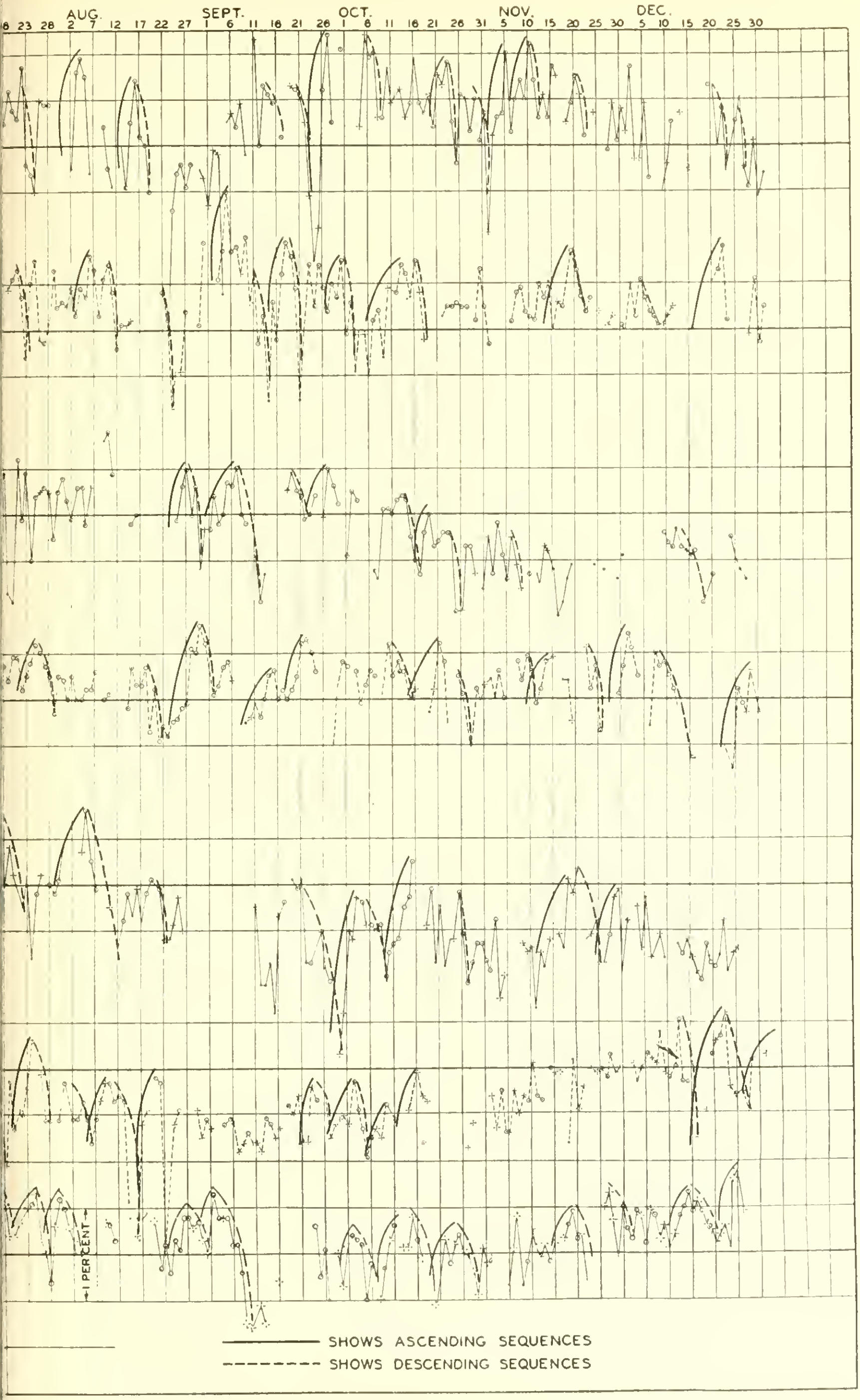


Fig. 1.—Daily observations at Montezuma, Chile, of the "Solar Constant of changing about the mean value, 1.94 calories. Circles, crosses, dots repr



" since 1924. Shows that the sun's gift of rays to warm the earth is frequently
ectively satisfactory, nearly satisfactory, and unsatisfactory observations.

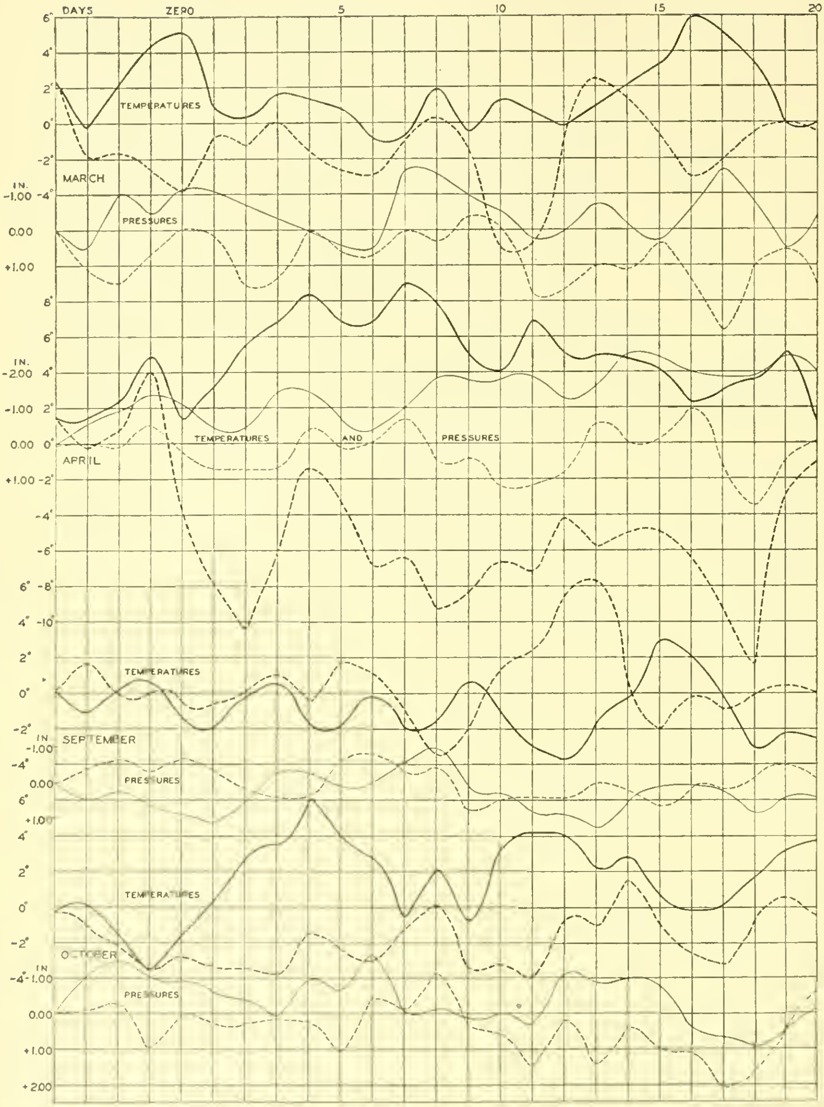


FIG. 2.—Average trends of temperature and pressure at Washington corresponding to average solar changes of 0.8 per cent. The solar changes culminate on the day "zero," but weather effects sometimes occur much later. Weather effects corresponding to rising solar radiation, full lines; to falling radiation, dotted.

TABLE I.—*Washington Mean Temperatures and Temperature Departures*

Ascending solar sequences reach their culmination on zero day

Month of March					Zero Day					5th Day					10th Day					15th Day					20th Day
1924........	29	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
	34.5	42.0	37.5	41.0	47.5	50.0	41.5	42.0	37.5	38.5	36.0	34.5	40.5	39.0	32.5	32.0	36.0	40.5	47.5	43.5	37.5	34.5	41.5	46.0	47.0
	0.0	7.5	3.0	6.5	13.0	15.5	7.0	7.5	3.0	4.0	1.5	0.0	6.0	4.5	—2.0	—2.5	1.5	6.0	13.0	9.0	3.0	0.0	7.0	11.5	12.5
1924........	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2
	38.5	36.0	34.5	40.5	39.0	32.5	32.0	36.0	40.5	47.5	43.5	37.5	34.5	41.5	46.0	47.0	44.5	46.0	44.0	56.5	61.5	60.5	43.0	34.0	35.5
	0.0	—2.5	—4.0	+2.0	+0.5	—6.0	—6.5	—2.5	+2.0	+9.0	+5.0	—1.0	—4.0	+3.0	+7.5	+8.5	+6.0	+7.5	+5.5	+18.0	+23.0	+22.0	+4.5	—4.0	—3.0
1928........	29	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
	45.5	41.0	37.0	36.0	37.5	33.5	32.0	43.5	43.5	38.5	38.5	38.0	46.0	49.5	50.5	46.0	39.5	37.0	36.5	35.5	38.5	40.5	50.0	56.0	59.5
	0.0	—4.5	—8.5	—9.5	—8.0	—12.0	—13.5	—2.0	—2.0	—7.0	—7.0	—7.5	+0.5	+4.0	+5.0	+0.5	—6.0	—8.5	—9.0	—10.0	—7.0	—5.0	+4.5	+10.5	+14.0
1928........	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
	33.5	32.0	43.5	43.5	38.5	38.5	38.0	46.0	49.5	50.5	46.0	39.5	37.0	36.5	35.5	38.5	40.5	50.0	56.0	59.5	67.5	65.0	51.5	45.5	48.5
	0.0	—1.5	+10.0	+10.0	+5.0	+5.0	+4.5	+12.5	+16.0	+17.0	+12.5	+6.0	+3.5	+3.0	+2.0	+5.0	+7.0	+16.5	+22.5	+26.0	+34.0	+31.5	+18.0	+12.0	+15.0
1928........	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9
	39.5	37.0	36.5	35.5	38.5	40.5	50.0	56.0	59.5	67.5	65.0	51.5	45.5	48.5	46.5	39.5	42.5	46.5	52.0	61.5	70.0	70.5	66.0	55.5	49.0
	0.0	—2.5	—3.0	—4.0	—1.0	+1.0	+10.5	+16.5	20.0	+28.0	+25.5	+12.0	+6.0	+9.0	+7.0	0.0	+3.0	+7.0	+12.5	+22.0	+30.5	+31.0	+26.5	+16.0	+8.5
1928........	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	56.0	59.5	67.5	65.0	51.5	45.5	48.5	46.5	39.5	42.5	46.5	52.0	61.5	70.0	70.5	66.0	55.5	49.0	41.5	38.0	50.5	57.5	64.0	46.5	40.0
	0.0	+3.5	+11.5	+9.0	—4.5	—10.5	—7.5	—9.5	—16.5	—13.5	—9.5	—4.0	+5.5	+14.0	+14.5	+10.0	—0.5	—7.0	—14.5	—18.0	—5.5	+1.5	+8.0	—9.5	—16.0
1929........	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13
	56.0	56.0	69.5	68.0	68.5	58.0	65.0	53.5	54.0	48.5	44.5	49.0	63.0	49.0	58.5	67.0	69.0	74.0	77.5	76.0	68.0	50.5	44.0	53.5	56.5
	0.0	0.0	+13.5	+12.0	+12.5	+2.0	+9.0	—2.5	—2.0	—7.5	—11.5	—7.0	+7.0	—7.0	+2.5	+11.0	+13.0	+18.0	+21.5	+20.0	+12.0	—5.5	—12.0	—2.5	+0.5
1930........	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6
	53.0	45.0	39.0	48.0	59.0	62.5	50.5	46.5	43.5	31.5	38.5	49.5	56.5	39.5	42.0	44.0	47.5	43.0	53.5	48.0	48.0	40.0	50.0	50.5	51.0
	0.0	—8.0	—14.0	—5.0	+6.0	+9.5	—2.5	—6.5	—9.5	—21.5	—14.5	—3.5	+3.5	—13.5	—11.0	—9.0	—5.5	—10.0	+0.5	—5.0	—5.0	—13.0	—3.0	—2.5	—2.0
1930........	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	43.5	31.5	38.5	49.5	56.5	39.5	42.0	44.0	47.5	48.5	43.0	53.5	48.0	40.0	50.0	50.5	51.0	53.5	45.0	46.5	51.5	69.0	65.5	58.5	64.5
	0.0	—12.0	—5.0	+6.0	+13.0	—4.0	—1.5	+0.5	+4.0	+5.0	—0.5	+10.0	+4.5	—3.5	+6.5	+7.0	+7.5	+10.0	+1.5	+3.0	+8.0	+25.5	+22.0	+15.0	+21.0
Means	0.0	—2.22	+0.39	+3.00	+4.06	+0.06	—0.06	+1.56	+1.67	+1.50	+0.17	—0.56	+3.61	+1.50	+3.56	+3.39	+2.89	+4.39	+5.94	+7.22	+10.33	+9.78	+8.39	+5.17	+5.61
Yearly march..	—2.40	—2.00	—1.70	—1.40	—1.10	—0.80	—0.40	—0.10	0.30	0.70	1.00	1.30	1.70	2.00	2.30	2.70	3.00	3.30	3.70	4.00	4.30	4.70	5.00	5.30	5.70
Corrected means ...	2.40	—0.22	2.09	4.40	5.16	0.86	0.34	1.66	1.37	0.80	—0.83	—0.74	1.91	—0.50	1.26	0.69	—0.11	1.09	2.24	3.22	6.03	5.08	3.39	—0.13	—0.11

TABLE 2.—*Washington Mean Temperatures and Temperature Departures*

Descending solar sequences reach their culmination on zero day

Month of March					Zero Day					5th Day					10th Day					15th Day					20th Day
1924	7 42.0 —0.0	8 37.5 —4.5	9 38.5 —3.5	10 36.0 —6.0	11 34.5 —7.5	12 40.5 —1.5	13 39.0 —3.0	14 32.5 —9.5	15 32.0 —10.0	16 36.0 —6.0	17 40.5 —1.5	18 47.5 +5.5	19 43.5 +1.5	20 37.5 —4.5	21 34.5 —7.5	22 41.5 —0.5	23 46.0 +4.0	24 47.0 +5.0	25 44.5 +2.5	26 46.0 +4.0	27 44.0 +2.0	28 56.5 +14.5	29 61.5 +19.5	30 60.5 +18.5	31 43.0 +1.0
1925	14 57.0 0.0	15 38.5 —18.5	16 39.5 —17.5	17 45.5 —11.5	18 49.5 —7.5	19 59.0 +2.0	20 48.0 —9.0	21 52.0 —5.0	22 50.5 —6.5	23 43.0 —14.0	24 47.0 —10.0	25 57.5 +0.5	26 58.0 +1.0	27 54.0 —3.0	28 43.5 —13.5	29 37.5 —19.5	30 41.0 —16.0	31 46.5 —10.5	1 46.0 —11.0	2 42.5 —14.5	3 51.0 —16.0	4 52.5 —4.5	5 50.5 —6.5	6 44.5 —12.5	7 49.0 —8.0
1925	19 59.0 0.0	20 48.0 —11.0	21 52.0 —7.0	22 50.5 —8.5	23 43.0 —16.0	24 47.0 —12.0	25 57.5 —1.5	26 58.0 —1.0	27 54.0 —5.0	28 43.5 —15.5	29 37.5 —21.5	30 41.0 —18.0	31 46.5 —2.5	1 46.0 —3.0	2 42.5 —16.5	3 51.0 —8.0	4 52.5 —6.5	5 50.5 —8.5	6 44.5 —14.5	7 49.0 —10.0	8 54.5 —4.5	9 51.5 —7.5	10 59.5 +0.5	11 59.0 0.0	12 63.0 +4.0
1927	25 42.5 0.0	26 47.5 +5.0	27 43.5 +1.0	28 44.0 +1.5	29 43.0 +0.5	30 46.0 +3.5	31 51.0 +8.5	1 44.0 +1.5	2 39.0 —3.5	3 42.0 —0.5	4 39.0 —3.5	5 41.0 —1.5	6 54.0 +11.5	7 49.0 +6.5	8 43.5 +1.0	9 39.0 —3.5	10 45.0 +2.5	11 48.5 +5.5	12 54.0 +11.5	13 52.0 +9.5	14 49.5 +7.0	15 53.5 +11.0	16 63.5 +21.0	17 64.5 +22.0	18 61.5 +19.0
1928	7 43.5 0.0	8 43.5 0.0	9 38.5 —5.0	10 38.5 —5.0	11 38.0 —5.5	12 46.0 +2.5	13 49.5 +6.0	14 50.5 +7.0	15 46.0 +2.5	16 39.5 —4.0	17 37.0 —6.5	18 36.5 —7.0	19 35.5 —8.0	20 38.5 —5.0	21 40.5 —3.5	22 50.0 +6.5	23 56.0 +12.5	24 59.5 +16.0	25 67.5 +24.0	26 65.0 +21.5	27 51.5 +8.0	28 45.5 +2.0	29 48.5 +5.0	30 46.5 +3.0	31 39.5 —4.0
1928	13 49.5 0.0	14 50.5 +1.0	15 46.0 —3.5	16 39.5 —10.0	17 37.0 —12.5	18 36.5 —13.0	19 35.5 —14.0	20 38.5 —11.0	21 40.5 —9.0	22 50.0 +0.5	23 56.0 +6.5	24 59.5 +10.0	25 67.5 +18.0	26 63.0 +15.5	27 51.5 +2.0	28 45.5 —4.0	29 48.5 —1.0	30 46.5 —3.0	31 39.5 —10.0	1 42.5 —7.0	2 46.5 —3.0	3 52.0 +2.5	4 61.5 +12.0	5 70.0 +20.5	6 70.5 +21.0
1928	19 35.5 0.0	20 38.5 +3.0	21 40.5 +5.0	22 50.0 +14.5	23 56.0 +20.5	24 59.5 +24.0	25 67.5 +32.0	26 65.0 +29.5	27 51.5 +16.0	28 45.5 +10.0	29 48.5 +13.0	30 46.5 +11.0	31 39.5 +4.0	1 42.5 +7.0	2 46.5 +11.0	3 52.0 +16.5	4 61.5 +26.0	5 70.0 +34.5	6 70.5 +35.0	7 66.0 +30.5	8 55.5 +20.0	9 49.0 +13.5	10 41.5 +6.0	11 38.0 +2.5	12 50.5 +15.0
1928	27 51.5 0.0	28 45.5 —6.0	29 48.5 —3.0	30 46.5 —5.0	31 39.5 —12.0	1 42.5 —9.0	2 46.5 —5.0	3 52.0 +0.5	4 61.5 +10.0	5 70.0 +18.5	6 70.5 +19.0	7 66.0 +14.5	8 55.5 +4.0	9 49.0 —2.5	10 41.5 —10.0	11 38.0 —13.5	12 50.5 —1.0	13 57.5 +6.0	14 64.0 +12.5	15 46.5 —5.0	16 40.0 —11.5	17 44.0 —7.5	18 44.5 —7.0	19 65.5 +14.0	20 56.0 +4.5
1930	16 48.0 0.0	17 59.0 +11.0	18 62.5 +14.5	19 50.5 +2.5	20 46.5 —1.5	21 43.5 —4.5	22 31.5 —16.5	23 38.5 —9.5	24 49.5 +1.5	25 56.5 +8.5	26 39.5 —8.5	27 42.0 —6.0	28 44.0 —4.0	29 47.5 —0.5	30 48.5 +0.5	31 43.0 —5.0	1 53.5 +5.5	2 48.0 0.0	3 40.0 —8.0	4 50.0 +2.0	5 50.5 +2.5	6 51.0 +3.0	7 53.5 +5.5	8 45.0 —3.0	9 46.5 —1.5
1930	25 56.5 0.0	26 39.5 —17.0	27 42.0 —14.5	28 44.0 —12.5	29 47.5 —9.0	30 48.5 —7.5	31 43.0 —13.5	1 53.5 —3.0	2 48.0 —8.5	3 40.0 —16.5	4 50.0 —6.5	5 50.5 —6.0	6 51.0 —5.5	7 53.5 —3.0	8 45.0 —11.5	9 46.5 —10.0	10 51.5 —5.0	11 69.0 +12.5	12 65.5 +9.0	13 58.5 +2.0	14 64.5 +8.0	15 56.0 —0.5	16 46.0 —10.5	17 44.5 —12.0	18 56.5 0.0
Mean	0.0	—3.70	—3.35	—4.00	—5.05	—1.55	—1.60	—0.05	—1.25	—1.90	—1.95	+0.30	+2.00	+0.75	—4.80	—4.10	+2.10	+5.75	+5.10	+3.30	+1.25	+2.65	+4.55	+5.30	+5.10
Yearly march	—2.40	—2.00	—1.70	—1.40	—1.10	—0.80	—0.40	—0.10	+0.30	+0.70	1.00	1.30	1.70	2.00	2.30	2.70	3.00	3.30	3.70	4.00	4.30	4.70	5.00	5.30	5.70
Corrected means	2.40	—1.70	—1.65	—2.60	—3.85	—0.75	—1.20	+0.05	—1.55	—2.60	—2.95	—1.00	0.30	—1.25	—7.10	—6.80	—0.90	2.45	1.40	—0.70	—3.05	—2.05	—0.45	0.0	—0.60

parency of our earth's atmosphere. No appreciable 12-month periodicity appears in the results. This is a good sign of their independence of atmospheric influences. Full and dotted curves in Figure 1 mark all the well-supported sequences of rising and of falling solar radiation. They occur in short intervals, averaging 5 days. All of those selected exceed 0.4 per cent in range, averaging 0.8 per cent. These rising and falling sequences are 111 and 106 in number, respectively. Many are lost because of unfavorable observing conditions.

Figure 2 shows average changes in the mean temperature and the barometric pressure at Washington, D. C., associated with these rising and falling sequences of solar radiation, during the months of March, April, September, and October. These meteorological exhibits are average values representing the work of 7 years, and of about 10 cases of each kind in each month.

The method of computing the curves shown in figure 2 is illustrated in tables 1 and 2 as regards temperatures of March. The temperatures (which are the mean of maximum and minimum at Washington as published by the U. S. Weather Bureau) are arranged in consecutive series of 25 days each. In each series, the fifth day is that on which the solar change examined reached its culmination. Departures of temperatures are always computed from the first day of the series as the base. The mean values of all the departures occurring in March in the years 1924 to 1930 are given at the foot of the table. They are corrected to eliminate the secular rise of temperature which, of course, occurs during any 25-day interval at that season of the year. The final result is plotted in figure 2. The reader will see that in all cases there is a marked opposition between curves corresponding to rising and falling solar radiation, respectively.

Eleven physicists to whom I have shown these results unanimously concur in advising me that the constant opposition of the weather effects following opposite solar causes demonstrates a physical connection between the weather of Washington and the changes in the solar constant of radiation as observed in Chile. Average changes of mean temperature of 5° Fahrenheit are found corresponding to solar changes averaging only 0.8 per cent. Hence we may suppose that on many occasions temperature effects caused by solar changes may reach 10°, and sometimes 15° or 20°. *That is to say, major changes in weather are due to short period changes in the sun.* So revolutionary is this conclusion for meteorology, that I hesitated to publish it until the unanimous approval of many competent critics encouraged me. I am further supported in this view by having found a similar opposition of relations prevailing not only at Washington but at Williston, North Dakota, and Yuma, Arizona, in all months of the year.

By what physical connection are these surprising meteorological results produced by such small solar changes? We must discard at once, I think, the idea that changes of ground temperature, directly produced, communicate the effects to the surface air. For firstly, by Stefan's law, in equilibrium conditions radiation varies as the fourth power of the absolute temperature. Hence a change of 1 per cent in radiation, if acting directly and in equilibrium conditions, should require but $\frac{1}{4}$ per cent change in the earth's temperature. Actually the change of temperature observed exceeds 1 per cent, reckoned from the absolute zero. Secondly, in March and some other months, a temperature effect at Washington is found to be nearly simultaneous with the solar change. The solid earth has too large a capacity for heat to follow in temperature thus quickly. Thirdly, large effects occur at Washington 10 or 12 days, and sometimes 16 or 17 days, after the solar cause ceases. Not all of these effects can be direct. Fourthly, in September a reversal of sign is observed.

Admitting that the meteorological effects are produced indirectly, let us recall: Firstly, that from 10 to 25 per cent of the solar radiation is primarily absorbed in the atmosphere itself, which has a very small capacity for heat. Secondly, that the atmosphere circulates in great cyclonic whirls. Thirdly, that the temperature of a station depends greatly on the prevailing wind direction. May it not be that the instantaneous changes of heat absorption in the atmosphere tend to displace centers of cyclones, and thereby to alter the wind direction at stations, thus altering their temperatures?

How shall we explain deferred effects occurring 10 or even 17 days after the culmination of solar sequences? May they not result from atmospheric waves drifting in a southeasterly direction from distant centers of action where primary effects are produced? If so, we must perceive that the average effects shown in tables 1 and 2 can form no trustworthy basis for forecasting individual cases. For primary and secondary effects, treading on each other's heels, as it were, must often interfere, and either augment or reduce expected weather changes.

SOLAR PERIODICITIES

It would be encouraging from a forecaster's standpoint if definite periodicities should be found in solar variations. In table 3 are given 10-day mean values of solar radiation from 1918 to 1930.[1] A tendency towards the recurrence of a certain form of 8 months' period was discovered in the 10-day means. To evaluate this periodicity, the 10-day mean values were arranged in a table of 9 lines of 24 consecutive values each, beginning with May, 1924. Mean values of the 24 columns being computed, they resulted thus:

8-month period

Direct Means[a]	40	41	42	41	44	41	41	42	41	43	42	40	41	42
Smoothed Means	40	41	42	42	43	42	42	42	42	42	41	41	41	41
Smoothed Departures	0	+1	+2	+2	+3	+2	+2	+2	+2	+2	+1	+1	+1	+1
Direct Means[a]	39	41	40	38	41	41	39	38	37	37				
Smoothed Means	41	40	40	40	39	39	39	38	37	37				
Smoothed Departures	+1	0	0	0	−1	−1	−1	−2	−3	−3				

[a] First two figures omitted. Thus for 1.940 calories, I substitute 40. Departures are given from 1.940, omitting three figures.

From these numbers a smoothed curve was drawn which gave the departures from 1.940 calories. Subtracting these departures, the original data were cleared of the 8-month periodicity from January, 1924, to December, 1930. It was then perceived that another periodicity of 11 months seemed present. By a similar arrangement in lines of 33 consecutive revised 10-day means of solar constant numbers, the following values were computed, representing the 11-month periodicity:

11-month period

Direct Means	40	41	39	38	38	36	38	39	35	37	37	34	38	40
Smoothed Means	41	40	39	38	38	37	37	37	36	36	36	37	38	39
Smoothed Departures	1	0	−1	−2	−2	−3	−3	−3	−4	−4	−4	−3	−2	−1
Direct Means	40	41	43	44	41	40	38	42	42	40	42	45	43	46
Smoothed Means	40	41	42	42	41	40	40	41	41	42	42	43	45	46
Smoothed Departures	0	1	2	2	1	0	0	1	1	2	2	3	5	6
Direct Means	44	45	43	43	41									
Smoothed Means	45	44	43	42	41									
Smoothed Departures	5	4	3	2	1									

As these two periodicities had been evaluated solely from results of 1924 to 1930, I desired to see whether they were also in evidence from 1918 to 1923. For this purpose, I made templates fitting the smoothed-curve departures for both periodicities. These templates I traced again and again in their proper phases to fill the entire period

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[1] The best values are those obtained since January, 1924. Prior to August, 1920, all observations were made in the outskirts of the city of Calama, amid dust and smoke, and with less perfect equipment than subsequently. Prior to January, 1919, there was only one observation per day and by the "long" method.

from August, 1918, to December, 1930. I then added their amplitudes algebraically. This produced a curve which obviously bore a considerable resemblance to the curve A of figure 3 throughout its whole extent. This indicated that both 8- and 11-month periodicities have prevailed in solar radiation since 1918.

I now desired to search for longer periodicities. It seemed better to use monthly mean values for this, as given in table 4 and figure 3, A. Having read from the curve of combined departures of 8-month and 11-month periodicities the departures for the second decade of each month from 1918 to 1930, I subtracted these from curve A, figure 3, and replotted the again-revised data. This curve seemed to indicate the existence of a periodicity of 45 months. Arranging the corrected solar values in lines of consecutive 45's, and proceeding as previously, the following result appeared:

45-month period

Direct Means	29	32	41	35	37	28	41	33	41	44	47	37	43	45
Smoothed Means	33	33	34	35	36	37	38	39	40	41	42	43	43	44
Smoothed Departures	−7	−7	−6	−5	−4	−3	−2	−1	0	+1	+2	+3	+3	+4
Direct Means	44	45	41	38	46	46	44	46	41	50	43	43	47	44
Smoothed Means	44	45	45	45	46	46	46	46	46	46	45	45	45	45
Smoothed Departures	+4	+5	+5	+5	+6	+6	+6	+6	+6	+6	+5	+5	+5	+5
Direct Means	44	39	40	40	38	48	40	47	47	41	41	39	40	39
Smoothed Means	45	45	45	44	44	43	43	42	41	41	40	39	37	36
Smoothed Departures	+5	+5	+5	+4	+4	+3	+3	+2	+1	+1	0	−1	−3	−4
Direct Means	36	35	31											
Smoothed Means	35	34	33											
Smoothed Departures	−5	−6	−7											

After removing the 45-month periodicity as in former cases, there seemed to exist a periodicity of 25 months, which by similar treatment resulted as follows:

25-month period

Direct Means	30	33	30	37	34	32	41	38	38	38	38	37	38	44
Smoothed Means	32	32	33	34	34	35	35	36	37	38	39	39	40	40
Smoothed Departures	−8	−8	−7	−6	−6	−5	−5	−4	−3	−2	−1	−1	0	0
Direct Means	41	44	43	40	43	42	42	43	42	40	33			
Smoothed Means	40	41	41	42	42	42	42	42	41	40	35			
Smoothed Departures	0	+1	+1	+2	+2	+2	+2	+2	+1	0	−5			

Removing the 25-month periodicity, as before, a nearly smooth curve resulted in which the 68-month period corresponding to a half sun-spot period was clearly seen. The coordinates of the five periods discovered are as follows:

Coordinates of Periods

Length in Months	Amplitude in Calories	Date of Zero Departure
68	.014	Dec. 15, 1929
45	.013	Sept. 15, 1930
25	.010	Nov. 15, 1929
11	.009	Dec. 1, 1929
8	.005	May 1, 1930

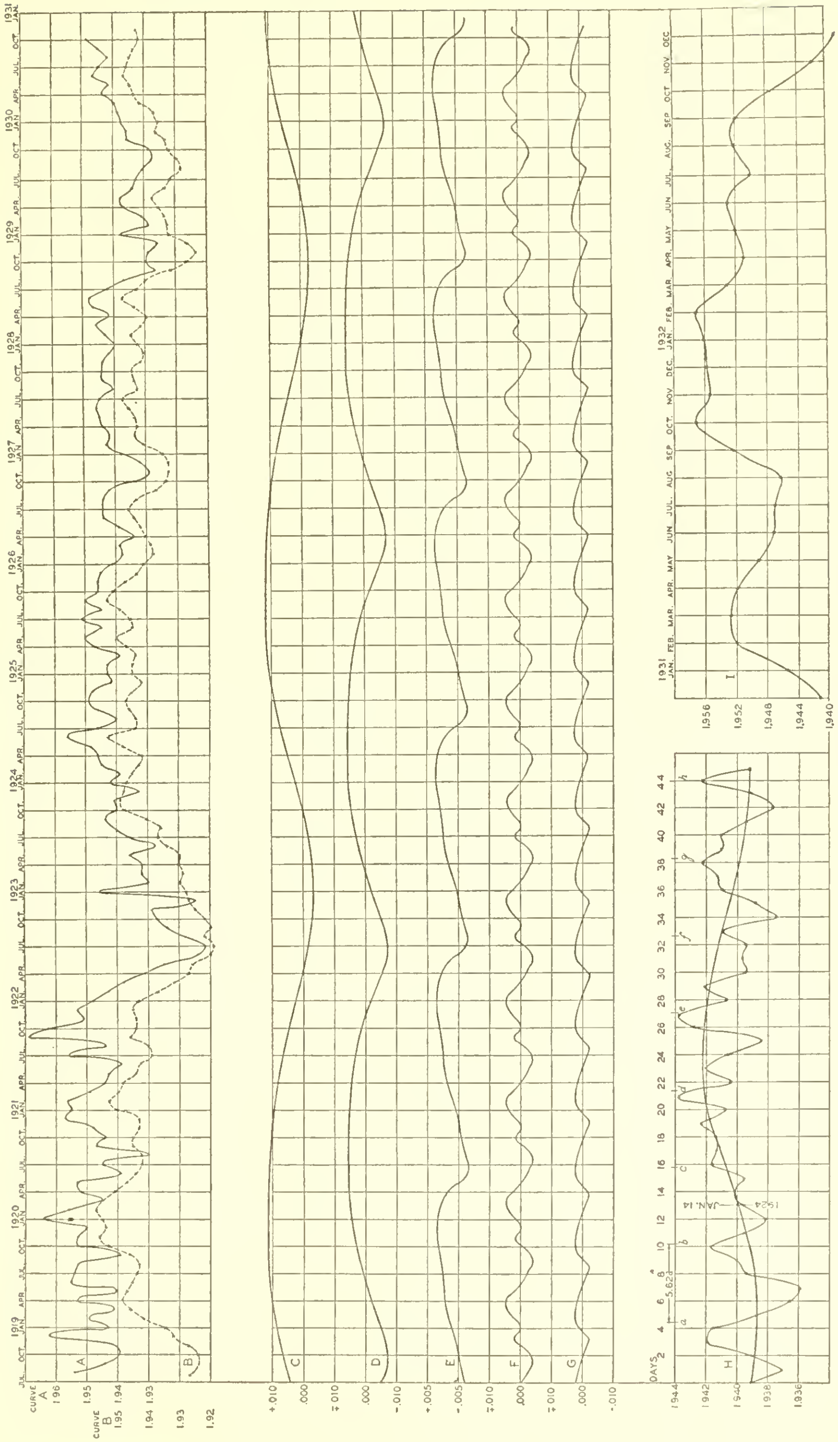

FIG. 3.—Periodicities in solar radiation.

I next made templates and traced the five periods hitherto described in a way to cover the entire interval 1918 to 1930. The total effect of the five periodicities is summed up algebraically in curve B, which will be seen to represent the main features and even most details of

TABLE 3.—*Ten-Day Solar Constant Values, 1918-1930*

Decade		1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930
Jan.	1		1.943	1.968	1.956	1.924	1.946	1.937	1.945	1.944	1.939	1.941	1.925	1.938
	2		1.948	1.967	1.953	1.946	.....	1.943	1.939	1.943	1.938	1.931	1.941	1.937
	3		1.938	1.959	.....	1.952	.....	1.944	1.947	1.933	1.931	1.942	1.939	1.929
Feb.	1		1.962	1.958	.....	1.911	1.934	1.938	.....	1.938	1.936	1.947	1.937	1.933
	2		1.951	1.954	1.952	1.947	1.951	1.943	1.951	1.939	1.946	1.941	1.925	1.939
	3		1.930	1.956	1.958	1.948	1.923	1.938	1.938	1.929	.....	1.934	1.925	1.942
Mar.	1		1.950	1.959	1.954	1.949	1.929	1.947	1.941	1.941	.....	1.950	1.932	1.940
	2		1.942	1.948	1.940	1.939	1.936	1.944	1.936	1.948	1.944	1.945	1.931	1.937
	3		1.931	1.932	.....	1.932	1.931	1.942	1.941	1.932	1.941	1.945	1.932	1.941
Apr.	1		1.943	1.948	1.951	1.930	1.934	1.942	1.945	1.927	1.941	1.946	1.932	1.941
	2		1.957	1.956	1.941	1.937	1.928	1.948	1.950	1.937	1.945	1.940	1.942	1.938
	3		1.961	1.952	1.934	1.925	1.934	1.947	1.946	1.939	1.945	1.940	1.938	1.941
May	1		1.953	1.950	1.946	1.924	1.934	1.944	1.946	1.937	1.947	1.943	1.936	1.945
	2		1.921	1.961	1.939	1.925	1.935	1.948	1.950	1.938	1.944	1.951	1.941	1.948
	3		1.945	1.950	1.941	.....	1.937	1.950	1.954	1.942	1.944	1.949	1.937	1.942
June	1		1.957	1.943	1.933	1.910	1.918	1.957	1.943	1.939	1.950	1.947	1.938	1.949
	2		1.938	1.934	1.936	1.913	1.934	1.956	1.943	1.946	1.943	1.948	1.932	1.944
	3		1.962	1.938	1.945	1.920	1.933	1.953	1.948	1.945	1.945	1.951	1.932	1.941
July	1		1.951	1.945	1.960	1.904	1.934	1.946	1.952	1.942	1.949	1.943	1.935	1.945
	2		1.961	1.940	1.957	1.913	1.928	1.951	1.954	1.949	1.942	1.942	1.931	1.949
	3	1.921	1.950	1.951	1.953	1.918	1.944	1.942	1.947	1.944	1.946	1.940	1.935	1.947
Aug.	1	1.955	1.961	1.930	1.944	1.919	1.942	1.950	1.949	1.945	1.942	1.943	1.931	1.946
	2	1.945	1.942	1.927	.....	1.916	1.940	1.940	1.941	1.942	1.941	1.937	1.932	1.947
	3	1.959	1.955	1.932	.....	1.921	1.941	1.933	1.942	1.942	1.941	1.932	1.930	1.943
Sept.	1	1.942	1.938	1.951	.....	.....	1.945	1.941	1.956	1.942	1.940	.....	1.926	1.942
	2	1.946	1.942	1.944	.....	1.932	1.944	1.950	1.946	1.940	1.942	1.938	1.928	1.929
	3	1.944	1.937	1.944	1.969	1.916	1.942	1.946	1.950	1.943	1.950	1.921	1.930	1.939
Oct.	1	1.951	1.947	1.942	1.959	1.926	1.940	1.953	1.942	1.938	1.945	1.930	1.928	1.939
	2	1.930	1.949	1.950	1.969	1.929	1.942	1.949	1.949	1.937	1.944	1.935	1.933	1.941
	3	1.933	1.960	1.943	1.966	.....	1.938	1.948	1.946	1.929	1.943	1.927	1.926	1.939
Nov.	1	1.928	1.958	1.951	1.953	1.929	1.934	1.948	1.944	1.931	1.945	1.924	1.932	1.942
	2	1.945	1.951	1.946	1.949	1.935	1.944	1.951	1.948	1.926	1.943	1.932	1.936	1.943
	3	1.947	1.948	1.945	1.952	1.920	1.944	1.945	1.944	1.930	1.944	1.930	1.939	1.949
Dec.	1	1.962	1.944	1.957	1.956	1.912	1.942	1.942	1.944	1.935	1.949	1.930	1.941	1.945
	2	1.969	1.949	1.957	1.938	1.916	1.942	1.947	1.945	1.931	1.935	1.924	1.939	1.948
	3	1.960	1.958	1.956	.....	1.912	1.921	1.939	1.946	1.935	1.939	1.927	1.940	1.951

TABLE 4.—*Monthly Mean Solar Constant Values, 1918-1930*

Month	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930
Jan.		1.943	1.964	1.955	1.948	1.946	1.942	1.943	1.941	1.938	1.940	1.938	1.936
Feb.		1.949	1.956	1.956	1.943	1.930	1.939	1.943	1.938	1.943	1.943	1.929	1.938
Mar.		1.941	1.945	1.949	1.938	1.932	1.945	1.939	1.939	1.942	1.946	1.931	1.939
Apr.		1.953	1.952	1.944	1.931	1.932	1.946	1.947	1.934	1.944	1.942	1.937	1.940
May		1.940	1.953	1.943	1.925	1.936	1.948	1.950	1.939	1.945	1.947	1.938	1.944
June		1.955	1.939	1.939	1.914	1.928	1.955	1.945	1.944	1.946	1.948	1.934	1.943
July	1.921	1.954	1.945	1.956	1.912	1.936	1.946	1.951	1.944	1.945	1.942	1.933	1.947
Aug.	1.954	1.953	1.930	1.944	1.918	1.941	1.940	1.945	1.944	1.941	1.937	1.931	1.945
Sept.	1.944	1.939	1.947	1.969	1.924	1.944	1.946	1.950	1.942	1.944	1.927	1.928	1.937
Oct.	1.939	1.953	1.944	1.962	1.927	1.940	1.949	1.946	1.934	1.944	1.930	1.929	1.940
Nov.	1.941	1.953	1.948	1.951	1.929	1.941	1.948	1.946	1.929	1.944	1.929	1.936	1.944
Dec.	1.962	1.950	1.957	1.953	1.915	1.933	1.942	1.945	1.932	1.942	1.926	1.940	1.947
Yearly Mean ..		1.949	1.948	1.952	1.927	1.937	1.946	1.946	1.938	1.943	1.938	1.934	1.942

curve A of figure 3. Inasmuch as three of the five periodicities which, combined, yield curve B are determined entirely from the work of 1924 to 1930, and the other two are to a large extent thus determined, the part of curve B from 1918 to 1923 may be regarded as if it were a forecast. Its good fit[1] encourages us to expect to see these five periodicities continue to hold until 1933, producing the general march of solar variation forecasted in curve I of figure 3.

In former publications dealing with possible solar periodicities, I was indebted to Dr. D. C. Miller for the use of his harmonic analyzing machine. Two of the periods which I then thought real, namely of about 25 months and 11 months, are re-discovered by my present method. I feel better satisfied, however, this time, because there is nothing arbitrary about my present analysis. It does not assume periods not indicated by the observations as does the ordinary method of harmonic analysis, which deals with submultiples of some arbitrarily assumed period.

I propose soon to apply a similar method to the individual daily observations, in the hope of discovering shorter periodicities. Thus far I have not gone very far in this line, and will reserve it for a later paper. At present, I will only mention that in the year 1924 there appeared to be continuing periodicities of 45 days and of the eighth part thereof, 5.6 days. These are illustrated in curve H of figure 3. Other periodicities seemed to hold from 2 to 4 months and then disappear.

So far, I have disclosed in solar radiation continuing periods of approximately $\frac{1}{2}$ and $\frac{1}{3}$ of the $11\frac{1}{4}$-year sun-spot cycle, and of 1/16, 1/36, and 1/50 of the Brückner cycle of 33 years. Besides these there were periodicities approximating 45 and 5.6 days in the year 1924, of which it is uncertain whether they belong to these families, though they approximate to 1/90 and 1/720 of the $11\frac{1}{4}$-year cycle.

WEATHER PERIODICITIES

If, as suggested by the title, weather is governed by solar variation, and if, as has just been shown, the solar variation from 1918 to 1930 comprises five definite continuing periodicities, we should expect to find these same periodicities in the weather.

For data to investigate this point, I took from " World Weather Records "[2] the Washington monthly mean temperatures from 1918

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[1] Regarding discrepancies of 1918 to 1920, see footnote on page 9.

[2] Smithsonian Misc. Coll., Vol. 79, 1927.

to 1923. I supplemented them to 1930 by taking monthly mean values of " Max." plus " Min.," as given in the " Climatological Data."[1] In some previous work I had prepared a plot of the average yearly march of Washington mean temperatures. From this smoothed curve I took values corresponding to the 15th day of each month, and subtracted from my monthly mean data. Thus I obtained the temperature-departures which constitute weather, as freed from the average march of events which constitutes climate. These results are plotted in curve A of figure 4 and given in column 9 of table 5.

I then analyzed these temperature-departure data in the manner already explained regarding the solar data. I employed in my analysis the same periods of 68, 45, 25, 11, and 8 months used in the solar work. These were found to represent to a surprisingly close approximation the variation of Washington temperature-departures since 1918. The agreement with observed data was somewhat improved by adding a sixth period of 18 months. These six periodicities are shown graphically in curves C, D, E, F, G, H of figure 4, and their summation in curve B. The actual data from which these curves are plotted are given in columns 1 to 8 of table 5.

The reader, I think, will agree with me that the similarity between curves A and B of figure 4 is both close and significant. Not only are the main trends of the original observations fairly well reproduced in the periodic summation, but many of the details also. Discrepancies, indeed, occur at several times, and unfortunately a principal one is found in 1930. One, therefore, hesitates to predict that the temperature departures of 1931 and following years will be defined by the same six periodicities without modifications of amplitudes or phases. Nevertheless the discrepancy of 1930 is not much more pronounced than several preceding ones, after which fair agreements returned.

It may be objected that the five solar periodicities alone were insufficient to give the best representation, without adding a sixth of 18 months not found conspicuously in solar variation. Is not this last periodicity possibly of terrestrial origin? May it not be due to some peculiarity of Washington surroundings which lends a predisposition to a periodicity of 18 months? For analogy, consider an automobile on a dirt road. It vibrates as the wheels strike the irregularities of the road, in a manner depending on these outside interferences. But

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[1] Issued monthly by the United States Weather Bureau, Washington, D. C.

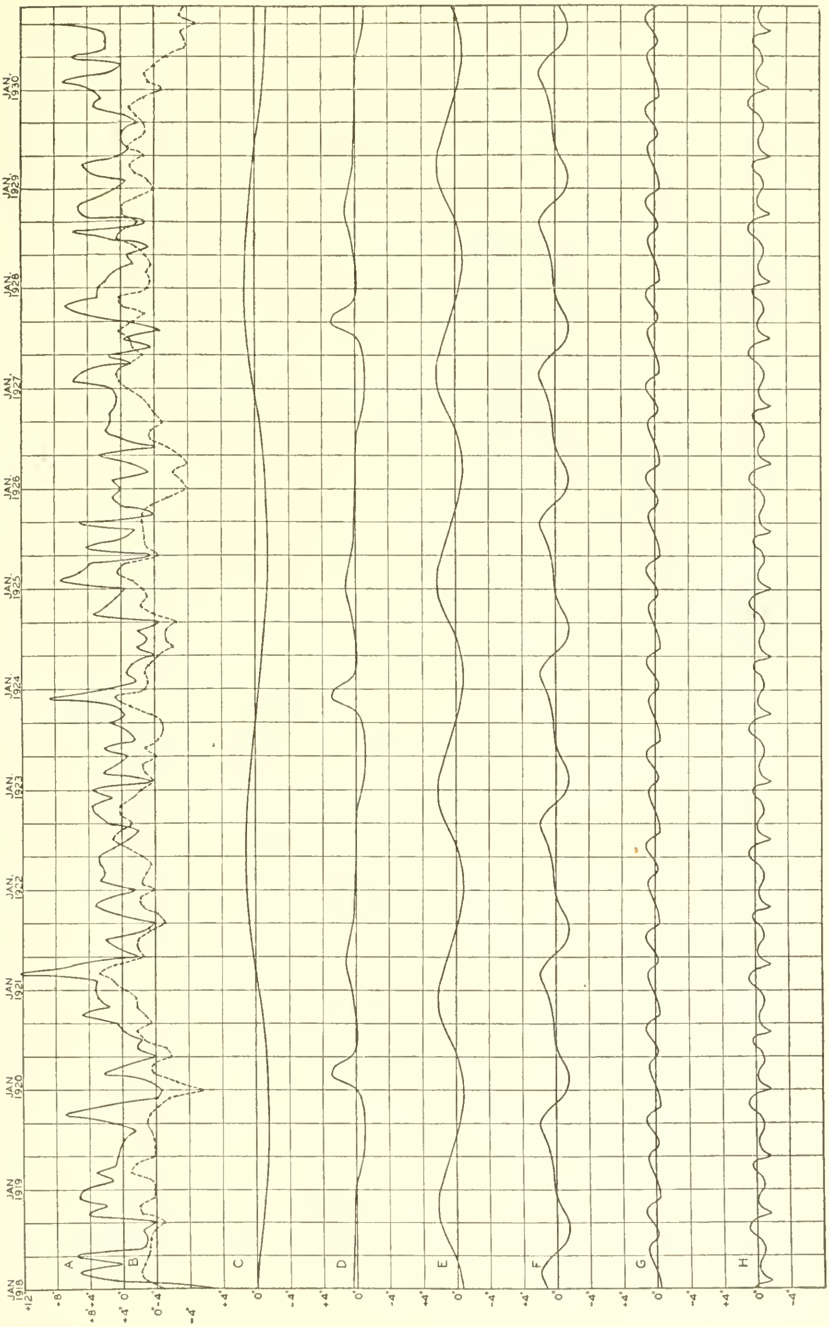

FIG. 4.—Periodicities in Washington mean monthly temperatures.

TABLE 5.—*Periodic Analysis of Washington Temperature Departures*

	Periodicities Degrees x 10 Fahr.							
	68 m	45 m	25 m	18 m	11 m	8 m	Sum °	Original data °
1918 Jan.	1	5	—7	14	—4	—16	—0.7	—9.7
Feb.	0	4	—5	19	—2	—3	1.3	0.8
Mar.	—1	3	—3	21	0	—1	1.9	5.1
April	—2	3	—1	16	5	—7	1.4	0.2
May	—3	3	3	7	8	—8	1.0	5.5
June	—4	2	8	—4	10	—3	0.9	—2.7
July	—5	2	13	—12	0	10	0.8	—2.9
Aug.	—6	2	17	—14	—2	6	0.3	2.5
Sept.	—7	2	21	—14	5	—16	—0.9	—4.0
Oct.	—8	2	23	—9	12	—3	1.7	4.1
Nov.	—9	1	23	—4	10	—1	2.0	2.0
Dec.	—10	1	23	0	—4	—7	0.3	5.2
1919 Jan.	—11	0	21	2	—2	—8	0.2	4.5
Feb.	—12	—1	17	3	0	—3	0.4	1.2
Mar.	—13	—3	14	4	5	10	3.0	3.1
April	—14	—6	11	5	8	6	2.4	0.8
May	—14	—9	7	7	10	—16	0.2	0.5
June	—15	—10	5	10	0	—3	0.2	0.4
July	—15	—10	2	14	—2	—1	0.3	—0.1
Aug.	—16	—11	0	19	5	—7	0.6	—1.5
Sept.	—15	—11	—3	21	12	—8	1.1	1.2
Oct.	—15	—10	—5	16	10	—3	0.8	6.8
Nov.	—15	—9	—7	7	—4	10	—0.3	2.5
Dec.	—14	—7	—8	—4	—2	6	—1.5	—4.2
1920 Jan.	—14	—3	—9	—12	0	—16	—5.4	—4.7
Feb.	—13	8	—7	—14	5	—3	—2.4	—3.3
Mar.	—13	29	—5	—14	8	—1	0.4	2.2
April	—13	25	—3	—9	10	—7	0.3	—0.4
May	—12	7	—1	—4	0	—8	—1.8	—3.9
June	—12	1	3	0	—2	—3	—1.3	—1.9
July	—11	0	8	2	5	10	1.4	—2.3
Aug.	—10	0	13	3	12	6	2.4	—0.3
Sept.	—9	0	17	4	10	—16	0.6	0.6
Oct.	—8	1	21	5	—4	—3	1.2	4.8
Nov.	—7	2	23	7	—2	—1	2.2	1.6
Dec.	—6	3	23	10	0	—7	2.3	2.9
1921 Jan.	—4	5	23	14	5	—8	3.5	3.2
Feb.	—3	8	21	19	8	—3	5.0	3.0
Mar.	—1	10	17	21	10	10	6.7	12.2
April	0	12	14	16	0	6	4.8	5.8
May	2	13	11	7	—2	—16	1.5	—1.8
June	4	13	7	—4	5	—3	2.2	0.7
July	6	11	5	—12	12	—1	2.1	2.0
Aug.	7	9	2	—14	10	—7	0.7	—2.5
Sept.	8	7	0	—14	—4	—8	—1.1	—3.8
Oct.	9	5	—3	—9	—2	—3	—0.3	0.6
Nov.	10	4	—5	—4	0	10	1.5	3.2
Dec.	11	3	—7	0	5	6	1.8	1.5
1922 Jan.	12	3	—8	2	8	—16	0.1	—1.4
Feb.	12	3	—9	3	10	—3	1.6	2.6
Mar.	12	2	—7	4	0	—1	1.0	2.1
April	13	2	—5	5	—2	—7	0.6	2.6
May	13	2	—3	7	5	—8	1.6	2.7
June	13	2	—1	10	12	—3	3.3	1.0
July	12	2	3	14	10	10	5.1	—0.7
Aug.	12	1	8	19	—4	6	4.2	—2.0
Sept.	12	1	13	21	—2	—16	2.9	1.7
Oct.	11	0	17	16	0	—3	4.1	3.0
Nov.	11	—1	21	7	5	—1	4.2	3.6
Dec.	10	—3	23	—4	8	—7	2.7	1.2
1923 Jan.	9	—6	23	—12	10	—8	1.6	3.4
Feb.	8	—9	23	—14	0	—3	0.5	—3.4
Mar.	7	—10	21	—14	—2	10	1.2	2.1
April	6	—10	17	—9	5	6	1.5	0.6
May	5	—11	14	—4	12	—16	0.0	—0.7
June	4	—11	11	0	10	—3	1.1	2.1
July	3	—10	7	2	—4	—1	—0.3	—1.6
Aug.	2	—9	5	3	—2	—7	—0.8	—0.7
Sept.	1	—7	2	4	0	—8	—0.8	1.4
Oct.	0	—3	0	5	5	—3	0.4	—0.3
Nov.	—1	8	—3	7	8	10	2.9	0.8
Dec.	—2	29	—5	10	10	6	4.8	8.6

TABLE 5.—*Periodic Analysis of Washington Temperature Departures*—(cont'd)

	Periodicities Degrees x 10 Fahr.							
	68 m	45 m	25 m	18 m	11 m	8 m	Sum °	Original data °
1924 Jan.	—3	25	—7	14	0	—16	1.3	1.8
Feb.	—4	7	—8	19	—2	—3	0.9	—1.7
Mar.	—5	1	—9	21	5	—1	1.2	—0.6
April	—6	0	—7	16	12	—7	0.8	—1.2
May	—7	0	—5	7	10	—8	—0.3	—3.9
June	—8	0	—3	—4	—4	—3	—2.2	—1.9
July	—9	1	—1	—12	—2	10	—1.4	—3.0
Aug.	—10	2	3	—14	0	6	—1.3	—2.0
Sept.	—11	3	8	—14	5	—16	—2.5	—4.4
Oct.	—12	5	13	—9	8	—3	0.2	3.3
Nov.	—13	8	17	—4	10	—1	1.7	1.7
Dec.	—14	10	21	0	0	—7	1.0	0.6
1925 Jan.	—14	12	23	2	—2	—8	1.3	—0.4
Feb.	—15	13	23	3	5	—3	2.6	7.3
Mar.	—15	11	23	4	12	10	4.5	4.9
April	—16	9	21	5	10	6	3.5	3.8
May	—15	7	17	7	—4	—16	—0.4	—3.4
June	—15	5	14	10	—2	—3	0.9	4.2
July	—15	4	11	14	0	—1	1.3	0.1
Aug.	—14	3	7	19	5	—7	1.3	—1.6
Sept.	—14	3	5	21	8	—8	1.5	5.0
Oct.	—13	3	2	16	10	—3	1.5	—3.9
Nov.	—13	2	0	7	0	10	0.6	—0.1
Dec.	—13	2	—3	—4	—2	6	—1.4	1.0
1926 Jan.	—12	2	—5	—12	5	—16	—1.4	0.1
Feb.	—12	2	—7	—14	12	—3	—2.2	1.0
Mar.	—11	2	—8	—14	10	—1	—2.2	—3.2
April	—10	1	—9	—9	—4	—7	—3.8	—1.2
May	—9	1	—7	—4	—2	—8	—2.9	2.5
June	—8	0	—5	0	0	—3	—1.6	—4.1
July	—7	—1	—3	2	5	10	0.6	—0.2
Aug.	—6	—3	—1	3	8	6	0.7	1.8
Sept.	—4	—6	3	4	10	—16	—0.9	1.3
Oct.	—3	—9	8	5	0	—3	—0.2	1.3
Nov.	—1	—10	13	7	—2	—1	0.6	0.7
Dec.	0	—10	17	10	5	—7	1.5	0.4
1927 Jan.	2	—11	21	14	12	—8	3.0	1.1
Feb.	4	—11	23	19	10	—3	3.2	5.7
Mar.	6	—10	23	21	—4	10	4.6	4.7
April	7	—9	23	16	—2	6	4.1	—1.2
May	8	—7	21	7	0	—16	1.3	1.5
June	9	—3	17	—4	5	—3	2.1	—3.5
July	10	8	14	—12	8	—1	2.7	—0.4
Aug.	11	29	11	—14	10	—7	4.0	—4.7
Sept.	12	25	7	—14	0	—8	2.2	—0.8
Oct.	12	7	5	—9	—2	—3	1.0	4.4
Nov.	12	1	2	—4	5	10	2.6	6.6
Dec.	13	0	0	0	12	6	3.1	2.9
1928 Jan.	13	0	—3	2	10	—16	0.6	2.8
Feb.	13	0	—5	3	—4	—3	0.4	1.9
Mar.	12	1	—7	4	—2	—1	0.7	0.9
April	12	2	—8	5	0	—7	0.4	—1.4
May	12	3	—9	7	5	—8	1.0	—0.8
June	11	5	—7	10	8	—3	2.4	—3.3
July	11	8	—5	14	10	10	4.8	1.4
Aug.	10	10	—3	19	0	6	4.2	5.7
Sept.	9	12	—1	21	—2	—16	2.3	—2.9
Oct.	8	13	3	16	5	—3	4.2	4.6
Nov.	7	11	8	7	12	—1	4.4	5.1
Dec.	6	9	13	—4	10	—7	2.7	3.1
1929 Jan.	5	7	17	—12	—4	—8	0.5	1.2
Feb.	4	5	21	—14	—2	—3	1.1	—0.5
Mar.	3	4	23	—14	0	10	2.6	3.7
April	2	3	23	—9	5	6	3.0	4.5
May	1	3	23	—4	8	—16	1.5	0.4
June	0	3	21	0	10	—3	3.1	—1.0
July	—1	2	17	2	0	—1	1.9	0.0
Aug.	—2	2	14	3	—2	—7	0.8	—0.2
Sept.	—3	2	11	4	5	—8	1.1	—2.0
Oct.	—4	2	7	5	12	—3	1.9	—0.4
Nov.	—5	2	5	7	10	10	2.9	3.3
Dec.	—6	1	2	10	—4	6	0.9	2.5

TABLE 5.—*Periodic Analysis of Washington Temperature Departures*—(cont'd)

	Periodicities Degrees x 10 Fahr.							
	68 m	45 m	25 m	18 m	11 m	8 m	Sum °	Original data °
1930 Jan.	—7	1	0	14	—2	—16	—1.0	3.5
Feb.	—8	0	—3	19	0	—3	0.5	6.9
Mar.	—9	—1	—5	21	5	—1	1.0	2.0
April	—10	—3	—7	16	8	—7	—0.3	0.0
May	—11	—6	—8	7	10	—8	—1.6	5.8
June	—12	—9	—9	—4	0	—3	—3.7	1.9
July	—13	—10	—7	—12	—2	10	—3.4	1.9
Aug.	—14	—10	—5	—14	5	6	—3.2	2.1
Sept.	—14	—11	—3	—14	12	—16	—4.8	8.3
Oct.	—15	—11	—1	—9	10	—3	—2.9	
Nov.	—15	—10	3	—4	—4	—1	—3.1	
Dec.	—15	—9	8	0	—2	—7	—2.5	

at some special speeds, there are sometimes encountered "sympathetic" vibrations due to the make-up of the car itself.

After all, the contribution of the 18-month periodicity to the fit between curves A and B is a minor feature. Is not their surprising agreement, which would still be striking if the 18-month curve F were omitted, significant because related to solar phenomena? Is it not indeed of promising import from the standpoint of long-range weather forecasting?

SUMMARY

1. Contrary to the prevailing view, the weather appears to be governed by variations in solar radiation.

2. Long-continuing periodicities in solar variation are found which give promise of value for purposes of long-range weather forecasting. They appear to be submultiples of 11¼ and 33 years.

3. All of these periodicities are found in Washington temperature-departures, and, combined, suffice to represent its main features.

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THE AVIFAUNA OF THE PLEISTOCENE IN FLORIDA

(With Six Plates)

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THE AVIFAUNA OF THE PLEISTOCENE IN FLORIDA

By ALEXANDER WETMORE

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(With 6 Plates)

Pleistocene deposits of fossils containing numerous bones of birds have been known for years in the western part of the United States in the Fossil Lake area in Oregon, and in the asphalt beds and caverns of California, but such material in other sections of our country to date has been decidedly rare and of limited amount. It is of interest, therefore, to discuss recent discoveries of abundant avian remains in Pleistocene beds in several localities in Florida, with representation of a far larger number of species than has been found at any previous time in the East.

Early report of birds in the Pleistocene in Florida came from the excavations at Vero on the east coast which initiated the argument regarding the antiquity of man in that area (see fig. 1). There were found here remains of a jabiru described by E. H. Sellards, and later there came another collection from which Shufeldt named as new a gull, a teal, and a heron. More recent excavations by J. W. Gidley and by F. B. Loomis, and subsequent work by Doctor Gidley and C. P. Singleton near Melbourne, not far from Vero, have brought to light many bird bones, while investigations initiated by Walter Wetmore Holmes near St. Petersburg on the west coast, in what is known as the Seminole Field, have uncovered the most extensive series of fossil bird bones that have as yet been found in the eastern part of our country. This series is supplemented by bones collected in several localities in Manatee County by J. E. Moore, by a few bird bones secured by Mr. Holmes from a Pleistocene cave deposit near Lecanto in central Florida, and by specimens from several localities in the collections of the Florida State Geological Survey.

The geologic conditions under which these fossils, other than those from the cave, are found are briefly as follows: At or below sea level on the east coast of Florida is a bed of cemented sand and broken marine shells that has been called the Anastasia formation, the Number One stratum, or the Coquina layer. At the Seminole Field near St. Petersburg, the corresponding layer is of fine white sand containing many mollusks, less compact than the beds at Melbourne and

Vero. This lower bed is overlaid by a stratum of fine white to light brown sand, from a few inches to several feet thick, containing occasional lenses or groups of marine shells and, locally, accumulations of fossilized bones. This is the Number Two layer, usually referred to as the bone bed, a deposit that is generally thicker on the east coast than on the west. From this bone bed have come fossil vertebrate remains. Above this bone bed appear Recent deposits of sand or humus that form the present surface, though in places the bone bed is exposed.

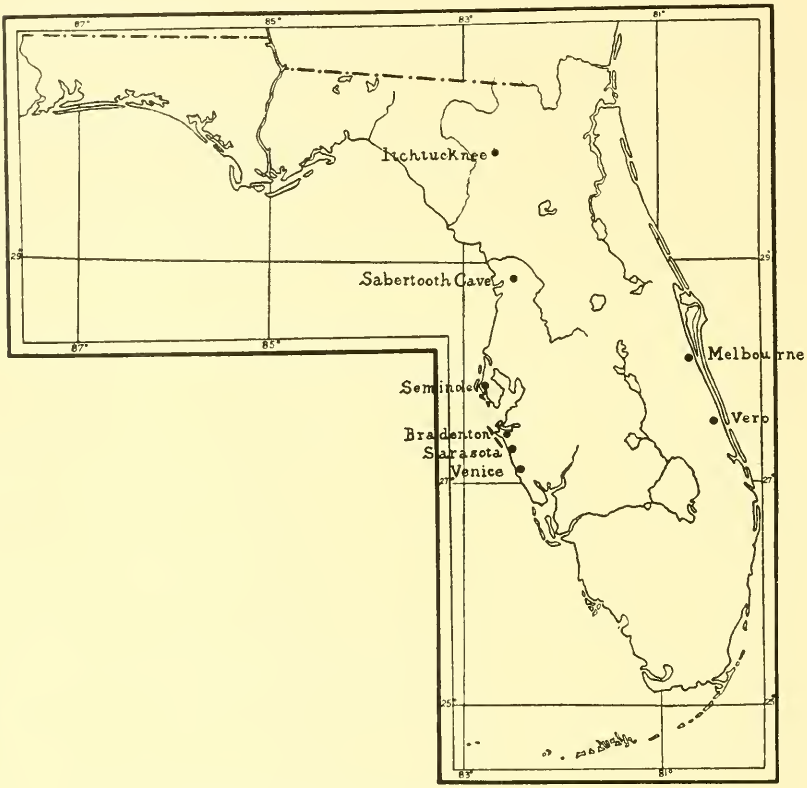

FIG. 1.—Localities where collections of fossil birds have been made in Florida.

The actual age of the specimens from the beds in question has been subject to some discussion. Dr. O. P. Hay[1] holds that the Number

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[1] Journ. Washington Acad. Sci., vol. 20, August 19, 1930, p. 335; and in earlier papers.

Two bed or stratum dates back to the early part of the Pleistocene, probably to the Aftonian period. In this he seems to be upheld by Dr. Wythe Cooke.[1] Dr. G. G. Simpson[2] considers it more probable that these deposits are of late Pleistocene age than that they date from the earlier part of that period. Doctor Simpson further concludes that the faunas from the Number Two bed of the east coast, from Sabertooth Cave, and from the Seminole area " represent a single phase of geologic time."

The writer cites these diverse opinions here without attempt to offer evidence from the bird material in favor of either one.

DISCUSSION OF THE AVIFAUNA

The five principal localities here considered with their fossils may be now treated briefly, but before taking these up in detail it is of interest to note that though grebes, cormorants, herons, ducks and geese, jabirus and other water loving birds are represented among the birds of these deposits, there have been found as yet no sandpipers, plovers, or other shorebirds, nor any terns or gulls (*Larus vero* of Shufeldt being the yellow-crowned night heron). The lack of gulls is of interest particularly since gulls are absent also from the Pleistocene of California, where only one bone of a gull has been identified in several hundred thousand specimens examined.[3]

In the present studies there have been identified 65 forms of birds from the Pleistocene of Florida. Of these three are fossil species of the Pleistocene, two of them, a teal, *Querquedula floridana,* and a turkey, *Meleagris tridens,* being known only from Florida, while the third, *Teratornis merriami,* was described originally from the deposits of Rancho La Brea in California.

There are nine forms that have not been reported from modern Florida. Among these is a shearwater, *Puffinus puffinus,* a pelagic species of wide range in the Atlantic Ocean and the Mediterranean Sea that comes here in all probability merely as a casual straggler. The trumpeter swan, *Cygnus buccinator,* now nearly extinct, bred formerly in the interior of the continent, ranging south in migration to Texas. The whooping crane, *Grus americana,* a breeding form of the interior of North America, now nearly extinct, has been reported uncertainly from Florida. A small gray crane may be the Cuban bird or the little brown crane of western North America. The California vulture,

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[1] Amer. Journ. Sci., vol. 12, 1926, pp. 449-452.

[2] Bull. Amer. Mus. Nat. Hist., vol. 54, February 19, 1929, p. 572.

[3] See Miller, Loye, Condor, 1924, pp. 173-174, and 1930, p. 117.

Gymnogyps californianus, comes only from the West Coast in modern times, while an eagle, *Geranoaëtus* sp., has a modern form in South America and fossils in the Pleistocene of California. The jabiru, *Jabiru mycteria,* Mexican turkey vulture, *Cathartes aura aura,* and wood-rail, *Aramides cajanea* are species known today from tropical America.

The 53 forms remaining that are found in modern Florida are listed below. Most of them are common today in the areas under study either as permanent residents or as migrants from the north during winter.

Colymbus auritus
Podilymbus podiceps
Phalacrocorax auritus
Anhinga anhinga
Ardea herodias
Casmerodius albus
Egretta thula
Hydranassa tricolor
Florida caerulea
Butorides virescens
Nycticorax nycticorax
Nyctanassa violacea
Botaurus lentiginosus
Plegadis sp.
Guara alba
Cygnus columbianus
Branta canadensis
Branta canadensis hutchinsi
Anas platyrhynchos
Anas rubripes
Anas fulvigula
Nettion carolinense
Nyroca valisineria
Nyroca affinis
Erismatura jamaicensis
Lophodytes cucullatus
Cathartes aura septentrionalis
Coragyps urubu
Buteo jamaicensis
Buteo lineatus
Buteo platypterus
Haliaeetus leucocephalus
Pandion haliaëtus
Polyborus cheriway
Falco sparverius
Colinus virginianus
Meleagris gallopavo
Grus canadensis (large form)
Aramus pictus
Rallus elegans
Rallus longirostris
Gallinula chloropus
Fulica americana
Zenaidura macroura
Tyto alba
Otus asio
Strix varia
Corvus brachyrhynchos
Corvus ossifragus
Agelaius phoeniceus
Megaquiscalus major
Quiscalus quiscula

Among these species there are 26 that have not before been recorded in the Pleistocene age, a considerable addition to the 114 modern species known previously from deposits of that period.

The fact that at this writing 140 species of the birds found living today in that area of North America included in the limits of the official Check-list of the American Ornithologists' Union are known as fossils in the Pleistocene illustrates clearly the stability in form of our existing species of birds, since this number is more than 15 per cent of the total living list (not counting subspecies) for the region in question. Progress in our knowledge of these matters has been so rapid that it may be confidently predicted that eventually all of our existing species, except those of small size, will be identified in Pleistocene deposits. As conditions are seldom favorable for preservation of small bones of fragile texture, not much can be known of the smaller birds as fossils, for their preservation in that state is highly fortuitous. We may dream, however, of the discovery of ancient caves, inhabited long ago by Pleistocene owls, with great accumulations of bones of small birds from the pellets of these nocturnal predators—caves that have been hermetically sealed for tens of thousands of years that chance may bring to attention and so give us unexpected information on a fascinating subject.

As his studies in avian paleontology have progressed the writer has become convinced that evolution of our existing birds so far as differentiation of species is concerned has taken place principally in the late Tertiary, and that variation since that time has been of slight degree, confined apparently to minor differences (in color and dimension) such as are used in our modern studies to distinguish the less definitely marked of geographic races or subspecies. As our information increases it appears that some of the differences that we consider today as of subspecific value were in existence in birds of the Pleistocene, for example in the gray cranes and in the turkey vultures, and have persisted to the present without apparent change, a striking example of stability in these groups.

The diversity in the bird life of North America at the time of the coming of the rigors of the Ice Age must have been truly remarkable since it would seem to have included most of our modern forms together with a host of others now extinct that are slowly becoming known from the fossil record. The entire period since the opening of the Pleistocene has been one of extermination rather than of evolution, a process that continued steadily until men appeared as the most active factor contributing to its progress.

THE SEMINOLE AREA

The region surrounding the small settlement of Seminole, not far from St. Petersburg, Pinellas County, Florida, has been designated as the Seminole area (see pl. 1). In 1924 Mr. Walter Wetmore Holmes discovered here a scute from the glyptodon *Chlamytherium septentrionale,* and through continued search during the succeeding 5 years unearthed numerous other fossil bones including among them many remains of birds. It is the Holmes collection of fossil birds that initiated the writer's present studies on the Pleistocene avifauna of Florida.

According to data secured from Mr. Holmes and from a paper on the mammals of these beds by Doctor Simpson[1] of the American Museum of Natural History, the fossil bones come originally from one deposit in the area in question, many of them being obtained by excavating in the original deposit, some coming from erosional wash and redeposit by Joe's Creek which runs through this area, and some from the dump along a drainage canal cut through this region. The bone-bearing layer is from 1 to 2 feet thick. According to Simpson "the lowest bed exposed is of white sand, with numerous marine shells, correlated by Cooke with the Anastasia formation of the east coast, and hence the equivalent of stratum No. 1 at Vero and Melbourne. Above this, sometimes with a barren sand layer intervening, is the bone bed, equivalent in age and character with stratum No. 2. This is generally overlain by a sandy soil, derived from it by weathering." Gidley has distinguished above this in places deposits of sand and muck that he considers equivalent to stratum Number Three of the east coast.

The list of mammals from this area as determined by Doctor Simpson is extensive and includes among its 49 species a capybara, a bear, *Arctodus floridanus,* a saber-tooth tiger, two ground-sloths, two glyptodons, tapirs, peculiar pigs, camelids, mastodon, and elephant that are considered typically Pleistocene species, in addition to opossums, moles, rabbits, rodents, skunks, minks, and deer of the same form as those occurring in the modern fauna.

The bird remains collected by Mr. Holmes include 52 forms, this being the largest assemblage of fossil species secured to date at any point in the eastern portion of North America. The importance of the collection is very evident from examination of the list that follows. A teal, *Querquedula floridana,* a huge condor, *Teratornis merriami,* and a turkey, *Meleagris tridens,* are extinct species of the Pleistocene, the first and last being known only from Florida. The jabiru, *Jabiru mycteria,* the Mexican turkey vulture, *Cathartes aura aura,* and the wood-rail, *Aramides cajanea,* are forms that at the present time range in tropical America and are not now known in the present limits of the United States. An eagle, *Geranoaëtus* sp., has its only living representative in South America though Pleistocene forms have been found in California. Most remarkable are remains of the California condor, *Gymnogyps californianus,* and a larger condorlike vulture, *Teratornis*

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[1] Simpson, George Gaylord, Pleistocene mammalian fauna of the Seminole Field, Pinellas County, Florida, Bull. Amer. Mus. Nat. Hist., vol. 54, February 19, 1929, pp. 561-599, 22 figs.

merriami. Bones of the former are abundant in the Pleistocene asphalt beds of California and the species is known today from northern Lower California north into California. It has never been recorded before in the eastern part of the country. *Teratornis* has been known previously only from the Pleistocene of California, its occurrence in beds of similar age in Florida indicating a former broad range that carried it clear across the continent. The occurrence of the whooping crane, *Grus americana,* and of two forms of the brown crane, one large and one small, is also of interest. There are 20 modern forms in the collection that have not previously been recorded as fossils.

Following is the list of species from this area:

Colymbus auritus
Podilymbus podiceps
Phalacrocorax auritus
Anhinga anhinga
Ardea herodias
Casmerodius albus
Hydranassa tricolor
Florida caerulea
Butorides virescens
Nyctanassa violacea
Botaurus lentiginosus
Jabiru mycteria
Plegadis sp.
Guara alba
Cygnus columbianus
Branta canadensis
Branta c. hutchinsi
Anas fulvigula
Anas sp.
Nettion carolinense
Querquedula floridana
Nyroca affinis
Nyroca sp.
Cathartes aura aura
Coragyps urubu
Gymnogyps californianus
Teratornis merriami
Buteo jamaicensis
Buteo lineatus
Buteo platypterus
Geranoaëtus sp.
Haliaeetus leucocephalus
Pandion haliaëtus
Polyborus cheriway
Meleagris gallopavo
Meleagris tridens
Grus americanus
Grus canadensis (large form)
Grus canadensis (small form)
Aramus pictus
Rallus elegans
Rallus longirostris
Aramides cajanea
Gallinula chloropus
Fulica americana
Zenaidura macroura
Strix varia
Corvus brachyrhynchos
Corvus ossifragus
Agelaius phoeniceus
Megaquiscalus major
Quiscalus quiscula

MANATEE COUNTY

From Mr. J. E. Moore of Sarasota, Florida, there have come three small collections of bones made at as many points in Manatee County.

The first of these was forwarded to me through Dr. George Gaylord Simpson, and comes from deposits near the mouth of Hog Creek near Sarasota, Florida. These are said[1] to have been found in a stratum

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[1] Simpson, G. G., Florida State Geol. Surv., 20th Ann. Rep., 1929, p. 274.

of blue clay 8 to 14 inches thick overlying limestone from 11 to 12 feet below the surface. The birds are accompanied by remains of *Smilodon floridanus, Megalonyx, Mylodon, Chlamytherium, Boreostracon, Tapirus,* elephant, mastodon, and other Pleistocene mammals. The bird bones are dull black in color and are heavily fossilized. The presence of the California condor is notable. The following species are represented:

Phalacrocorax auritus
Botaurus lentiginosus
Gymnogyps californianus
Meleagris gallopavo

A second collection forwarded by Mr. Moore was obtained from a canal within the city limits of Bradenton, the locality being known as the Florida Avenue pit. The type material of *Parelephas floridanus* Osborn[1] came from this point. Mr. Moore (in a letter) states that remains of *Chlamytherium, Glyptodon* and *Bison latifrons* were obtained here also. The bird bones examined vary from dull brown to dull black in color and are well fossilized. The night heron and ruddy duck are here first recorded from the Pleistocene of Florida and from these excavations come the best remains of *Teratornis.* The following species are represented:

Ardea herodias
Egretta thula
Nycticorax nycticorax
Anas fulvigula
Teratornis merriami
Meleagris gallopavo
Grus canadensis
Fulica americana

The third collection was obtained by Mr. Moore at Venice Rocks, two miles south of Venice, Florida. The material is fragmentary and varies from light brown to black in color, some bones being more heavily mineralized than others. Following is the complete list of species:

Buteo jamaicensis
Buteo lineatus
Haliaeetus leucocephalus
Casmerodius albus
Anas sp.
Querquedula floridana
Nyroca affinis
Erismatura jamaicensis
Jabiru mycteria

SABER-TOOTH CAVE

According to information supplied by Mr. W. W. Holmes, and a published account by Dr. George Gaylord Simpson[2] the sink known as Saber-tooth Cave (see pl. 2) is located in a bed of Ocala limestone

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[1] Amer. Mus. Nov., No. 393, December 24, 1929, p. 20.

[2] Pleistocene mammals from a cave in Citrus County, Florida, Amer. Mus. Nov., No. 328, October 26, 1928, pp. 1-16, 11 figs.

(Eocene) 1 mile northwest of Lecanto, Citrus County, Florida, on property belonging to Mr. D. J. Allen. Several years ago Murray Davis with some companions obtained there the canine tooth of a saber-tooth tiger (*Smilodon* sp.) which was sent to the Florida State Geological Survey. Subsequently Mr. Holmes made arrangements for a thorough examination through the cooperation of Mr. Herman Gunter, Mr. J. E. King, and Mr. Allen. The work was done under Mr. Holmes' direction in February and March, 1928.

The entrance to this cave is described[1] as being " through a broad sink terminating in two vertical shafts. Immediately under these the floor of the cave was from 25 to 40 feet below the shaft mouths and there apparently has never been an entrance practicable for large living mammals. On the floor below the sink and in pockets elsewhere was a deposit of red earth or clay in which were found numerous remains of Pleistocene animals, apparently representing a distinct unit fauna. There also occurred in the cave a younger bed of sand and humus containing no extinct mammals but with numerous remains of the recent white-tailed deer of the region."

The bird bones from these deposits are relatively few in number and are all fragmentary. They are light in color, somewhat stained by the reddish earth in which they were found, and present the chalky appearance usual in bones from limestone caves.

The 10 species of birds identified offer little worthy of remark as all are found in the same area at the present time. The barn owl, *Tyto alba,* regularly inhabits caves. The two vultures, *Cathartes* and *Coragyps*, sometimes nest in or about caverns. Occurrence of the other species must be considered as due to chance except that possibly the screech owl and barred owl may have sought shelter in the cave.

The bird bones are associated with remains of the saber-tooth tiger, a capybara, a fossil dog, ground sloth, horse, tapir, a camelid, and mastodon among Pleistocene species, together with a number of mammals that occur at the present time in this area.

The list of species follows:

Nyroca affinis
Cathartes aura septentrionalis
Coragyps urubu
Haliaeetus leucocephalus
Falco sparverius
Colinus virginianus
Meleagris gallopavo
Tyto alba
Otus asio
Strix varia

COLUMBIA COUNTY DEPOSITS

From collections in the Florida State Geological Survey obtained in Columbia County about 3 miles northwest of Fort White, Mr. Herman Gunter has forwarded a number of bird bones for examination. Dr. G. G. Simpson, who has reported on the mammals from this deposit, states[1] that part of this material was collected by J. Clarence Simpson of High Springs, with additional specimens obtained by L. G. Getzen and J. D. Lowe. The site is about a mile below the springs at the head of the Itchtucknee River. Following these earlier collections a considerable number of bird bones were obtained by Mr. and Mrs. H. H. Simpson of High Springs during the latter months of 1930. These latter specimens came to hand as the present report was being completed and have added decidedly to information concerning birds from this area. The bird bones are brown in color and are heavily fossilized. Associated mammalian remains include *Hydrochoerus, Mylodon, Equus, Tapirus, Mylohyus, Mastodon,* and *Archidiskidon columbi.*

Notable among the birds are the jabiru, the extinct teal, *Querquedula floridana,* and the trumpeter swan. Curiously enough the collection contains no remains of hawks or vultures.

Following is the list of identified species:

Colymbus auritus
Podilymbus podiceps
Phalacrocorax auritus
Ardea herodias
Nycticorax naevius
Jabiru mycteria
Cygnus buccinator
Branta canadensis
Branta canadensis hutchinsi
Anas platyrhynchos
Anas rubripes
Anas fulvigula
Querquedula floridana
Nyroca valisineria
Nyroca affinis
Lophodytes cucullatus
Pandion haliaëtus
Meleagris gallopavo
Grus americanus
Aramus pictus
Rallus elegans
Gallinula chloropus
Fulica americana

VERO AND MELBOURNE DEPOSITS

The deposits at Vero have attracted the greatest public attention because remains of man were found there associated with bones of mammals currently considered of Pleistocene age. Among other specimens secured at this locality were a few bones of birds that were described by Shufeldt in 1916.[2] In this account there are listed the turkey vulture, *Cathartes aura,* barn owl, *Tyto alba,* great blue heron, *Ardea herodias,* and several other species not certainly identified. Three forms were described as new, a teal, *Querquedula floridana,* a

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[1] Florida State Geol. Surv., 20th Ann. Rep., 1929, p. 270.

[2] Florida State Geol. Surv., 9th Ann. Rep., 1917, pp. 35-41.

supposed heron, *Ardea sellardsi,* and a supposed gull, *Larus vero,* the two latter proving invalid (see beyond under *Meleagris gallopavo* and *Nyctanassa violacea*).

Two bones forwarded by Mr. Gunter to the present writer include the cormorant, *Phalacrocorax auritus,* and turkey, *Meleagris gallopavo.* Mammal remains from this area include *Hydrochoerus, Canis ayersi, Smilodon floridanus, Felis veronis, Megalonyx jeffersonii, Mylodon harlani, Chlamytherium septentrionale, Tatu bellus,* three species of *Equus, Tapirus veroensis, Mylohyus,* a camelid, *Archidiskidon columbi,* and *Mastodon americanus.*

Near Melbourne (see pl. 3) in Brevard County, Dr. F. B. Loomis of Amherst College located a further deposit which was worked partly in cooperation with Dr. J. W. Gidley of the United States National Museum. Subsequently Doctor Gidley carried on extensive work in this general region during three winters, being assisted by Mr. C. P. Singleton of Melbourne. Later Mr. Singleton worked in these excavations for the Museum of Comparative Zoölogy. Bird material obtained has been scattering but has included some important finds. All of the specimens secured have been available for the present study. The specimens vary in state of preservation, some being heavily fossilized and others having a chalky texture. The latter are quite fragile. The bones vary from light to dark brown in color.

The shearwater that comes first on the list may be a species of accidental occurrence as it ranges regularly at sea or about islands. The jabiru and the extinct teal, *Querquedula floridana,* are represented, as are a large and a small form of the gray crane, *Grus canadensis.* These birds accompanied species of mammals of supposed Pleistocene age.

Following is a list of the birds that have been identified:

Puffinus puffinus
Phalacrocorax auritus
Ardea herodias
Casmerodius albus
Nyctanassa violacea
Jabiru mycteria
Branta canadensis hutchinsi
Querquedula floridana
Cathartes aura septentrionalis
Buteo jamaicensis
Buteo lineatus
Haliaeetus leucocephalus
Polyborus cheriway
Colinus virginianus
Meleagris gallopavo
Grus americanus
Grus canadensis (large and small forms)
Strix varia

ACKNOWLEDGMENTS

In the identification of these specimens the writer is indebted to the American Museum of Natural History for the loan of a skeleton of the jabiru, and to Dr. Hildegarde Howard, of the Los Angeles Museum of History, Science and Art, for bones of *Teratornis* and certain other important material for comparison.

Mr. W. W. Holmes, in addition to his specimens which he has most generously placed in the United States National Museum, has supplied much important information both in letters and in personal conversations. Ornithologists stand greatly indebted to him for the care and effort that he has given to the collection of his material which has caused such an increase in our knowledge of the fossil birds of this area. Photographs illustrating the Seminole area and Sabertooth Cave were obtained from him. Thanks are due to Mr. J. E. Moore for important specimens that he has forwarded for the national collections. Dr. Thomas Barbour has kindly forwarded for study material collected by C. P. Singleton. Dr. J. W. Gidley has furnished data with regard to the deposits on the east coast and has supplied certain photographs. Drawings illustrating this report have been made by Mr. Sidney Prentice.

ANNOTATED LIST

Order COLYMBIFORMES

Family COLYMBIDAE

COLYMBUS AURITUS Linnaeus

Horned grebe

Colymbus auritus Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 135.

In the Holmes collection from near St. Petersburg there are one complete and several broken humeri. Part of another humerus is contained in collections from the Itchtucknee River, Columbia County, in the Florida State Geological Survey. All are similar to those of the modern birds. The species is known previously from the Pleistocene of Fossil Lake, Oregon, and from cavern deposits in Tennessee.

PODILYMBUS PODICEPS (Linnaeus)

Pied-billed grebe

Colymbus podiceps Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 136.

In the Holmes collection from the Seminole Field there are limb bones of several individuals of this species which are similar to those of modern individuals. Other bones are found in the series from the Itchtucknee River, Columbia County, in the Florida State Geological Survey. This grebe today ranges throughout North and South

America. As it has been recorded in Pleistocene beds in Oregon and California (McKittrick) its presence in deposits of that age in Florida indicates a similar wide distribution for North America during the Ice Age.

Order PROCELLARIIFORMES

Family PROCELLARIIDAE

PUFFINUS PUFFINUS (Brünnich)

Manx shearwater

Procellaria puffinus Brünnich, Orn. Bor., 1764, p. 29.

A left metacarpal with the fourth metacarpus missing was secured by J. W. Gidley near Melbourne, March 18, 1929. This shearwater as a species now ranges from Norway south into the Mediterranean, breeding in Iceland, the Azores and other islands, and at least casually on Bermuda. At the present time it occurs rarely along the coasts of North America. It has not been recorded previously as fossil nor has it been known before from Florida.

Order PELECANIFORMES

Family PHALACROCORACIDAE

PHALACROCORAX AURITUS (Lesson)

Double-crested cormorant

Carbo auritus Lesson, Traité Orn., 1831, p. 605.

Cormorants of this type apparently were as widely distributed in Florida during the Pleistocene as they are today, for in the collections here under review there are found the lower end of a tibio-tarsus and part of an ulna from stratum Number Two at Melbourne secured by J. W. Gidley, part of an ulna from Hog Creek, near Sarasota, obtained by J. E. Moore in 1928, and a sacrum and three fragments of humeri from the Holmes collections in the Seminole Field. In the collections of the Florida State Geological Survey there are a complete humerus, part of an ulna and other bones from the Itchtucknee River, Columbia County, another humerus, white in color, from Rock Springs in Orange County that is very doubtfully Pleistocene in age, and still another humerus from the north bank of the canal west of the railroad bridge at Vero.

The resident cormorant of this group found now in Florida, *Phalacrocorax auritus floridanus*, is smaller than the bird from farther north and west, *Phalacrocorax auritus auritus*, which comes to Florida as a migrant during the winter season. It is interesting to observe that the distal ends of two humeri in the Holmes collection from the west coast differ decidedly in size, the transverse breadth across the trochleae in one being 15.8 mm. and in the other 18.2 mm., thus exhibiting differences similar to those that mark the larger and smaller modern races. It appears possible that differentiation between these two forms may have occurred in the Pleistocene, though on the other hand these two specimens may be merely extremes of individual variation existing at that time. On this scanty material the writer does not venture to identify the two as belonging certainly to distinct subspecies.

Family ANHINGIDAE

ANHINGA ANHINGA (Linnaeus)

Snake-bird, water-turkey

Plotus anhinga Linnaeus, Syst. Nat., ed. 12, vol. 1, 1766, p. 218.

The snake-bird is represented by the distal end of a left humerus collected in the Number Two bed near Melbourne by Doctor Gidley on May 3, 1929.

This species has not been recorded previously as a fossil.

Family ARDEIDAE

ARDEA HERODIAS Linnaeus

Great blue heron

Ardea herodias Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 143.

The genus *Ardea* is represented by four cervical vertebrae and two fragmentary metatarsi from Melbourne, collected by Gidley; by the lower end of a metatarsus and the upper part of a coracoid from the Seminole Field collected by Holmes; and by the lower end of a tibio-tarsus from Bradenton collected by J. E. Moore. The upper and lower ends of metatarsi and a broken tibio-tarsus are included in collections in the Florida State Geological Survey from the Itchtucknee River, Columbia County. All are referred here to the species *herodias* without consideration of the possible occurrence of the great white heron, *Ardea occidentalis,* confined today to southern Florida, since so far as present information goes these two supposed species are indistinguishable in their skeletons. The two specimens from the Seminole Field are larger than any modern bird seen, suggesting that possibly there was a larger heron of this type in existence in the Pleistocene. The differences are shown in the following measurements: Modern *Ardea herodias* (seven specimens, including two from Florida); metatarsus, transverse breadth of trochleae 16.2-17.3 mm., smallest transverse breadth of shaft 5.9-7.0 mm.; coracoid, transverse breadth of head 13.8-15.7 mm. Fossils from Seminole Field: metatarsus, transverse breadth of trochleae 18.4 mm., smallest transverse breadth of shaft 8.2 mm.; coracoid, transverse breadth of head 17.3 mm. The material is considered too fragmentary for further consideration at this time.

CASMERODIUS ALBUS (Linnaeus)

Egret

Ardea alba Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 144.

The lower end of the left tibio-tarsus of a young individual is found in the collections made by W. W. Holmes in the Seminole Field. Another was identified in material collected near Venice by J. E. Moore. An ulna of an individual of large size was included in collections made near Melbourne by C. P. Singleton, in 1928, for the Museum of Comparative Zoölogy.

This species has not been recorded previously as a fossil, the only other reference to its possible occurrence in the Pleistocene being that of Shufeldt,[1] where a fragmentary metatarsus is listed as possibly from this species.

EGRETTA THULA (Molina)

Snowy heron

Ardea thula Molina, Sagg. Stor. Nat. Chili, 1782, p. 235.

A partly complete metatarsus collected at Bradenton by J. E. Moore is the first record of this species as a fossil. The specimen comes from a small individual. The snowy heron is fairly common in Florida at the present time, and formerly existed there in large numbers. It has not been recorded previously as a fossil.

HYDRANASSA TRICOLOR (Müller)

Louisiana heron

Ardea tricolor Müller, Vollst. Naturs. Suppl., 1776, p. 111.

The lower end of a right metatarsus comes from the Seminole Field near St. Petersburg.

The present species is here first recorded as a fossil.

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[1] Florida Geol. Surv., Ninth Ann. Rep., 1917, pp. 40-41.

FLORIDA CAERULEA (Linnaeus)

Little blue heron

Ardea caerulea Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 143.

This species, common in modern Florida, is represented by the lower end of a right tibio-tarsus and the distal portion of a right femur secured by W. W. Holmes in the Seminole Field.

This heron is here first reported certainly in fossil deposits.

BUTORIDES VIRESCENS (Linnaeus)

Little green heron

Ardea virescens Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 144.

A right metatarsus and the lower end of a left tibio-tarsus were collected in the Seminole Field deposits by W. W. Holmes. The metatarsus measures 51.7 mm. in length.

The green heron is here found fossil for the first time.

NYCTICORAX NYCTICORAX (Linnaeus)

Black-crowned night heron

Ardea nycticorax Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 142.

The lower end of a tibio-tarsus was obtained by J. E. Moore, at Bradenton, and a similar specimen was collected at the Itchtucknee deposit by Mr. and Mrs. H. H. Simpson. This heron, which is common in Florida now, has been found previously in the Pleistocene of Rancho La Brea in California.

NYCTANASSA VIOLACEA (Linnaeus)

Yellow-crowned night heron

Ardea violacea Linnaeus, Sys. Nat., ed. 10, vol. 1, 1758, p. 143.
Larus vero Shufeldt, Journ. Geol., vol. 25, Jan.-Feb. (Jan.), 1917, p. 18; Florida State Geol. Surv., Ninth Ann. Rep., 1917, p. 40, pl. 2, fig. 21.

The proximal ends of two left coracoids represent this heron in the material obtained by W. W. Holmes in the Seminole Field.

The type of *Larus vero* Shufeldt, a left metacarpal secured at Vero, Florida (U. S. Nat. Mus. Div. Vert. Pal. No. 8832), on examination proves to be the yellow-crowned night heron. This species has not been recorded before in the Pleistocene.

BOTAURUS LENTIGINOSUS (Montagu)

American bittern

Ardea lentiginosa Montagu, Suppl. Orn. Dict., 1813, text and plate.

Parts of two humeri were obtained by W. W. Holmes in the Seminole area, and of another by J. E. Moore on Hog Creek near Sarasota, Florida. This inhabitant of marshes is widely distributed in Florida at the present time.

Family CICONIIDAE

JABIRU MYCTERIA (Lichtenstein)

Jabiru

Ciconia mycteria Lichtenstein, Abhandl. Kön. Akad. Wiss. Berlin (Phys. Klass.), for 1816-1817, 1819, p. 163.

Jabiru? weillsi Sellards, Florida State Geol. Surv., 8th Ann. Rep., 1916, p. 146; pl. 26, figs. 1-4, text-fig. 15.

Apparently the great jabiru stork was common in Florida during the Pleistocene as it is represented in the present collections by many fragments of bones from a number of localities. In the Seminole Field near St. Petersburg W. W. Holmes obtained a number of fragmentary specimens, including parts of the tibio-tarsus, coracoid, scapula, ulna, and metacarpus. Most of these are well fossilized though one fragment appears quite modern. A fragment from the head of a tibio-tarsus was obtained by J. E. Moore near Venice. A perfect metacarpal, a coracoid, and part of a metatarsus are found in collections from the Itchtucknee River, Columbia County, in the Florida State Geological Survey. At Melbourne in the excavations on the golf links J. W. Gidley secured the lower end of a right metatarsus, and parts of an ulna and a metacarpus from the Number Two stratum. In the collection made at Melbourne by C. P. Singleton for the Museum of Comparative Zoölogy there are parts of three right and one left tibio-tarsi and both extremities of a right metatarsus with the central part of the shaft gone.

After careful comparison of the type specimen of *Jabiru weillsi*, a right humerus obtained at Vero, Florida, there is nothing evident to separate it from the modern *Jabiru mycteria*. It was differentiated in the original description principally on larger size, but, though large, it is equalled by modern birds in dimension, and is similar to them in its conformation. The original description gives the total length of the type humerus as 280 mm. Since then the bone has been broken and restored, in this process being lengthened until now it is 293 mm.

long, the extra length being obviously due to crushing of the shaft and the separation of these parts. In a previous publication[1] the present writer indicated that *sellardsi* was probably equivalent to modern *mycteria,* a belief that is now substantiated.

The fossil material indicated above shows the same range in individual variation in size as is found in the modern material examined.

The jabiru is also known from the Pleistocene of Cuba.[1]

Family THRESKIORNITHIDAE

PLEGADIS sp.

Glossy ibis

The lower end of a left tibio-tarsus from the Seminole Field collected by W. W. Holmes is from a juvenile bird and shows little evidence of fossilization. It is not practicable to determine whether it represents *Plegadis falcinellus* or *P. guarauna,* both of which occur in Florida.

GUARA ALBA (Linnaeus)

White ibis

Scolopax alba Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 145.

The distal ends of right and left humeri, of two right ulnae, and the lower end of a left tibio-tarsus were collected by W. W. Holmes in the Seminole Field. The white ibis is locally common in Florida at the present time.

This ibis is here first reported as a fossil.

Order ANSERIFORMES

Family ANATIDAE

CYGNUS COLUMBIANUS (Ord)

Whistling swan

Anas columbianus Ord, in Guthrie's Geogr., 2d Amer. ed., 1815, p. 319.

The proximal ends of right and left coracoids were obtained by W. W. Holmes in collecting in the Seminole Field. In modern times this swan is found in winter occasionally in Florida, mainly along the Gulf Coast, its principal winter range in eastern North America being farther north.

The whistling swan has been known previously as a fossil only from the Pleistocene beds at Fossil Lake, Oregon.

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[1] Amer. Mus. Nov., No. 301, Feb. 29, 1928, pp. 2-3.

CYGNUS BUCCINATOR Richardson

Trumpeter swan

Cygnus buccinator Richardson, Faun. Bor.-Amer., vol. 2, 1831, (1832), p. 464

One entire and three fragmentary humeri, a metacarpal, a coracoid, and a tibio-tarsus are included in the Florida State Geological Survey collections from near the head of the Itchtucknee River in Columbia County (Catalog nos. V-4576; V-4589; V-4599; V-4598, 2 specimens; V-4599 and V-4826). These bones are in an excellent state of preservation, part being dark and part light in color. They agree perfectly with the modern bird, and are larger and stronger than the corresponding bones in the whistling swan. This fine bird, known previously from the Pleistocene of Fossil Lake, Oregon, formerly ranged widely through interior and western North America but at the present time is at so low an ebb of abundance as to be nearly extinct. It wintered formerly from southern Indiana and southern Illinois to Texas but has not been reported previously from Florida.

BRANTA CANADENSIS (Linnaeus)

Canada goose

Anas canadensis Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 123.

From the Seminole Field this goose, a common species on the northern part of the Gulf Coast of modern Florida, is represented by the lower end of a left tibio-tarsus and the distal ends of right and left ulnae. Two ulnae and a broken metacarpal are found in collections in the Florida State Geological Survey from near the head of the Itchtucknee River in Columbia County.

BRANTA CANADENSIS HUTCHINSI (Richardson)

Hutchins' goose

Anser hutchinsii Richardson, Faun. Bor.-Amer., vol. 2, 1831 (1832), p. 470.

In the Holmes collection from the Seminole Field near St. Petersburg there is a distal end of a left ulna of the *Branta* type that is a counterpart of *B. canadensis* except for its smaller size. Part of an ulna comes from the Itchtucknee River, and material secured near Melbourne for the Museum of Comparative Zoölogy by C. P. Singleton includes a right humerus that also has the same characters. These are identified as from the Hutchins' goose, a species rarely recorded from modern Florida. Current custom in recognizing this bird as a subspecies of the Canada goose is here followed though some doubt may be expressed as to whether the two are not specifically distinct.

This form is here identified certainly for the first time in a fossil state, the only previous records being open to question. Shufeldt[1] has recorded it uncertainly from the Pleistocene of Fossil Lake, Oregon, listing it in his final table with a query.[2]

ANAS PLATYRHYNCHOS Linnaeus

Mallard

Anas platyrhynchos Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 125.

Two humeri of the mallard, strong and robust bones, were collected in the Itchtucknee River deposits in Columbia County by Mr. and Mrs. H. H. Simpson.

Remains of other ducks of the mallard type from the Seminole Field, collected by W. W. Holmes, include parts of humeri, an ulna, a metacarpal, and parts of several coracoids, all in such fragmentary form that it is not expedient to attempt to identify them specifically. Parts of two humeri of similar status were obtained by J. E. Moore near Venice. Probably the black duck and mallard are both represented.

The mallard is a regular migrant to Florida.

ANAS RUBRIPES Brewster

Black duck

Anas obscura rubripes Brewster, Auk, 1902, p. 184.

Collections from the Itchtucknee River, Columbia County, made by Mr. and Mrs. H. H. Simpson, include a humerus and a metatarsus of this species, which has not been recorded previously as a fossil.

Like the mallard the black duck comes regularly to winter in Florida.

ANAS FULVIGULA Ridgway

Florida duck

Anas obscura var. *fulvigula* Ridgway, Amer. Nat., vol. 8, February, 1874, p. 111.

A metacarpal and the proximal and distal ends of two humeri are equal in size to a female of this species and are identified as this bird. These specimens come from the Holmes collection from the Seminole Field. In material obtained by J. E. Moore at Bradenton there is part of another humerus.

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[1] Bull. Amer. Mus. Nat. Hist., vol. 32, July 9, 1913, pp. 147, 156, pl. 33, fig. 414.

[2] See also Shufeldt, Auk, 1913, p. 39, and Science, vol. 37, February 21, 1913, p. 307, where this same record is given as *Branta canadensis hutchinsi* (?).

Collections in the Florida State Geological Survey from near the head of the Itchtucknee River, Columbia County, contain two entire and four broken humeri, a coracoid, and two radii (the last being identified tentatively on basis of agreement in size and contour). Apparently the species was common in that area. These represent the first records for the Florida duck in a fossil state. This species breeds abundantly in Florida at the present time.

NETTION CAROLINENSE (Gmelin)

Green-winged teal

Anas carolinensis Gmelin, Syst. Nat., vol. 1, pt. 2, 1789, p. 533.

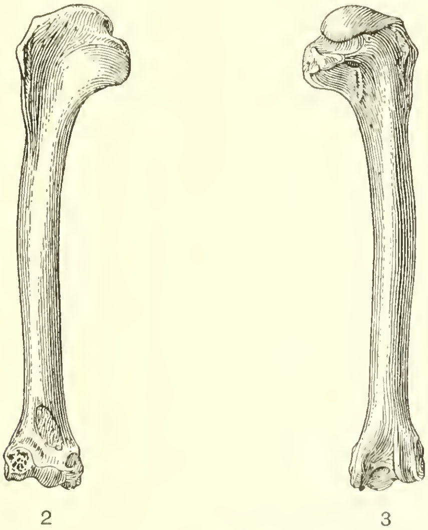
In material collected by W. W. Holmes in the Seminole Field there are parts of two right and two left humeri, of right and left ulnae, and a left coracoid. The humerus in this species is distinctly shorter than in the blue-winged teal.

This duck has been reported previously from the Pleistocene of Oregon, and from several localities in California.

QUERQUEDULA FLORIDANA Shufeldt

Querquedula floridana Shufeldt, Florida State Geol. Surv., Ninth Ann. Rep., 1917, p. 36, pl. 1, fig. 4, pl. II, fig. 25.

The type specimen of this teal (figs. 2-3) was collected in stratum Number Two at Vero, Florida, and is now in the collections of the



Figs. 2-3.—Type of *Querquedula floridana* Shufeldt (natural size).

United States National Museum. While closely similar to the humerus of the living blue-winged teal, *Querquedula discors*, the fossil is heavier and stronger throughout both in the shaft and in the proximal and distal ends. It thus bears out the characters assigned to it in the original description.

In the Holmes collection from the Seminole Field there is one right and one left humerus nearly complete, and the fragments of three or more others that correspond very closely to the type specimen. With them are three broken metacarpals. A portion of a humerus was secured by J. E. Moore near Venice. The proximal half of a right humerus was collected by C. P. Singleton at Melbourne for the Museum of Comparative Zoölogy. There are also a number of bones from the Itchtucknee River deposits, Columbia County, in the collections of the Florida State Geological Survey.

Following are measurements of the four complete humeri at hand.

Type, Vero, Florida, total length 65.8, transverse diameter through trochleae 9.9, transverse diameter through head 16.1, transverse diameter of shaft at center 5.4 mm.

Two specimens, Seminole Field, total length 65.7-70.2, transverse diameter through trochleae 10.3-10.5, transverse diameter through head 15.3-15.6, transverse diameter of shaft at center 5.1-5.3 mm.

Three modern *Querquedula discors*, two males and one female, measure as follows: total length 65.4, 65.9, 61.8, transverse breadth through trochleae 9.7, 10.0, 9.2, transverse breadth through head 13.8, 14.0, 13.1, transverse diameter of shaft at center 4.7, 4.8, 4.6 mm.

NYROCA VALISINERIA (Wilson)

Canvasback

Anas valisineria Wilson, Amer. Orn., vol. 8, 1814, p. 103, pl. 70, fig. 5.

A complete ulna is found in collections made by Mr. and Mrs. H. H. Simpson on the Itchtucknee River in Columbia County.

This species in Florida is a winter migrant from the north.

NYROCA AFFINIS (Eyton)

Lesser scaup duck

Fuligula affinis Eyton, Monogr. Anatidae, 1838, p. 157.

A left humerus collected in the Number Two bed at Melbourne by J. W. Gidley in 1926, with a right metatarsus in the Holmes collection from the Seminole Field, part of an ulna obtained near Venice by J. E. Moore, and four complete and one fragmentary humeri, two ulnae, a metacarpal, and a tibio-tarsus from the head of the Itchtucknee River, Columbia County, constitute definite record of this duck. Some miscellaneous fragments from near St. Petersburg belong probably to this species but cannot be certainly identified. There is also a complete ulna from Saber-tooth Cave near Lecanto, collected in 1928 by W. W. Holmes. These form the only certain Pleistocene records for this duck which is found in abundance in Florida during winter at the present time.

ERISMATURA JAMAICENSIS (Gmelin)

Ruddy duck

Anas jamaicensis Gmelin, Syst. Nat., vol. 1, pt. 2, 1789, p. 519.

The ruddy duck is represented by a metacarpal collected near Venice by J. E. Moore. This species is a common visitor to Florida during the winter.

LOPHODYTES CUCULLATUS (Linnaeus)

Hooded merganser

Mergus cucullatus Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 129.

A humerus was obtained on the Itchtucknee River, Columbia County, by Mr. and Mrs. H. H. Simpson.

Order FALCONIFORMES

Family CATHARTIDAE

CATHARTES AURA AURA (Linnaeus)

Mexican turkey vulture

Vultur aura Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 86.

In the Holmes collection from the Seminole Field there is the distal end of a right tibio-tarsus and the shaft of a left coracoid of a turkey vulture that are decidedly smaller than these bones in the modern bird of the United States, but that agree exactly in dimension with a specimen of the Mexican form from Matamoras. They are identified as typical *aura* which is here first recorded from within the limits of the United States, its modern range being from Mexico south to Panama and Columbia, including Cuba and Jamaica. The transverse breadth of the distal end of the tibio-tarsus in the Pleistocene specimen is 11.0 mm. The modern specimen of *aura* from Matamoras (U. S. N. M. 1442) is exactly similar. In a series of eight modern birds of *septentrionalis* from Florida, Virginia, Maryland, and Pennsylvania this measurement ranges from 12.2 to 13.1 mm. with an average of 12.6 mm. The fossil bone in form is exactly like the modern *aura*.

The existence of remains of two evidently distinct races of the turkey vulture in the Pleistocene deposits of Florida, of which one is now northern and the other southern in range is puzzling. Since the two forms are found in different deposits, *septentrionalis* coming from Vero and Melbourne on the east coast and Lecanto in the central part of the state, and *aura* from near St. Petersburg, if it is assumed that the record of *aura* is not due to a stray individual out of its normal range, it seems probable that the bone deposits in question were formed at different periods during the Ice Age.

CATHARTES AURA SEPTENTRIONALIS Wied

Turkey vulture

Cathartes septentrionalis Wied, Reis. Nord-Amer., vol. 1, 1839, p. 162.

The distal part of a left ulna obtained near Melbourne by C. P. Singleton in 1928 for the Museum of Comparative Zoölogy, and a fragment of a left metacarpal collected by W. W. Holmes in Saber-tooth Cave at Lecanto, Florida, are similar in size to the turkey vulture found today in Florida. Shufeldt[1] has reported this bird from Vero, Florida, and from his figured specimen it is evident that the large northern bird was the one represented.

This form ranges today throughout the greater part of the United States, being absent only in the north, and has had extended range for a long period of time, since it is known from the Pleistocene deposits of California.

CORAGYPS URUBU (Vieillot)

Black vulture

Vultur urubu Vieillot, Ois. Amer. Sept., vol. 1, 1807, p. 23, pl. 2.

Numerous fragments of bone from the Seminole Field include parts of metatarsus, tibio-tarsus, coracoid, humerus, and metacarpal, while from Saber-tooth Cave at Lecanto there are two bones, the distal part of a tibio-tarsus and the upper portion of a metatarsus, the latter from a juvenile individual. All this material was collected by W. W. Holmes. These remains are similar in size and form to those of modern individuals.

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[1] Journ. Geol., 1917, p. 18; Florida State Geol. Surv., Ninth Ann. Rep. 1917, p. 36, pl. 1, fig. 2.

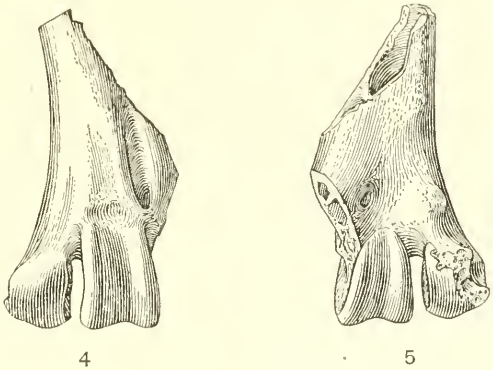
The greater abundance of remains of the black vulture over those of the turkey vulture in these deposits is worthy of comment as indicating possibly the relative abundance of these two birds during the Pleistocene. The black vulture is first known as a fossil from this area.

GYMNOGYPS CALIFORNIANUS (Shaw)

California condor

Vultur californianus Shaw, Nat. Misc., vol. 9, 1797, pl. 301.

In the material secured on Hog Creek, near Sarasota, Florida, by J. E. Moore in 1928, there is part of the distal end of a left metatarsus (see pl. 4, and figs. 4-5) that agrees so exactly in form and dimension with two modern specimens of the California condor that there is no hesitancy in identifying it as that species. It may be remarked that *Gymnogyps* has the middle trochlea of the metatarsus decidedly smaller than the South American condor *Vultur*, this serving to distinguish the metatarsus in these two genera without difficulty.



Figs. 4-5.—Fragmentary metatarsus of California Condor (*Gymnogyps californianus*) from near Sarasota (natural size).

In collecting in the Seminole area W. W. Holmes obtained a bit of a right humerus comprising the ulnar trochlea with the adjacent external parts, and the distal end of a right radius that are identified as remains of this species.

The previously known range of the California condor has been entirely western as it has been found living in the coast ranges of California from Santa Clara County south into northern Lower California, ranging in earlier days north to the Columbia River. Though it has been reported casually east to Arizona, according to Swarth[1] these records lack confirmation. Miller[2] has identified an ulna from cave deposits of uncertain age near Las Vegas, Nevada. The same author[3] in writing of the occurrence of this species in the Pleistocene asphalt beds of Rancho La Brea at Los Angeles, California, says that it is the most common of the American vultures in these deposits, its remains occurring in almost incredible abundance. With large series of Pleistocene material for examination he found remarkable uniformity when compared with bones from modern specimens.

The report of this species from the Pleistocene of Florida is the first note of the occurrence of a condor-like bird in eastern North America and gives an entirely unexpected extension of range for this species during the Ice Age. Discovery of further remains will be awaited with interest.

Family TERATORNITHIDAE

TERATORNIS MERRIAMI L. H. Miller

Teratornis

Teratornis merriami L. H. Miller, Univ. California Publ. Geol., vol. 5, September 10, 1909, p. 307, figs. 1-9.

Among fossils collected by W. W. Holmes in the Seminole area there were found a number of small fragments of bones from what was evidently a very large form of bird. After some study it was clear that these were from some large vulture so that on preliminary examination they were placed among remains assigned to the condors. Critical study indicated certain puzzling differences from both the California and the South American condors and it was with much surprise that they were found to come from the great Teratornis known previously only from California where its remains have been found in the asphalt deposits at Rancho La Brea, McKittrick and Carpinteria.

As stated above the remains from the Holmes collection are all highly fragmentary. The distal end of a left ulna (figs. 9-11), one of the most characteristic bits, agrees minutely in its somewhat intricate details with two specimens of *Teratornis* from California. Two bits of humeri include the articular surface of the head and the radial trochlea of a left humerus. There are further the distal ends

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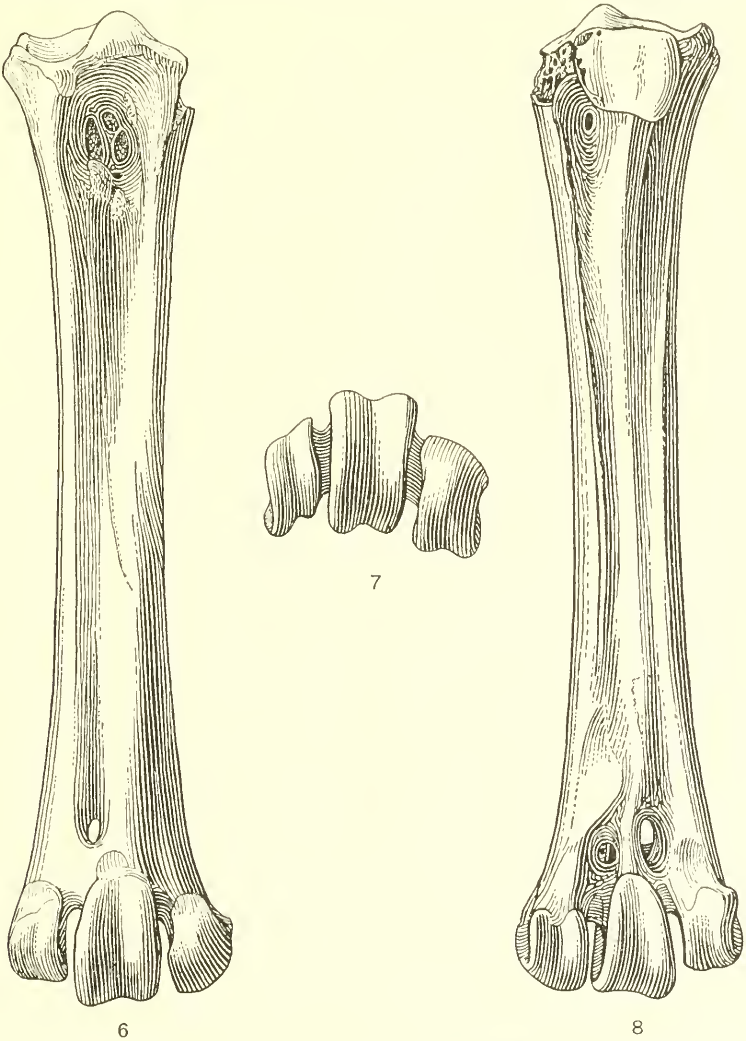
[1] Pac. Coast Avif., No. 10, May 25, 1914, p. 83.

[2] Condor, 1931, p. 32.

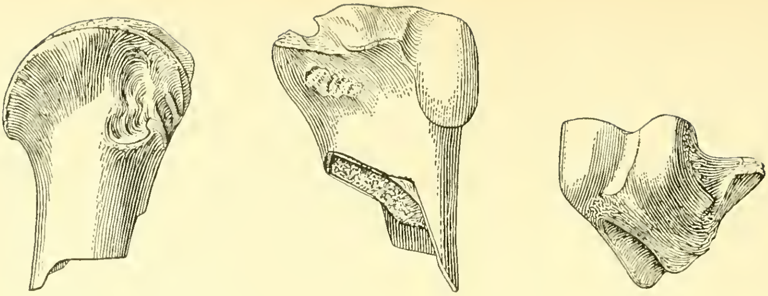
[3] Carnegie Inst., Washington, Publ. No. 349, August, 1925, p. 81.

of left and right radii and the lateral facets from the head of a left coracoid. These likewise in size and detail are like the corresponding parts in *Teratornis.* In fact the agreement is so close that there is no basis for differentiating the Florida bird from that of California.



FIGS. 6-8.—Metatarsus of *Teratornis merriami* from Bradenton (natural size).

With the material described above at hand it has been highly gratifying to find in specimens collected by J. E. Moore at Bradenton a nearly complete metatarsus (pl. 5, and figs. 6-8) and a broken femur (fig. 12) that likewise agree in close detail with the bird of California.



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Figs. 9-11.—Distal end of ulna of *Teratornis merriami* from the Seminole area (natural size).

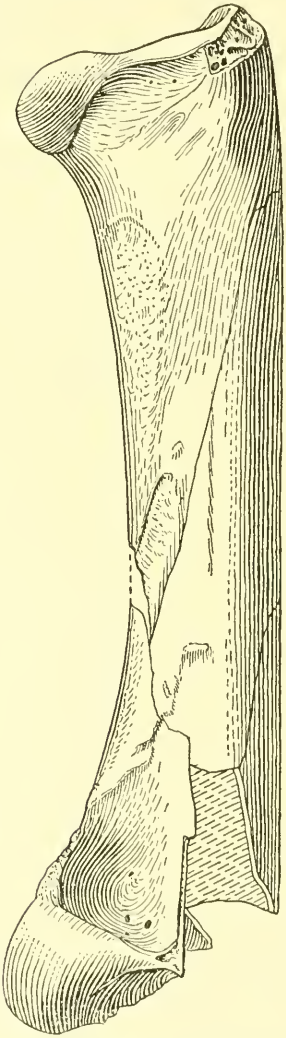

Fig. 12.—Femur of *Teratornis merriami* from Bradenton (natural size).

The femur was in a fragile condition and was received in several pieces. These have been so skillfully joined by N. H. Boss that they illustrate well the form of the bone.

The identification of this form from Florida is one of the most unexpected results of this study of the Pleistocene from Florida and indicates a wide range in Pleistocene times for this peculiar bird.

Family ACCIPITRIDAE

BUTEO JAMAICENSIS (Gmelin)

Red-tailed hawk

Falco jamaicensis Gmelin, Syst. Nat., vol. 1, pt. 1, 1788, p. 266.

The red-tailed hawk is represented in the W. W. Holmes collection from the Seminole Field by the distal end of a left metatarsus, the lower ends of two left tibio-tarsi, and a left coracoid. J. E. Moore secured part of an ulna near Venice. Gidley collected the lower portion of a left humerus in the lower part of the Number Two bed on the golf links at Melbourne. The species occurs today in Florida, and has been recorded previously as fossil in the Pleistocene of California.

The red-tailed hawk has been known for many years as *Buteo borealis*, the original reference being *Falco borealis* Gmelin, Syst. Nat., vol. 1, pt. 1, 1788, p. 266, where it is species No. 75. The preceding species, No. 74, *Falco jamaicensis* on the same page is based on the cream-colored buzzard of Latham[1] described from a specimen from Jamaica, evidently an immature of the red-tailed hawk. As the name *jamaicensis* comes first on the page in question in Gmelin's work it will replace the familiar *borealis* as the specific name for this hawk.

BUTEO LINEATUS (Gmelin)

Red-shouldered hawk

Falco lineatus Gmelin, Syst. Nat., vol. 1, pt. 1, 1788, p. 268.

The red-shouldered hawk was apparently as common in Pleistocene times as today, for it is represented by a number of fragmentary bones. Holmes obtained a left humerus lacking the head and the distal ends of two tibio-tarsi from the Seminole area. J. E. Moore secured part of a metatarsus near Venice. In excavations on the golf links at Melbourne Gidley secured a nearly complete left metatarsus in 1926, a fragment of another in 1928, and a broken left femur in 1930. The red-shouldered hawk is represented in modern Florida by a resident form *Buteo lineatus alleni* that besides differing in color

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[1] Gen. Syn. Birds, vol. 1, pt. 1, 1781, p. 49.

from the northern race is slightly smaller, and by a migrant form *Buteo lineatus lineatus* that is present in winter and is slightly larger. The specimens from the west coast are from slightly smaller birds than those from Melbourne, suggesting that possibly two forms are presented in the fossil material. This cannot be definitely decided from the bones now at hand.

The red-shouldered hawk is here first recorded in fossil form.

BUTEO PLATYPTERUS (Vieillot)

Broad-winged hawk

Sparvius platypterus Vieillot, Tabl. Encycl. Méth., vol. 3, 1823, p. 1273.

In the Seminole Field in Pinellas County, W. W. Holmes obtained the distal end of a left humerus, and the proximal part of a left metacarpus. This species has not been recorded previously as a fossil.

The broad-winged hawk today is a winter visitor to Florida arriving from the north in October and departing in March.

GERANOAËTUS sp.

Eagle

The distal ends of three ulnae obtained by W. W. Holmes in the Seminole Field come from an eagle of this genus, which was represented in the Pleistocene of California by two species *G. fragilis* and *G. grinnelli* and of which there is one living species *G. melanoleucus* in South America. The bones from Florida agree in size with the latter. The material is considered too fragmentary to warrant specific determination at the present time. The genus is here first recorded from eastern North America.

HALIAEETUS LEUCOCEPHALUS (Linnaeus)

Bald eagle

Falco leucocephalus Linnaeus, Syst. Nat., ed. 12, vol. 1, 1766, p. 124.

The bald eagle is represented by fragments from the Seminole Field, and by two broken radii from Saber-tooth Cave, near Lecanto, collected by W. W. Holmes, as well as by part of an ulna collected near Venice by J. E. Moore and a number of bones from near Melbourne, obtained by Gidley and Singleton. The collection made by Singleton for the Museum of Comparative Zoölogy contains part of a metacarpal. Several of the Melbourne specimens are practically complete, and show no differences from the modern bird which is common at present in Florida.

PANDION HALIAËTUS (Linnaeus)

Osprey

Falco haliaëtus Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 91.

A nearly complete left metatarsus was obtained by J. W. Gidley on April 5, 1929, in the Number Two bed at Melbourne where it was associated with remains of a peculiar extinct bear, *Arctodus floridanus*. In 1930 a femur was secured in the Itchtucknee deposits by Mr. and Mrs. H. H. Simpson. These are the first reports of the osprey in the Pleistocene of our continent.

Family FALCONIDAE

POLYBORUS CHERIWAY (Jacquin)

Audubon's caracara

Falco (cheriway) Jacquin, Beytr. Gesch. Vögel, 1784, p. 17, pl. 4.

On the golf course near Melbourne, Gidley collected an ulna that is identical with that of modern birds. On the west coast W. W. Holmes obtained numerous remains in the Seminole Field, these including parts of humeri, ulnae, a femur, a tibio-tarsus, and several metatarsi. Two fragmentary humeri and the lower end of a tibiotarsus are similar in size to small modern specimens of the caracara from Florida. Parts of four metatarsi agree in having the distal trochleae distinctly smaller than in any of the three modern birds seen. Ulnae and part of a femur also seem smaller than usual. It will be recalled that two subspecies of this caracara are now recognized, *Polyborus cheriway cheriway* of northern South America, and *Polyborus cheriway auduboni* of Florida and the southwestern part of the United States south into Mexico, the former being smaller in size. The smaller fossil bones here under discussion seem to show approach to the modern race of South America.

Remains of the caracara are common in the Pleistocene deposits of California but are here reported for the first time outside that State. In Florida the species at the present time is peculiar to the prairies of the Okeechobee and Kissimmee regions, where it is locally common.

FALCO SPARVERIUS Linnaeus

Sparrow hawk

Falco sparverius Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 90.

Material collected in Saber-tooth Cave at Lecanto, Florida, in 1928 by W. W. Holmes includes parts of right and left tibio-tarsi of this species, a common bird in this area at the present time.

Order GALLIFORMES

Family PERDICIDAE

COLINUS VIRGINIANUS (Linnaeus)

Bob-white

Tetrao virginianus Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 161.

In material collected by W. W. Holmes in the Seminole area remains of the quail may be said to be common since this species is represented by six humeri more or less complete and part of an ulna. It is likewise common in the collection from Saber-tooth Cave near Lecanto where two humeri, a metatarsus and two femora were obtained. In excavations on the golf links at Melbourne in February, 1928, Gidley secured two humeri at the line of contact between stratum Number One and stratum Number Two.

These bones all appear similar to those of modern quail. The species is abundant in Florida, and has been previously reported as a fossil from Pleistocene cavern deposits in Tennessee.

Family MELEAGRIDIDAE

MELEAGRIS GALLOPAVO Linnaeus

Turkey

Meleagris gallopavo Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 156.
Ardea sellardsi Shufeldt, Journ. Geol., Jan.–Feb. (publ. Jan.), 1917, p. 19.

In the series of bird bones obtained in the Seminole area, Pinellas County, by W. W. Holmes, remains of the wild turkey far outnumber those of any other species represented; they include 98 fragments of metatarsi, tibio-tarsi, femora, coracoids, humeri, ulnae, and metacarpi. Most of these have been broken into small bits. The specimens exhibit the usual variation in size found in series of wild turkey bones, and do not differ from modern specimens. In the material collected on Hog Creek, near Sarasota, by J. E. Moore in 1928 there is included parts of a femur and a tibio-tarsus, the latter considerably worn. The proximal end of a metatarsus has been forwarded by Mr. Moore as taken at Bradenton. In Saber-tooth Cave near Lecanto Holmes obtained a single spur core from the metatarsus of a male individual. Collections in the Florida State Geological Survey from near the head of the Itchtucknee River, Columbia County, include metatarsi, femora, humerus, ulnae, and other bones, all more or less fragmentary, and part of a sternum. There is part of a metatarsus in the same collections from the north bank of the canal between the Florida East Coast Railroad and the highway at Vero. Gidley collected a broken metatarsus near Melbourne March 1, 1928, and Singleton in the same year working in this same deposit for the Museum of Comparative Zoölogy secured parts of humerus, metatarsus, and tibio-tarsus. The wild turkey must have been abundant in Florida during the Ice Age.

The type specimen of *Ardea sellardsi* Shufeldt,[1] the distal end of a right tibio-tarsus, proves on examination to be from a wild turkey. The bone is from an individual apparently barely adult and of small size, possibly from a young female. The condyles are worn and abraded in such a manner as to mask their true form, leading to error in the earlier identification. The type in question is equalled in size by the smallest in a considerable series of modern wild turkey bones examined. *Ardea sellardsi* thus becomes a synonym of *Meleagris gallopavo*. The specimen was taken in Pleistocene deposits in stratum Number Three, near Vero, Florida.

MELEAGRIS TRIDENS sp. nov.

Characters.—Metatarsus (pl. 6, and fig. 13) similar to that of *Meleagris gallopavo* Linnaeus [2] but male with three-pointed spur core.

Description.—Type, U. S. Nat. Mus. No. 12052. Central portion of shaft of right metatarsus, collected by W. W. Holmes, in the Seminole area, Pinellas County, Florida. Shaft strong, flattened anteroposteriorly below, and more rounded above; anterior face with a wide, shallow groove that becomes obsolete at level of central spur; below this the anterior face is ridged and shallowly grooved by tendons leading to the toes; external side of shaft rounded; internal side more flattened, spurs rising from a common base in a broad buttress of bone projecting obliquely inward from the inner side of the posterior surface; central spur strong and heavy (tip partly broken away); with an accessory spur above and below of smaller size, the upper one slightly more acute than a right triangle in outline, relatively broad transversely, with the distal extremity widened laterally so that in form it is like a cog in a cogwheel; distal accessory spur longer, more slender, with a conical, rather sharp point; outer surface of buttress supporting spurs broadly grooved for the passage of tendons that in life passed down the back of the metatarsus; a distinct, rather narrow,

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[1] Journ. Geol., Jan.–Feb. (publ. Jan.), 1917, p. 19. See also Florida State Geol. Surv., 1917, Ninth Ann. Rep., pp. 38-39, pl. 2, fig. 15.

[2] *Meleagris gallopavo* Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 156.

shallow groove across the base of the spur core buttress on the anterior side, to allow passage of another tendon. Bone brown in color, well fossilized.

Remarks.—In size and form the specimen here described is similar to the ordinary turkey, *Meleagris gallopavo,* except for the three points of the spur core. Description of it as a new species has been withheld for 2 years to allow careful consideration of its peculiarities. These are susceptible of three interpretations: (1) that the bone is pathological and therefore aberrant, (2) that it is simply an individual variant, and (3) that it represents a distinct species.

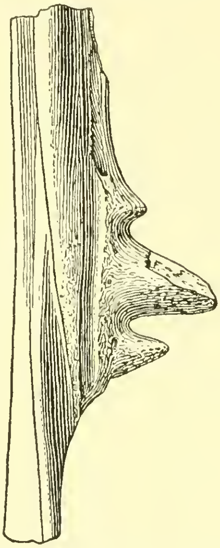

FIG. 13.—Fragmentary metatarsus (type) of *Meleagris tridens* (natural size).

With regard to the first it needs only casual inspection to determine that the entire bone, including the spur cores is entirely normal and without any indication of disease. The very regularity and symmetry of its development indicate that the increased number of spurs is not due to any injury. As for the second supposition, in the past two years the writer has examined critically all of the specimens of wild turkeys that have been available to him, has seen the tarsal bones of a considerable number, one hundred or more, that have come from Indian pueblos in the Southwest and elsewhere, has seen several hundreds of domestic turkeys, and has talked with persons who have reared domestic turkeys for years without learning of any instance where a male turkey had more than a single spur. Under these circumstances it has seemed entirely logical to consider this specimen as representative of a peculiar species. Among numerous other tarsal bones in the material from the Florida Pleistocene it stands unique, indicating probable rarity. It is possible that some of the bones from other parts of the skeleton that have been identified as *Meleagris gallopavo* belong to *M. tridens* but this cannot be determined.

It may be remarked that multiple spurs are not unusual among gallinaceous birds of the Old World, though hitherto unknown in any American species. The pheasants of the genus *Ithaginis* regularly have two or more pairs of spurs in the male. The same is true of *Polyplectron*, while according to Ogilvie-Grant[1] duplicate spurs occur in *Haematortyx*, *Caloperdix*, and *Galloperdix*. The vulturine guinea fowl, *Acryllium vulturinum*, frequently has two to four lumpy spur-like processes on the tarsus.

The type of *Meleagris tridens* is so fragmentary that it affords few measurements. The transverse diameter of the shaft just below the spurs is 9.0 mm. The buttress supporting the spurs is 30.6 mm. long. The form may be ascertained from the accompanying figure.

Order GRUIFORMES

Family GRUIDAE

GRUS AMERICANA (Linnaeus)

Whooping crane

Ardea americana Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 142.

Remains of cranes obtained by W. W. Holmes in the Seminole Field, Pinellas County, include fragments of metacarpus, tibio-tarsus and femur, and of three ulnae. Two fragmentary ulnae and one radius are in the collections of the Florida State Geological Survey from the Itchtucknee River area in Columbia County. Gidley collected part of an ulna from stratum Number Two at Melbourne in 1930, and Singleton secured part of another ulna in the same beds in June, 1929, when collecting for the Museum of Comparative Zoölogy. All are easily distinguished from the bones of other cranes found with them by their much greater size.

Though the whooping crane was recorded from Florida by early ornithologists, in recent years doubt has been cast upon these reports and the species seems not to have been certainly found in modern

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[1] Cat. Birds Brit. Mus., vol. 22, 1893, pp. 221, 222, 260.

times south of Georgia. These records from the Pleistocene are therefore of exceptional interest. This species is now nearly extinct, only a few individuals being known to exist in the interior of our country. It has not been recorded previously as a fossil.

GRUS CANADENSIS (Linnaeus)

Gray crane

Ardea canadensis Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 141.

Remains of gray cranes are common in the deposits at Melbourne and in the Seminole area, and contain representatives of two forms, one large in size and the other small. The large form has the dimensions of *Grus canadensis pratensis* Meyer, the Florida crane, which is resident in Florida today, and is supposed to be that race. There is now recognized however another race, *Grus canadensis tabida* Peters, of more northern and western range that resembles *pratensis* in size, but differs in coloration, so that there is no certainty as to the form that ranged in Florida during the Pleistocene. This larger bird is represented in the Pleistocene collections by a coracoid, a femur, and part of a metacarpal, all secured by Gidley near Melbourne, and the head of a metatarsus and the symphysis of a lower mandible collected by Holmes in the Seminole area, as well as by part of a tibio-tarsus secured by Moore at Bradenton.

The smaller race from the Florida Pleistocene has the dimensions of the little brown crane, *Grus canadensis canadensis,* that now ranges in the western half of the United States, and might be supposed to be that form were it not that the Cuban crane, *Grus canadensis nesiotes,* is a bird of equally small dimension. In fact the differences between *G. c. canadensis* and *G. c. nesiotes* seem to rest on color characters that appear not to have been definitely worked out. The small form is represented in the Pleistocene collections at hand by the distal end of a humerus, parts of two radii, and two coracoids from Melbourne, obtained by Gidley, and the distal end of a humerus secured by Holmes in the Seminole area.

The occurrence of these two races in the Pleistocene of Florida is suggestive of the modern condition in the western part of the United States, where a large gray crane and a small one occur together during migration over a considerable area.

Family ARAMIDAE

ARAMUS PICTUS (Meyer)

Limpkin

Tantalus pictus Meyer, Zool. Ann., vol. 1, 1794, p. 287.

The distal end of a left humerus was collected by W. W. Holmes in the Seminole area. Parts of five metatarsi and a broken tibiotarsus are found in collections from the Itchtucknee River deposits in Columbia County, the specimens being in the Florida State Geological Survey. All these are similar to the corresponding bones in modern birds. The species is of regular occurrence in Florida at the present time. It has not been recorded previously as a fossil.

Family RALLIDAE

RALLUS ELEGANS Audubon

King rail

Rallus elegans Audubon, Birds Amer. (folio), vol. 3, 1834, pl. 203.

In the Seminole area W. W. Holmes secured a complete right femur, and Mr. and Mrs. H. H. Simpson obtained a humerus in the Itchtucknee beds in Columbia County. These bones of this species are distinguished from the clapper rail by larger size.

This rail, common in Florida now, inhabits mainly fresh-water marshes. It has not been recorded previously as a fossil.

RALLUS LONGIROSTRIS Boddaert

Clapper rail

Rallus longirostris Boddaert, Tabl. Planch. Enl., 1783, p. 52.

The distal end of a humerus comes from the Seminole area, collected by W. W. Holmes. The clapper rail is a sedentary species inhabiting salt-water marshes that is common at the present time along the coast of Florida, where several subspecies, slightly differentiated from one another, occur in different geographic areas.

It has not been reported previously as a fossil.

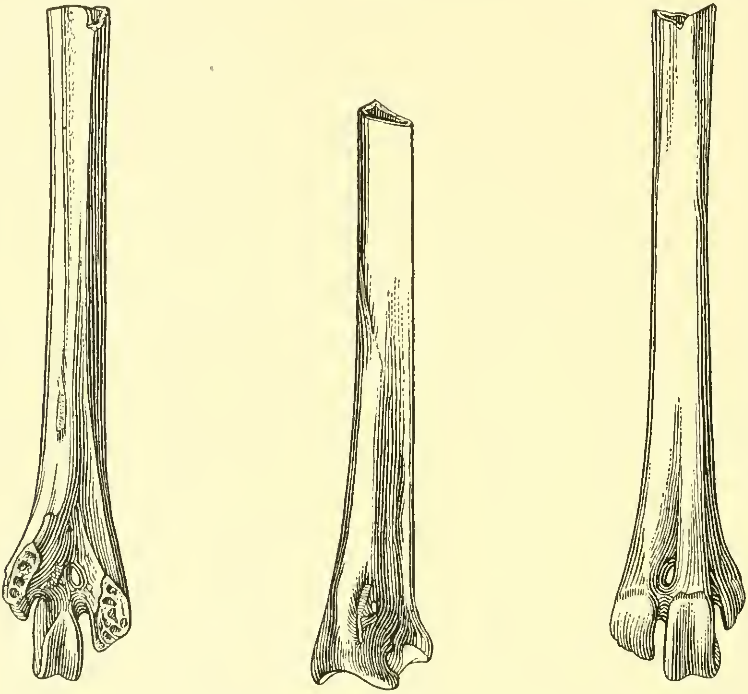
ARAMIDES CAJANEA (Müller)

Wood rail

Fulica cajanea Müller, Vollst. Nat. Suppl., 1776, p. 119.

The determination of two fragmentary metatarsi (see figs. 14-16) and a nearly complete femur collected by W. W. Holmes in the Seminole area as belonging to a form of wood rail, a group of birds comprising several forms that range now from southeastern Mexico south to Argentina, has been another of the unexpected finds in the present collection. The two metatarsal bones are well fossilized, one being black in color and the other brown. The femur contains somewhat less mineral.

Identification to species of these bones has been difficult owing to lack of material for comparison. That they are not related to the large *A. ypecaha* and *A. saracura* of the area from southern Brazil southward is obvious. Likewise it is evident on close study that they are from a bird larger than *A. axillaris* and its allies, which are among the smallest forms of the group. They are smaller than *albiventris,* but agree with *A. cajanea,* which now ranges in two or more subspecies from Panama southward into Brazil, and are identified as of that group on this basis. The genus has not been previously recorded north of southeastern Mexico nor has it been previously encountered as a fossil. Its occurrence in the Pleistocene of Florida is quite in keeping with the various types of mammals of South American affinity that come from these same beds.



14 15 16

FIGS. 14-16.—Metatarsi of the wood rail *Aramides cajanea* from the Seminole area (natural size).

GALLINULA CHLOROPUS (Linnaeus)

Gallinule

Fulica chloropus Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 152.

Parts of four humeri were collected by W. W. Holmes in the Seminole field on the west coast, and another humerus was secured on the Itchtucknee River, Columbia County, by Mr. and Mrs. H. H. Simpson. The species, abundant in present day Florida, has not been recorded previously as a fossil.

FULICA AMERICANA Gmelin

Coot

Fulica americana Gmelin, Syst. Nat., vol. 1, pt. 2, 1789, p. 704.

Bones of this species collected in the Seminole area by W. W. Holmes include one entire and two fragmentary humeri and the distal ends of two tibio-tarsi. Parts of a humerus and a coracoid were obtained by J. E. Moore at Bradenton. A number of other limb bones are found in the collections of the Florida State Geological Survey from the Itchtucknee River area in Columbia County.

The coot is found now in abundance in Florida in winter and a few remain to nest during summer. The species has been reported previously from the Pleistocene of Oregon.

Order COLUMBIFORMES

Family COLUMBIDAE

ZENAIDURA MACROURA (Linnaeus)

Mourning dove

Columba macroura Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 164.

Two metacarpals and the proximal end of an ulna from the Seminole Field, obtained by W. W. Holmes, are in size similar to the modern forms of the mourning dove of North America, being larger than the bird of the West Indies.

Order STRIGIFORMES

Family TYTONIDAE

TYTO ALBA (Scopoli)

Barn owl

Strix alba Scopoli, Annus I. Hist.-Nat., 1769, p. 21.

In the collection obtained by W. W. Holmes in Saber-tooth Cave at Lecanto in 1928 there are a number of fragmentary bones of the barn owl, including parts of the femur, tibio-tarsus, metatarsus, and ulna. The species is quite common in modern Florida.

Family STRIGIDAE

OTUS ASIO (Linnaeus)

Screech owl

Strix asio Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 92.

Parts of two humeri of the screech owl were collected by W. W. Holmes in Saber-tooth Cave near Lecanto. This bird is common and widely distributed in Florida.

STRIX VARIA Barton

Barred owl

Strix varius Barton, Fragm. Nat. Hist. Penn., 1799, p. 11.

The barred owl, a common species in Florida at the present time, seems to have had equally wide distribution during the Pleistocene. In the Seminole area W. W. Holmes obtained a number of fragments including parts of the metatarsus, humerus, ulna, and metacarpus. In the excavation of Saber-tooth Cave at Lecanto Mr. Holmes further obtained a nearly complete femur. J. W. Gidley secured part of a metatarsus in the golf links area at Melbourne. The species has not been previously recorded as a fossil.

Order PASSERIFORMES

Family CORVIDAE

CORVUS BRACHYRHYNCHOS Brehm

Crow

Corvus brachyrhynchos Brehm, Beitr. Vogelk., vol. 2, 1822, p. 56.

Numerous remains of the common crow were secured by W. W. Holmes in the Seminole area, indicating that this species was as common during the Pleistocene as it is in Florida at the present time. Crows have been recorded previously from Ice Age deposits in California but not before from the Pleistocene of eastern North America.

CORVUS OSSIFRAGUS Wilson

Fish crow

Corvus ossifragus Wilson, Amer. Orn., vol. 5, 1812, p. 27, pl. 37, fig. 2.

A humerus, lacking the head, was obtained by W. W. Holmes in the Seminole area, this being the first report of this species for the

Pleistocene. The bone is similar to that of the common crow but is decidedly smaller. The fish crow is widely distributed through the Florida Peninsula today.

Family ICTERIDAE

AGELAIUS PHOENICEUS (Linnaeus)

Red-winged blackbird

Oriolus phoeniceus Linnaeus, Syst. Nat., ed. 12, vol. 1, 1766, p. 161.

A right humerus lacking the distal end, and a left one with part of the head missing, were secured in the Seminole area by W. W. Holmes. This is a common resident of marshes throughout much of North America and abounds today in Florida. It has not been identified certainly before from the Pleistocene.

MEGAQUISCALUS MAJOR (Vieillot)

Boat-tailed grackle

Quiscalus major Vieillot, Nouv. Dict. Hist. Nat., vol. 28, 1819, p. 487.

The proximal portion of a right humerus found by W. W. Holmes in the Seminole area comes from an individual of small size. These grackles are common in Florida, ranging mainly about water. The species has not been recorded before from the Pleistocene.

QUISCALUS QUISCULA (Linnaeus)

Crow blackbird

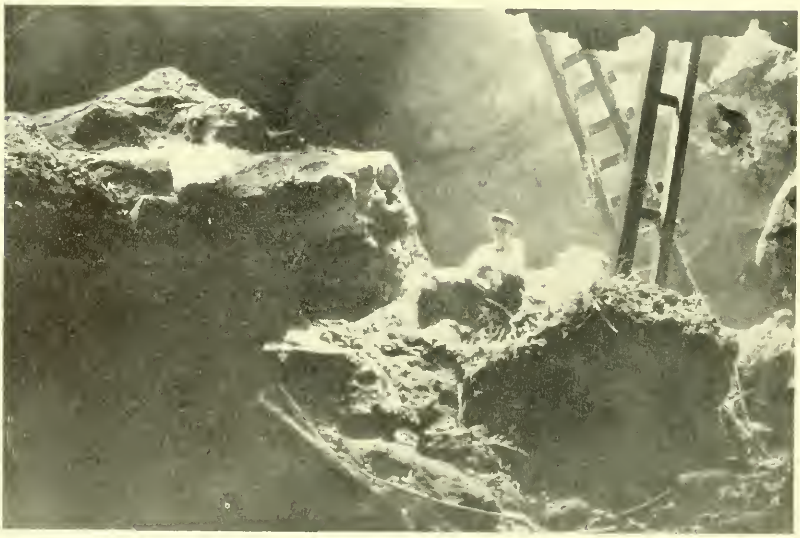
Gracula quiscula Linnaeus, Syst. Nat., ed. 10, vol. 1, 1758, p. 109.

A nearly complete left humerus secured by W. W. Holmes in the Seminole Field comes from an individual of small size. This grackle, common in modern Florida, has not been recorded previously from the Pleistocene.

1. General view of the Seminole area with excavation in foreground. Photograph by W. W. Holmes.

2. Stratification in excavation at Seminole with the bone bearing layer indicated by two trowels at center. Photograph by W. W. Holmes.

1. Entrance to Saber-tooth Cave near Lecanto, Fla.



2. Excavations in Saber-tooth Cave.

1. Stratification at Melbourne, the bone bearing layer being the dark band through the center. Photograph by J. W. Gidley.

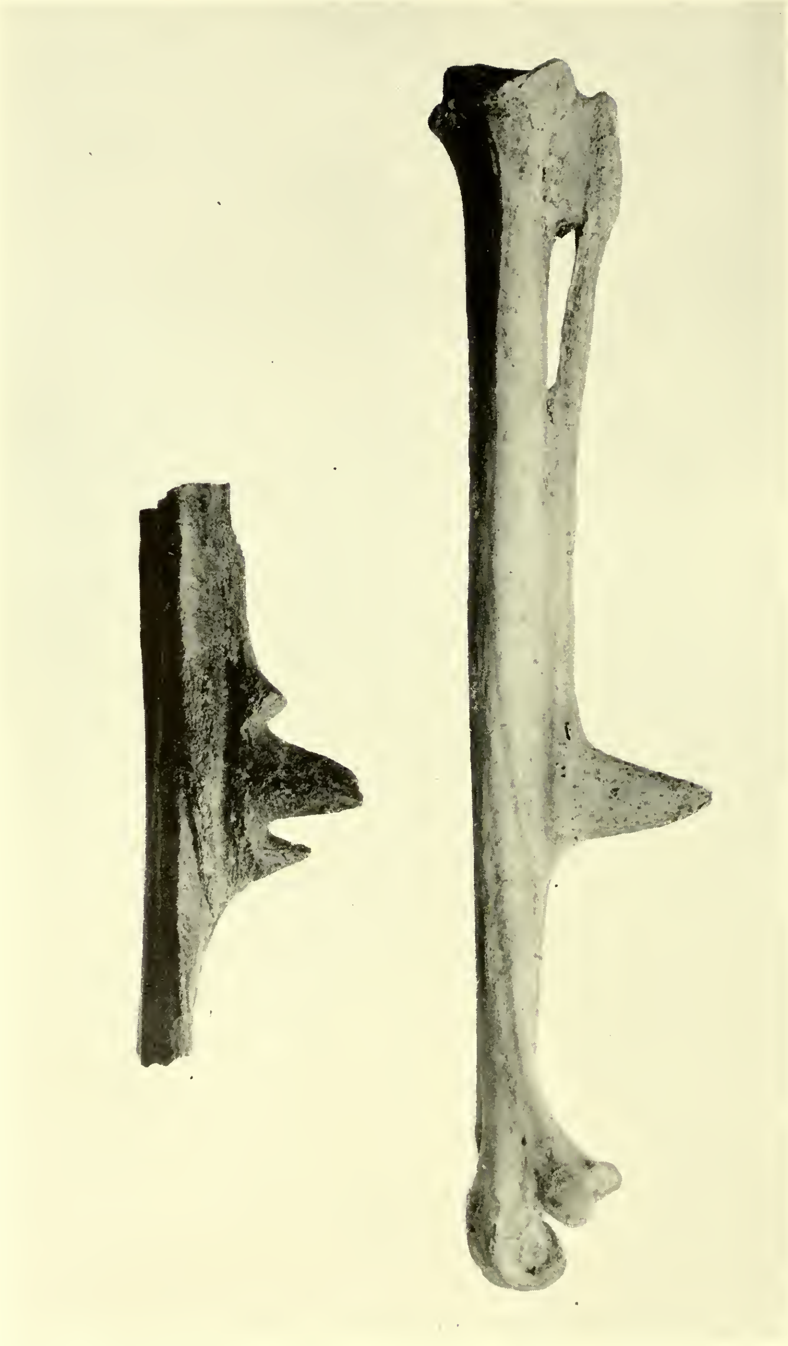
2. Excavations on the golf links at Melbourne, Fla. Photograph by J. W. Gidley.

At left fragmentary metatarsus of California condor, collected by J. E. Moore at Venice, Fla., compared with modern specimen at right. (Natural size.)

1

2

1. Metatarsus of *Teratornis merriami* obtained by J. E. Moore at Bradenton, Fla. (Natural size.)
2. Femur of *Teratornis merriami* obtained by J. E. Moore at Bradenton, Fla. (Natural size.)



At left type of *Meleagris tridens*, compared with metatarsus of modern male *Meleagris gallopavo merriami.* (Natural size.)

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VOLUME 85, NUMBER 3

ADDENDA TO DESCRIPTIONS OF BURGESS SHALE FOSSILS

(WITH 23 PLATES)

BY
CHARLES D. WALCOTT
(With Explanatory Notes by Charles E. Resser)

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PREFATORY STATEMENT

Shortly after his discovery of the remarkable Burgess shale fossils in British Columbia in 1910, Dr. Charles D. Walcott described the more striking species of the major classes of animals and plants represented, to bring to the attention of the scientific world their exceptionally well preserved anatomic details. Subsequent quarrying at the locality yielded many additional specimens of the described forms as well as examples of rarer species not secured in the first season's work.

During my 13 years' association with Doctor Walcott he frequently dwelt upon the fact that he considered his papers on the Burgess shale forms rather in the nature of announcements than as completed studies of these wonderfully preserved fossils. He always intended to return to the study of the described species and to publish more detailed descriptions and interpretations of their form and structure. However, the stress of war times and advancing years prevented a realization of this hope. Nevertheless, from time to time, he had photographs prepared or made notes of his observations regarding structure, all of which were preserved with the collections.

At the request of the National Museum authorities I have assembled these notes and illustrations for publication so that they may not be lost to science. It must be remembered that none of the statements, and particularly none of the interpretations, in the following pages should be regarded as Doctor Walcott's final opinion, since he recognized many of them as tentative. He more than once stated that fully 15 years' work remained to be done on the 35,000 Burgess shale specimens in the National Museum's collections.

All generic and specific names, having been created by Doctor Walcott, are, of course, to be credited to him, and not to us jointly.

In order to show clearly exactly what Doctor Walcott wrote and, on the other hand, what I have added—chiefly by way of explanation—two type faces are used. Doctor Walcott's manuscript is printed in 10-point type, while the explanations added by me appear in the smaller 8-point type.

Charles E. Resser.

INTRODUCTION

It is obvious that one person cannot cover, even in a very cursory manner, the entire field of Cambrian stratigraphy and paleontology, especially with such rich faunas as the Burgess shale extant. Again, in the case of the Burgess shale faunas, none but a trained student in biology can do more than merely assign specific and generic names to the gross forms. Further, it is doubtful if any biologist, however versatile, could by long years of study perceive everything to be learned from these wonderful fossils. In view of these facts it has seemed advisable to encourage specialists to study the various classes represented rather than attempt to monograph the subject as a whole. Accordingly, such a study by Dr. G. E. Hutchinson has recently been printed[1] and one by Dr. Rudolf Ruedemann has been submitted for publication.[2] In this way we may hope to carry on the work suspended by the passing of the discoverer of these unique forms.

The following descriptions either were prepared entirely by Doctor Walcott or are based on notes and illustrations left by him.

Formation and locality.—For every species described in this paper, the formation and locality are as follows: Middle Cambrian, Burgess shale: (Loc. 35k) on the west slope of the ridge between Mount Field and Wapta Peak, 1 mile (1.6 km.) northeast of Burgess Pass, near Field, British Columbia.

DESCRIPTION OF GENERA AND SPECIES

MARGARETIA, new genus

The characters of this strange organism are presented in the specific description or shown in the illustrations.

Genotype.—*M. dorus,* new species.

MARGARETIA DORUS, new species

Plate 1, figs. 1-6

More than 70 specimens of this peculiar organism have been assembled from the Burgess shale collections. In the following description comparisons are made with algae. Other notes by Doctor Walcott, apparently his latest, together with suggestions by Mr. A. H. Clark, and particularly the presence in the same drawer of specimens of *Titanideum suberosum,* indicate that Doctor Walcott's latest opinion was that *M. dorus* might really be an Alcyonarian.

Description.—Mass forming a thin membranous perforated sheet, narrow at the base and expanding to a width of 1.5 cm. in 2 cm. distance; length of narrow base about 1.5 cm. and of wider portion 4 cm.; the perforations are elongate oval and apparently arranged on longitudinal and obliquely transverse lines; tegument presumably

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[1] Restudy of Some Burgess Shale Fossils. Proc. U. S. Nat. Mus., vol. 78, art. 11, pp. 1-24, pl. 1, year ?

[2] Some New Middle Cambrian Fossils from British Columbia. To be printed in the Proc. U. S. Nat. Mus.

leathery as it is a black film with irregular, broken, longitudinal lines with more or less scaly edges.

Microscopic structure undetermined.

Observations.—The perforations in the tegument are not unlike those of the living alga *Agarum turneri* Post and Ruprecht, and one might imagine that a fragment of the strong frond of this species is similar to *M. dorus,* but the resemblance is only general; the perforations of *M. dorus* are more uniform than those of the beautifully perforate living alga *Kallymenia perforata* Agardh, which also has a far more delicate tegument.

Holotype and paratypes.—U. S. N. M., Nos. 83922, 83923a-e.

REDOUBTIA Walcott 1918

REDOUBTIA POLYPODIA Walcott

Plate 2, figs. 2-3

Redoubtia polypodia Walcott, 1918, Smithsonian Misc. Coll., vol. 68, no. 12, p. 5, fig. 5.

The holotype is refigured since it was first published in the popular account of field explorations issued annually by the Smithsonian Institution, which does not reach paleontologists generally.

Accompanying the original figure is the following statement, "An elongate creeping holothurian with numerous tube feet and tentacles."

Whether the second specimen really represents the same species appears somewhat doubtful inasmuch as the tube feet are smaller and more numerous. The larger appendages above the specimen, as posed on the plate, are parts of another animal.

Holotype and paratype.—U. S. N. M., Nos. 83924 and 83925.

PORTALIA Walcott 1918

PORTALIA MIRA Walcott

Plate 3, figs. 2-3

Portalia mira Walcott, 1918, Smithsonian Misc. Coll., vol. 68, no. 12, p. 6, figs. 6, 7.

Another holothurian first figured in the explorations account for 1918 is also refigured, to give it wider availability. This form differs from the preceding *Redoubtia polypodia* in having fewer and longer tube feet and in their apparently different grouping.

Holotype.—U. S. N. M., No. 83927.

MISKOIA Walcott 1911[1]

MISKOIA PLACIDA, new species

Plate 2, fig. 1

Comparing this form with *M. preciosa* Walcott, the genotype, the new species is stouter and shorter. As none of the specimens referred to the type species preserves the rear end, it is not possible to determine whether the lobate termination of *M. placida* is also characteristic of the first species. The annulations of the body are clearly marked in the specimen illustrated, particularly on the counterpart, which is a mold of the exterior. Teeth are shown around the mouth as bright, shiny, curved, chitinous hooks.

Holotype.—U. S. N. M., No. 83928.

CANADIA Walcott 1911

CANADIA SPINOSA Walcott

Plate 4; plate 5; plate 6, figs. 1-2

Canadia spinosa Walcott, 1911, Smithsonian Misc. Coll., vol. 57, no. 5, p. 118, pl. 23, figs. 4-7.

Original description.—" Body slender, formed of 20 to 21 segments that, when flattened on the shale, are a little longer than wide; each segment has a pair of parapodia with a dorsal and ventral bundle of strong non-jointed setae. The setae are finely illustrated by figures 4, 6, and 7. Head minute, with a pair of large tentacles curving outward from the front anterior margins; a bundle of fine setae occurs on each side of the head back of the base of the large tentacles. A straight slender enteric canal is indicated on several specimens. Mouth and anus not seen, but probably at or near the end of the annelid.

" *Dimensions.*—The largest adult specimen has a length of 34 mm., with a width of the body at the seventh segment from the head of 1.5 mm."

Fortunately many additional specimens of this interesting spiny worm were found after 1911. Those first illustrated give a fairly good conception of the general features; however, illustrations of additional specimens may show features particularly desired by the biological student at places where the other specimens are faulty.

Plesiotypes.—U. S. N. M., Nos. 83929a-e.

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[1] Walcott, C. D., Smithsonian Misc. Coll., vol. 57, no. 5, p. 114, pl. 18, figs. 1-5, 1911.

CANADIA SETIGERA Walcott

Plate 7, figs. 1, 4; plate 8, fig. 3

Canadia setigera Walcott, 1911, Smithsonian Misc. Coll., vol. 57, p. 119, pl. 23, figs. 1-3.

Canadia setigera Walcott, 1916, Ann. Rep. Smithsonian Inst., 1915, pl. 12, figs. 1-3.

The original description states that "this species differs from *C. spinosa* in being more elongate, slender, and with much smaller bundles of finer setae." It is further stated that a series of 36 specimens shows gradation between the two types originally illustrated. It seems, however, that in reality several distinct forms are included in the species as now constituted.

Plesiotypes.—U. S. N. M., Nos. 83930a-c.

CANADIA GRANDIS, new species

Plate 9, fig. 10

A single wide *Canadia* that shows the body annulations very well and that has numerous setae seems to differ from *C. spinosa* mainly in the larger bundles of setae.

Holotype.—U. S. N. M., No. 83932.

CANADIA IRREGULARIS Walcott

Plate 6, figs. 4-6; plate 7, fig. 3

Canadia irregularis Walcott, 1911, Smithsonian Misc. Coll., vol. 57, p. 120.

Original description.—"A slender species not over 20 mm. in length. The setae are irregular in size and appearance and suggest partially worn macerated specimens of the slender forms of *C. setigera*."

The specimens on which this description was based are now illustrated for the first time. A study of the figures, however, causes some doubt to arise regarding specific differentiation from *C. grandis*.

Lectotype and paratypes.—U. S. N. M., Nos. 83933 and 83934a and b.

CANADIA SPARSA Walcott

Plate 6, fig. 3

Canadia sparsa Walcott, 1911, Smithsonian Misc. Coll., vol. 57, p. 119.

Original description.—"A slender form with only two strong setae on each very short parapodia. Finer setae may occur but they are not shown in the one specimen."

This form is another that was not illustrated in 1911. In this case two questions may be raised: First, the specific identity of all the specimens seems doubtful, and second, the generic reference to *Canadia* is also uncertain.

Holotype.—U. S. N. M., No. 83935.

CANADIA DUBIA Walcott

Plate 7, fig. 2; plate 8, figs. 1-2; plate 9, fig. 8

Canadia dubia Walcott, 1911, Smithsonian Misc. Coll., vol. 57, p. 119.

Original description.—" This species is proposed to include a small chaetiferous annelid not over 10 mm. in length. One specimen shows a bundle of very fine setae on each side near the head."

Four of the original specimens are illustrated.

Cotypes.—U. S. N. M., Nos. 83936a-d.

CANADIA SIMPLEX, new species

Plate 9, fig. 9

A tiny organism that appears as a slender tube with a termination surrounded by a ring of setae constitutes the material to which Doctor Walcott attached this name.

Holotype.—U. S. N. M., No. 83937.

WIWAXIA Walcott 1911

WIWAXIA CORRUGATA (Matthew)

Plate 3, fig. 1

Orthotheca corrugata Matthew, 1899, Trans. Roy. Soc. Canada, 2d ser., vol. 5, sec. 4, p. 42, pl. 1, fig. 3.

Orthotheca corrugata Walcott, 1908, Canadian Alpine Journ., vol. 1, no. 2, p. 246, pl. 1, fig. 11.

Wiwaxia corrugata Walcott, 1911, Smithsonian Misc. Coll., vol. 57, no. 5, p. 123, pl. 21, figs. 1-4.

A particularly fine example of this remarkable spined worm turned up in some of the more recent collections. Its picture is included since it may represent a relatively undistorted specimen with most of the plates retained.

Plesiotype.—U. S. N. M., No. 83938.

OTTOIA Walcott 1911

OTTOIA MINOR Walcott

Plate 9, figs. 1-7

Ottoia minor Walcott, 1911, Smithsonian Misc. Coll., vol. 57, p. 129, pl. 22, figs. 5-6.

Original description.—" This species differs from *O. prolifica* in its proportionally more slender form when elongated and straighter outline both when elongated and contracted. The hooks are also much finer and extend farther back on the anterior end. The annular lines and interspaces are also finer and more irregular."

Several specimens, among the many found subsequent to 1911, preserve some of the structure features very well, and illustrations were prepared by Doctor Walcott to show them. However, it is very doubtful whether the forms shown on plate 9, figures 2 and 4, belong to this species.

Plesiotypes.—U. S. N. M., Nos 83939a-g.

PIKAIA Walcott 1911

PIKAIA GRACILENS Walcott

Plate 8, figs. 4-5

Pikaia gracilens Walcott, 1911, Smithsonian Misc. Coll., vol. 57, p. 132, pl. 20, figs. 1-2.

Original description.—" Body elongate, slender, and tapering at each end. It is formed of many segments that are defined by strong annular shiny lines. Head small with two large eyes and two tentacles as shown by figure 1. Back of the head the first five segments carry short parapodia that appear to be divided into two parts.

" The enteric canal extends from end to end without change in character. It is relatively large along the central portions and tapering toward the ends. Judging from such specimens as the one illustrated by figure 2, its annulations correspond in size with those of the body.

" Surface apparently smooth. Two entire adult specimens and several fragments of others indicate a length of about 5 cm."

Two additional figures are presented at this time.

Plesiotypes.—U. S. N. M., Nos. 83940a-b.

SELKIRKIA Walcott 1911

SELKIRKIA MAJOR (Walcott)

Plate 10

Orthotheca major Walcott, 1908, Canadian Alpine Journ., vol. 1, p. 246, pl. 1, fig. 11.

Selkirkia major Walcott, 1911, Smithsonian Misc. Coll., vol. 57, p. 120, pl. 19, fig. 6.

This species was first described from the Stephen formation on Mount Stephen. Later Doctor Walcott found apparently the same shell at the Burgess Pass quarry, but in this instance the soft body of the animal was preserved and therefore, in the 1911 discussion, he removed it from the Hyolithidae to the polychaetous annelids.

Photographs of two exceedingly well preserved individuals with the body extending beyond the shell are printed here for the first time.

Plesiotypes.—U. S. N. M., No. 83941a-b.

AYSHEAIA Walcott 1911

AYSHEAIA PEDUNCULATA Walcott

Plate 11

Aysheaia pedunculata Walcott, 1911, Smithsonian Misc. Coll., vol. 57, p. 117, pl. 23, figs. 8-9.

Aysheaia pedunculata Hutchinson, 1930, Proc. U. S. Nat. Mus., vol. 78, art. 11, p. 14.

This fossil has perhaps attracted wider attention than any other. Recently G. E. Hutchinson, of Yale University, studied this peculiar form and concluded that *Aysheaia* is an extinct Onychophora. Unfortunately, Mr. Hutchinson did not see the two individuals here illustrated, as they were buried away among numerous specimens of *Ottoia*. As the present assemblage of material progressed they came to light and are now illustrated, especially as they are perhaps the best preserved specimens available.

At the time these photographs were found among the notes Doctor Walcott intended using in further publications relating to this animal, two letters were discovered, both suggesting that *Aysheaia* may be an Onychophora or a Peripatus. The first letter, dated September 21, 1911, was written by Prof. W. M. Wheeler of Harvard University, and reads as follows:

> "I wish to thank you for your very interesting publications on the Middle Cambrian Annelids. On plate 23, I noticed two figures of *Aysheaia pedunculata*. This creature bears the most extraordinary resemblance to *Peripatus*, except for the head, and judging from the figures the 'head' may be something which does not belong to the fossil. I have just shown these figures to Mr. C. T. Brues, who has been working on *Peripatus*, and he also was struck with the remarkable resemblance. Is there any possibility that it might be *Peripatus* instead of an Annelid? If this should prove to be the case it would be a matter of the very greatest interest."

The second letter dated October 25, 1911, was written by Prof. Charles Schuchert, of Yale University, and contains the following:

> "The other point is one that Lull has called my attention to and refers to figures 8 and 9 of plate 23 which you call *Aysheaia pedunculata*. The question that I want to ask is, have you considered it as a possible Onychophora or related to *Peripatus?* Of course if one looks at your illustrations and compares them with the illustration of *Peripatus* given by Parker and Haswell in their Text-book of Zoology, page 607, in the edition of 1910, one can see considerable differences and yet there are in your figures several points in common to make one wonder whether you have not a marine ancestor of this land-living arthropod."

This rather lengthy historical account is presented to show that at least three authorities arrived at the same conclusions independently.

Plesiotypes.—U. S. N. M., Nos. 83942a-b.

LEANCHOILIA Walcott 1912

LEANCHOILIA SUPERLATA Walcott

Plate 12; plate 13, figs. 1-2; plate 14, figs. 4-5

Leanchoilia superlata Walcott, 1912. Smithsonian Misc. Coll., vol. 57, p. 170, pl. 31, fig. 6.

Original description.—"Body elongate, with clearly defined head shield and nine strong body segments up to the point where the posterior part of the body is broken off. The anterior pointed end of the head is broken off in such a manner that the presence of a frontal appendage is suggested. The large opening on the side of the head indicates a large pedunculated eye comparable with that of *Opabinia regalis* (pl. 28, fig. 1).

"*Appendages.*—Of the head appendages, the antennae are the best preserved. These are large and composed of several strong joints, of which three now show from beneath the carapace; the second of these bears a long slender branch on its inner margin, and the third two branches, one of which is similar to that of the second joint. These two branches appear to be composed of one very long slender joint followed at the end by several short small joints that curve upward and presumably gave the branches flexible extremities; the third and lower branch has a similar slender proximal joint that at its outer end has three slender, jointed branches. This structure makes a very effective clasper of each of the antennae. Back of the right antennae are two narrow appendages that may be the ends of one of the third and fourth pairs of head appendages.

"The thoracic legs terminate in flat, elongate, broad, lanceolate joints. The terminal joint is about three-fifths the entire length of the leg, and has a fringe of strong setae on its outer and posterior margin. The condition of preservation is such that the details of structure of the other portions of the leg cannot clearly be determined."

The illustrations presented herewith apparently were prepared by Doctor Walcott to exhibit the detailed structure of this interesting crustacean.

Plesiotypes.—U. S. N. M., Nos. 83943a-g.

LEANCHOILIA MAJOR, new species

Plate 13, fig. 3

Several specimens, of which the best is illustrated, were labeled *Leanchoilia major* by Walcott. Just why he should have chosen this specific name is not readily apparent as these individuals are not sufficiently larger than *L. superlata* to warrant the designation. In fact there is but little difference between this form, which happens to be flattened out horizontally, and the specimen shown in figure 2, plate 13, referred to the genotype.

Holotype.—U. S. N. M., No. 83944.

NARAOIA Walcott 1912

NARAOIA COMPACTA Walcott

Plate 13, fig. 4; plate 14, figs. 1-3; plate 15, figs. 2-3

Naraoia compacta Walcott, 1912, Smithsonian Misc. Coll., vol. 57, no. 6, p. 175, pl. 28, figs. 3, 4.

Many specimens of this interesting form have been found since its preliminary description in 1912, but none shows the cephalic appendages in position or an uninjured trunk limb. The carapace is thicker than that of *Burgessia bella* and the body is firmly attached to the fused segments forming the posterior dorsal shield, and there is a close union between the body of the cephalic region and the carapace that extends from the anterior ventral margin of the latter back to the line of the anterior margin of the posterior dorsal shield. In the restoration (text figs. 1, 2) I have made an attempt to incorporate all information available.

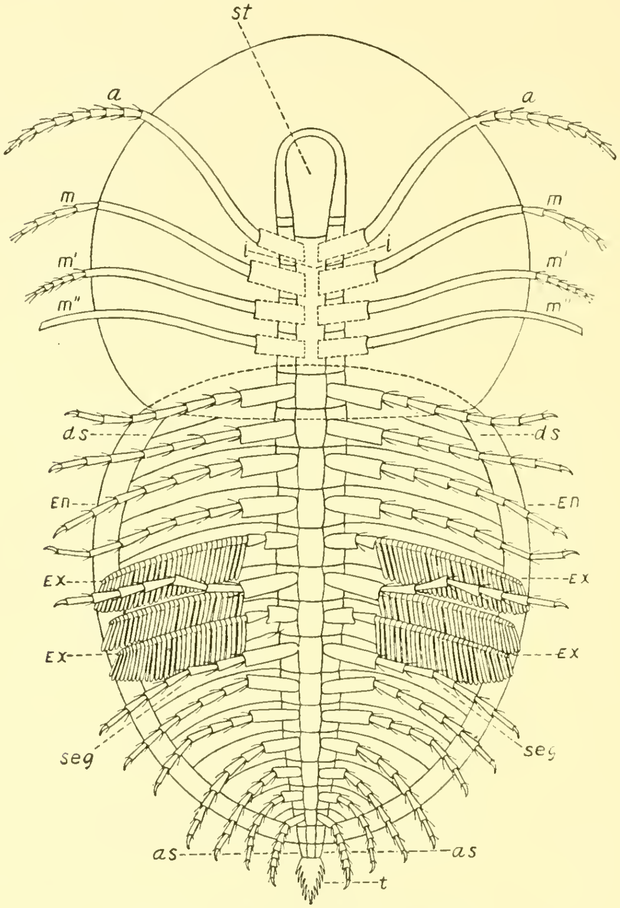

FIG. 1.—*Naraoia compacta* Walcott.

a, antennae; *as*, anal segment; *ds*, reflex margin of posterior carapace; *en*, endopodite; *ex*, exopodite; *i*, intestine; *m*, mandible; *m'*, maxilla; *m"*, maxillula; *seg*, segmented posterior carapace; *st*, stomach; *t*, telson.

(About × 5.) Diagrammatic outline of ventral view of appendages, etc.

Exoskeleton.—The dorsal exoskeleton as seen from its dorsal side is formed of a carapace and a posterior segmented shield. The true cephalic carapace or shell fold is attached to the cephalic somites near its anterior portion, probably as in the recent Apodidae or the associated *Burgessia* and also along the line of the body as far back as the anterior margin of the posterior dorsal carapace. The carapace is not known to have had a reflected anterior margin with a labrum attached as in *Burgessia*, but it may have had, as none of the specimens shows the ventral side of this part in an uninjured condition. The carapace is broader than long, with a somewhat uniformly rounded outline except posteriorly where it is nearly transverse; it probably had a ventral as well as dorsal membrane between which the great hepatic caeca were located very much as are the shell glands in the Apodidae.[1] For some unknown reason the anterior portion of the carapace is usually distorted by being crowded back so as to wrinkle and shorten it.

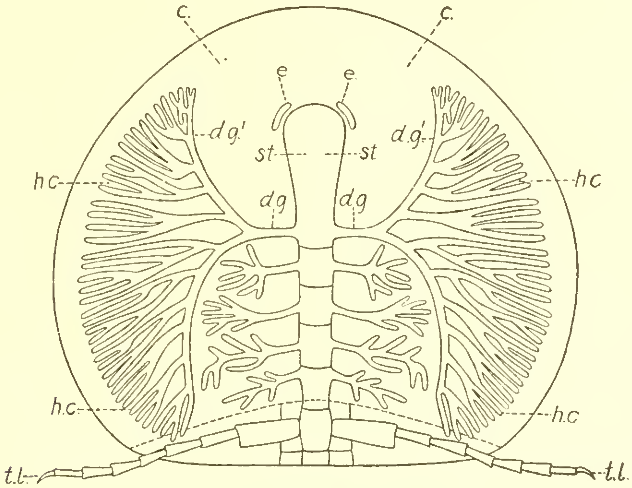

FIG. 2.—*Naraoia compacta* Walcott.

c, carapace; *g*, digestive glands; *d.g.*, lateral digestive glands; *c*, eye; *h.c.*, hepatic caeca; *st*, stomach; *t.l.*, thoracic limb.
(About × 5.) Diagrammatic outline of the digestive organs.

The large shield of the posterior part of the exoskeleton is composed of 14 fused segments with a narrow border. It has the appearance of the many-segmented pygidium of the trilobite belonging

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[1] In no other manner can I explain the wonderful preservation of the digestive tubes and caeca.

to the genera *Ogygopsis* or *Orria*,[1] except that the median lobe is not as strongly marked. These two genera are mentioned as they occur in correlative Middle Cambrian formations and one of them in the Stephen formation which is nearly contemporaneous with the Burgess shale. The dorsal carapace and shield also appear similar in outline to the dorsal exoskeleton of the freshly hatched young of *Limulus polyphemus* as figured by Packard.[2] The posterior shield has each of the thoracic body segments, excepting the two posterior which project beyond it, attached directly to it, and it forms the dorsal side of the exoskeleton of the body segments. The exoskeleton of the free posterior segments and telson, of the cephalic segments, and of the ventral side of the trunk segments was so exceedingly delicate as to leave only a slight trace on the shale. Both the anterior carapace and posterior segmented shield were very thin and readily distorted.

The anterior carapace slightly overlapped the posterior shield and the two were closely held together by the strong body as evidenced by their rarely being found separated. The telson is short and marked by fine short spines.

Dimensions.—The largest specimen had a length of about 40 mm., the carapace being shortened by compression. A specimen that has been slightly narrowed by compression has the following dimensions:

	mm.
Length of carapace	16
Width of carapace	15
Length of posterior dorsal shield	17
Width of posterior dorsal shield	14

Eyes.—The eyes are represented by two small crescent-shaped bright spots a little in advance of the anterior end of the stomach as illustrated by the restoration (fig. 2). The position and form correspond quite closely to the paired eyes of the recent *Apus lucasanus* Packard.[3]

Cephalic appendages.—The antennae are uniramous, short jointed, and slender in their distal portion, and have a large proximal joint; the intermediate joints are unknown. Of the cephalic limbs only slight indications were found of the proximal joints of three pairs, and a few terminal joints extending from beneath the carapace, nothing of their original form being preserved. All traces of cephalic ap-

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[1] Smithsonian Misc. Coll., vol. 64, no. 5, figs. 1 and 2, pl. 66, 1916.

[2] Mem. Boston Soc. Nat. Hist., vol. 2, pl. 5, figs. 25, 25*d*, 1871.

[3] Twelfth Ann. Rep., U. S. Geol. and Geog. Surv. Territories, Hayden, Pt. 1, pl. xvi, fig. 2, 1883.

pendages are posterior to the hepato-pancreatic tubes passing from the stomach to the hepatic caeca.

There is no clearly defined line between the cephalic and trunk limbs, but from the relations of the limbs in *Burgessia* and *Marrella* it is assumed that it is between the third pair of cephalic limbs and the supposed first pair of trunk limbs. The specimens are too much obscured by the compression they have undergone to permit of recognition of the detailed structure of the limbs.

Thoracic limbs.—The specimen represented by figure 3, plate 14, has the distal ends of 17 thoracic or trunk limbs projecting beyond the left margin of the posterior shield; the shield in this specimen has not more than 14 fused segments outlined on it, so it is probable that the three anterior limbs belong with the body segments between the anterior segment of the posterior shield and the third pair of cephalic limbs. Another alternative is that the distal portion of the two anterior limbs extending beyond the margin of the shield belong to the maxilla and maxillula, which would leave only one pair of limbs from the segment anterior to the posterior shield and posterior to the cephalic limbs. The limbs were so subject to displacement, however, that any deduction is very uncertain. The distal portion of the thoracic or trunk limbs shows an endopodite with a slightly curved terminal spine with a slender section back of it corresponding to the slender distal joint of the endopodite of *Marrella* and *Burgessia;* and then the joints broaden towards the coxopodite with slight indications of five joints between the distal joint and coxopodite.

The exopodite is represented by many slender filaments that were attached to a multi-jointed arm or support similar in appearance to that of the exopodite of *Marrella.* The filaments are relatively broad, as they occur flattened on the shale. There are strong indications of large coxopodites, but none show their original form or the exact point of attachment of endopodite or exopodite, and the joints of the endopodites have been so crushed down as to be no longer definitely recognizable. The exopodites were nearly as long as the endopodites, and the filaments of the former are usually extended out to the end of the endopodites or beyond.

Digestive organs.—The exact location of the mouth is unknown, but from the apparent position of the antennae and proximal joints of the cephalic limbs, it was posterior to the point of entrance of the hepatic tubes, back of which the intestine was large with minor hepatic caeca opening into it through four small tubes, all of which are anterior to the posterior dorsal shield as indicated in the diagrammatic restoration (fig. 2); beneath the posterior dorsal shield the intestine is slightly constricted at the union of the trunk segments and extends back to the anal segment which protrudes posteriorly from beneath the shield; the gullet connecting the mouth and the stomach must have extended forward and upward.

The large hepatic glands and caeca are somewhat similar to those of *Burgessia bella* (text fig. 5); a short, strong tube with a well-marked anterior and posterior tube leads out from the stomach, and branching from these lateral tubes are a series of hepatic caeca. The small hepatic caeca are located between the long posterior tubes of the hepatic glands and the intestine and posterior to the main hepatic tube.

Owing to the excellent state of preservation of many of the specimens showing the hepatic caeca it is probable that they were situated between the dorsal and ventral membrane of the carapace and thus held in position and protected from destruction; that they are preserved at all is one of the wonders of this remarkable Burgess shale fauna.

Functions of appendages.—These were presumably the same as for similar organs in *Marrella* and *Burgessia,* and the mode of occurrence is essentially the same.

Diagrammatic restorations.—The diagrammatic restoration (fig. 2) presents the outline of the carapace and posterior shield with the stomach, intestine, hepatic tubes and caeca of the digestive system outlined, also the thoracic trunk, the telson and the thoracic limbs as far as known and interpreted. The data for this diagram are very good except the jointing of the endopodites and the exact form of the coxopodites and proximal joints of the exopodites. In figure 1, the endopodites on each side have been omitted and the exopodites drawn in so as to show their structure and position above the endopodites and below the ventral membrane of the posterior dorsal shield. The sixth limb has both the endopodite and exopodite attached; this should be compared with the thoracic limb of *Marrella splendens* (text fig. 9).

We know so little of the cephalic limbs of *Naraoia compacta* that I hesitate to give a diagrammatic sketch of them, and it would not be of even tentative value if we did not have the cephalic limbs of *Marrella* and *Burgessia* for suggestion; from the latter and from the evidence afforded by a few specimens, the outline of figure 1 is drawn.

Comparison with crustaceans.—*Naraoia* has many characters in common with the trilobite and some in common with *Marrella, Burgessia,* and *Waptia,* which will be spoken of in the discussion of this group of genera.

Plesiotypes.—U. S. N. M., Nos. 83945a-e.

NARAOIA SPINIFER, new species

Plate 15, fig. 1

Three specimens referred to this species are known, of which the one figured shows best the spines on the margin of the posterior dorsal shield; another preserves both the carapace and dorsal shield, the latter having marginal spines while the carapace has a smooth margin. On the third specimen the test of the dorsal shield is nearly all exfoliated on the left side so as to expose the body, several of the fringed exopodites, and coming from beneath them the distal portions of the endopodites.

This species differs from *Naraoia compacta* in having eight short, small spines on the outer margin of the dorsal shield equally spaced between the anterior margin and a large posterior median spine; all three of the known specimens of the posterior dorsal shield are also larger than those of *N. compacta,* as they average 25 mm. in length exclusive of the posterior median spine. The one specimen preserving the carapace indicates that it was similar to the carapace of *N. compacta,* the recognized differences between the two species being confined to the posterior dorsal shield.

Holotype.—U. S. N. M., No. 83946.,

BURGESSIA Walcott 1912

BURGESSIA BELLA Walcott

Plate 15, figs. 4-7; plate 16; plate 17; plate 18, fig. 1

Burgessia bella Walcott, 1912, Smithsonian Misc. Coll., vol. 57, no. 6, p. 177, pl. 27, figs. 1-3; pl. 30, figs. 3-4.

Since the publication of the original description of *Burgessia bella* Walcott, a large number of more or less well preserved specimens have been collected from the Burgess shale, a few of which preserve details of structure that make it possible to draw a diagrammatic restoration indicating the increase in our information of the cephalic and thoracic appendages (text figs. 3, 4).

Exoskeleton.—The exoskeleton is very delicate and the carapace is so thin as to be almost membranaceous. The segment to which the telson is attached appears to be partly covered ventrally by a heart-shaped plate that is attached to the anterior margin of the segment or to the posterior limb-bearing segment of the thorax; it suggests a supra-anal plate.

There appear to be five cephalic, eight thoracic, and one abdominal segment, also a long, slender telson with numerous joints. One example 21 mm. in length has 30 joints.

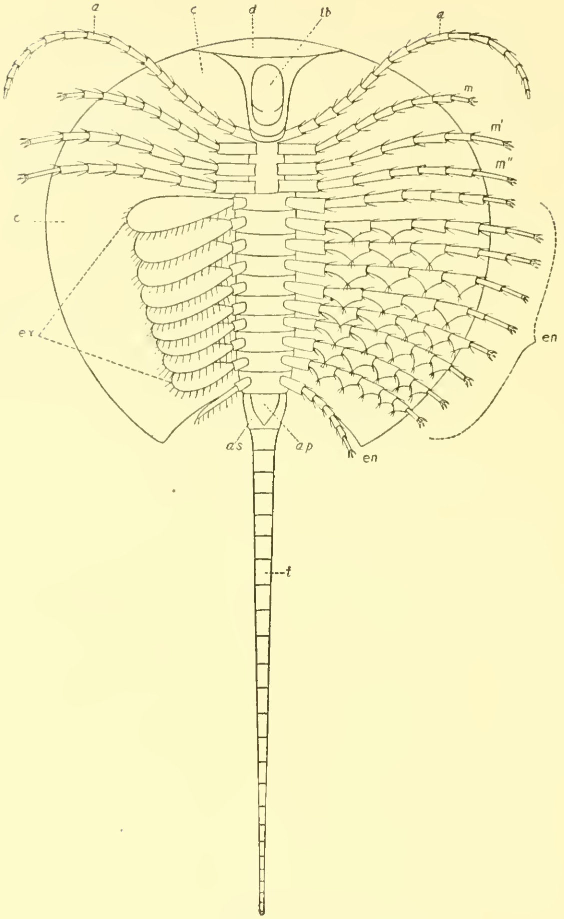

FIG. 3.—*Burgessia bella* Walcott.

a, antennae; *ap*, anal plate; *as*, anal somite; *c*, carapace; *d*, doublure; *en*, endopodite; *ex*, exopodite; *lb*, labrum; *m*, mandibles; *m'*, maxillae; *m''*, maxillulae; *t*, telson.

(About × 7.) Diagrammatic outline of ventral side with appendages. Much of the data on which this figure is based are shown by the specimens illustrated on plates 16 and 17. The exact form and position of the proximal joints of the cephalic limbs is unknown, but their general outline and position are about as outlined. The thoracic limbs, especially the endopodites, are well preserved in several specimens, but the exopodites are rarely seen and then only as faint and delicate impressions on the shale. The protopodites are fairly well defined, also the trunk segments and telson. The posterior endopodite and exopodite both differ from those anterior to them.

Carapace.—Carapace semicircular, with a deep notch on the posterior side. It appears to have had an upper (dorsal) and lower (ventral) membrane between which the irregular ramifications of the hepatic caeca were located. The shell glands, so conspicuous in the Apodidae, have not been recognized in *Burgessia.*

Labrum.—The labrum is attached to the reflected anterior rim (doublure) of the ventral side of the carapace and extends back nearly one-third its length; the labrum is rounded posteriorly and has a shallow obliquely transverse furrow on each side just in advance of its posterior margin; it was thin, readily distorted by pressure and is rarely preserved; one of the best examples is illustrated by figure 3, plate 17; it appears to have covered the anterior portion of the mouth.

Eyes.—The eyes are indicated by a minute round spot on each side of the dorsal median axis of the carapace and a short distance within the anterior margin.

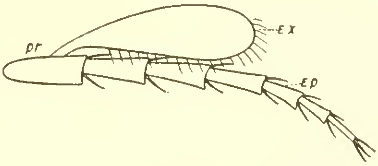

FIG. 4.—Diagrammatic outline of a thoracic limb of *Burgessia.*

pr, protopodite; *en*, endopodite; *ex*, exopodite.

The outline is based on the examination of many specimens aided by the known form of the endopodite of *Marrella* which is somewhat similar.

Dimensions.—The average length of the larger specimens is about 10 mm. A few are 12 and many are 6 to 8 mm. in length exclusive of the long telson. The relative proportions of the carapace, thorax, and abdomen are indicated by the diagrammatic restoration (text fig. 3).

Cephalic appendages.—These consist of well-marked antennae (figs. 3, 4) and three pairs of limbs situated between the antennae and the hepato-pancreas tubes; there is evidence that the basal or proximal joints of the cephalic limbs are relatively large and the remaining joints slender, but their exact position in relation to the labrum and their details of form and structure are not determined. It is quite probable that they represent the mandibles, maxillulae, and maxillae very much as in *Marrella,* and I have so represented them in the diagrammatic restoration of the ventral view of the species (text fig. 3).

Thoracic limbs.—The ten pairs of biramous thoracic limbs are uniform in character with the exception of the posterior pair, which are relatively smaller and more slender. Each limb has a strong proximal joint (coxopodite) to which the endopodite is attached; the latter is formed of four stout joints and two slender joints with two or three short spines at the end of the distal joints; the four joints between the proximal and slender sixth joint may have a flattened extension on the ventral side as in the endopodite of *Marrella* that gives them a greater transverse diameter, and this may also occur in the sixth joint; the distal joint is slender and probably cylindrical; the exopodite has not been seen attached to the protopodite, but from a number of specimens showing their position there is little doubt of their having been attached as on the thoracic limb of *Marrella*. The exopodite is an elongate oval, apparently unjointed lobe as seen in the specimen represented by figure 4, plate 17; a fringe of fine, short filaments occurs on the ventral and outer margins; the delicate structure and small size makes it difficult to determine its exact nature, but as far as known it recalls the exopodite of *Neolenus*. One specimen indicates that there may have been an anterior support for the exopodite that extended beyond the flat filamentous lobe and terminated in two minute spines; the proximal portion of the endopodites has been flaked off in this specimen so as to expose the exopodites; the slender distal extensions may belong to the exopodites or they may be the ends of the endopodites of the opposite side flexed under. I am inclined, however, to think that they belong with the exopodites. What may be a modified exopodite has been seen in one specimen; it projects from beside the posterior thoracic endopodite and consists of a central axis with seven sharp spines projecting from its posterior side and a terminal spine; or it may be an endopodite showing the edges of plate-like joints in the same manner as those of *Marrella splendens* (pl. 22, figs. 6, 7).

Digestive organs.—The mouth was situated at the ventral side and probably bounded in front by the labrum and on the sides by the mandibles; the mouth presumably opened into a gullet that passed into a large stomach apparently divided or forked anteriorly; from the rear of the stomach a straight intestine extended back to the anus. A strong, relatively large tube is given off from each side of the stomach at about the fifth segment; these have strong branches at the proximal end, one extending forward and another backward, both of which have short bifurcating branches on both the outer and inner sides. In nearly all well-preserved specimens the large tube and often the large connecting tubes are rounded as though they were distended when buried in the sediment; this would accord with the view that these were large digestive glands that contained food in process of digestion, the ultimate or hepatic caeca secreting a digestive juice as in *Lepidurus* and other crustaceans having such glands.[1]

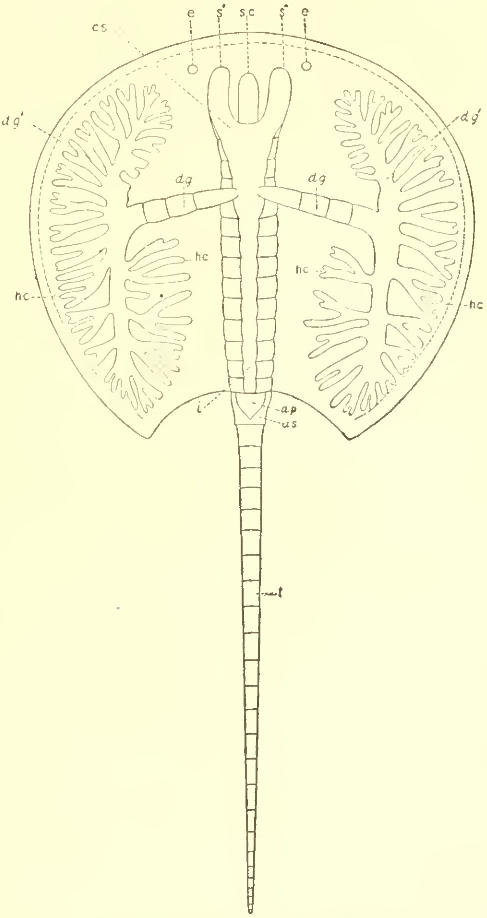

Fig. 5.—*Burgessia bella* Walcott.

ap, anal plate; *as*, anal somite; *cs*, central stomach; *d. g.*, digestive glands; *d. g'.*, lateral digestive glands; *e*, eye; *h. c.*, hepatic caeca; *i*, intestine; *s'* and *s''*, anterior lobes of stomach; *sc*, anterior central lobe of stomach; *t*, telson.

(About × 7.) Diagrammatic outline of digestive organs. Most of the data on which this figure is based are shown by the specimens illustrated on plate 16, figures 1, 3 and 4. The exact relations of the anterior central lobe of the stomach to the central stomach are unknown as there appears to be a line separating them.

The anus is supposed to have been at the last thoracic segment beneath the platelike structure shown on figure 3, plate 17.

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[1] Parker and Haswell, Text-book of Zool., vol. 1, p. 491, 1897.

Functions of appendages.—The functions of the cephalic and thoracic limbs were probably similar to the functions of those of *Marrella splendens.*

Mode of occurrence.—This delicate and beautiful little crustacean occurs abundantly in association with *Marrella splendens* and *Waptia fieldensis,* and is quickly recognized, even when distorted and crushed, by its carapace and strongly marked hepatic caeca. The carapace is almost always outlined on the shale, as are frequently the body and telson; the large strong endopodites are usually more or less clearly marked, although their jointed structure has generally been lost in the flattening in the shale; the exopodites were so delicate that they are rarely preserved, and the same is true of the labrum and eyes.

Comparison with crustaceans.—*Burgessia* has certain characters in common with *Marrella* and *Naraoia* and belongs in a group with them which will be discussed later (p. 37).

Diagrammatic restorations of ventral surface.—I have endeavored to present, in text figures 3, 4, and 5, interpretations of the structure of my *Burgessia bella.*

Plesiotypes.—U. S. N. M., Nos. 83947a-o.

WAPTIA Walcott 1912

WAPTIA FIELDENSIS Walcott

Plate 18, figs. 2-5; plate 19; plate 20; plate 21, fig. 2

Waptia fieldensis Walcott, 1912, Smithsonian Misc. Coll., vol. 57, no. 6, 1912, p. 181, pl. 27, figs. 4, 5.

The general characters of this species were described in 1912, since when a large number of specimens have been collected from the Burgess shale, a few affording data from which a fairly accurate diagrammatic restoration of the animal may be drawn (text fig. 6).

Exoskeleton.—The exoskeleton of the carapace, trunk, and caudal furca was very thin and readily distorted. The trunk consists of 5 to 7 short cephalic segments; 8 narrow thoracic segments, each bearing a pair of uniramous appendages; 6 long abdominal segments and 2 broad lobelike terminal caudal furca or rami; the latter have three transverse lines indicating four fused segments. The posterior margin of the abdominal segments bears four or more strong spines with a fringe of small, short, sharp spines between them. The last or anal segment has a minute anal opening on a slightly rounded elevation near its posterior ventral margin. The abdominal segments have often been narrowed and lengthened, or broadened and shortened by distortion in the shale.

Carapace.—The carapace when viewed from its dorsal side is elongate, narrowed anteriorly, expanded posteriorly, and has the outline of two broad lobes by the incurving of the rounded posterior margin towards the median line; when folded over on its longitudinal axis each side is a long semi-oval with the narrow end in front; there is no evidence of the presence of a longitudinal median line or hinge in the many specimens collected from the Burgess shale.

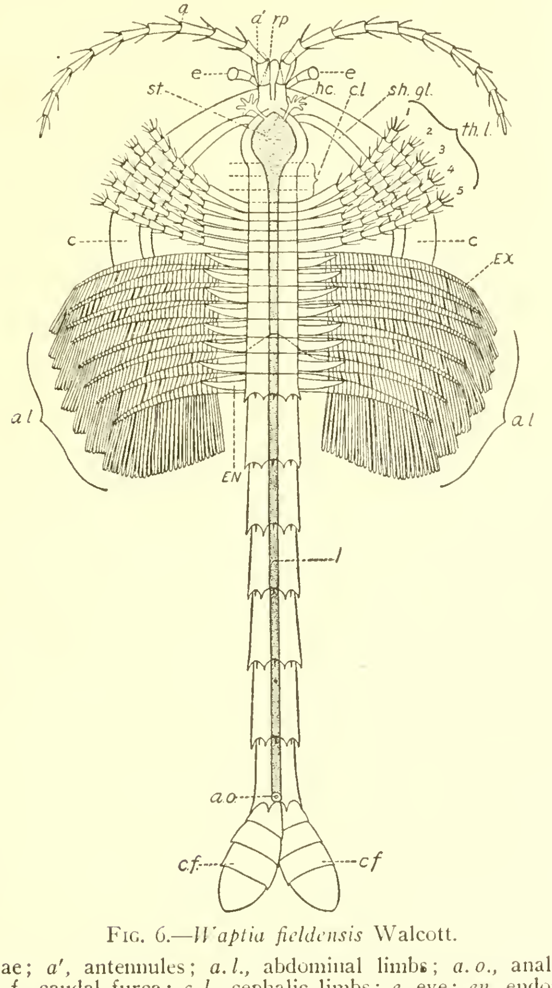

Fig. 6.—*Waptia fieldensis* Walcott.

a, antennae; *a'*, antennules; *a. l.*, abdominal limbs; *a. o.*, anal opening; *c*, carapace; *c. f.*, caudal furca; *c. l.*, cephalic limbs; *e*, eye; *en*, endopodite (??); *ex*, exopodite; *h. c.*, hepatic caeca; *i*, intestine; *r. p.*, rostral plate; *sh. gl.*, shell gland; *st*, stomach; *th. l.*, thoracic leg.

(About × 3.5.) Diagrammatic outline of ventral view of appendages and digestive organs. Most of the data on which this figure is based are shown by specimens illustrated on plates 19 and 20.

Rostral plate.—A small triangular rostral plate with narrow, sharp, longitudinal median ridge has been seen in four specimens (see fig. 3, pl. 19; fig. 2, pl. 20); it is located in the median line between the antennae.

Dimensions.—The average length of an entire adult specimen is from 40 to 50 mm., the carapace being about 16 mm. in length with a width when flattened of 15 mm. The general proportions of the various parts are shown by figure 4, plate 27, of the 1912 paper.

Eyes.—The eyes are relatively large and placed at the end of a stalk or peduncle that projects from beneath and on each side of the rostral plate as seen from above. The peduncles are slender at their proximal end and expanded in a broad oval outline on the distal third of their length, the expanded section carrying the elongate oval visual surface; the peduncle appears to have had at least one joint at about the inner third of its length and to have been attached to a prostomium at its proximal end.

Cephalic appendages.—These consist of a pair of long jointed antennae that project forward beside and beneath the median rostral plate, and a pair of short lobelike antennules appear to be represented close to the eye and above the antennae (see fig. 3, pl. 19; fig. 2, pl. 20) in several specimens. Traces of three pairs of cephalic limbs have been observed but their structure and form are unknown.

Thoracic limbs.—A number of specimens have five strong thoracic limbs that extend from their union with the body trunk forward and outward beyond the edge of the carapace (see fig. 2, pl. 18); the distal joint is short and has three strong and two small curved spines projecting from its outer end and fine spines along its margin; the three next joints are rather short and spiniferous, but the detailed character of the remaining joints is unknown. The limb observed is assumed to be the endopodite of a biramous limb, but the exopodite was not developed or it was so small and delicate as not to be preserved in the fossil state.

Abdominal limbs.—Each of the abdominal limbs is represented by long, multi-jointed exopodites bearing long, slender filaments (see fig. 3, pl. 20). The proximal joint was probably short and without fringing filaments, but none of the specimens proves this to have been the case; the exopodites are rather large at the proximal end, tapering gradually to a slender, flexible terminal section; the filaments of the terminal section are sometimes gathered in tufts or bundles as shown by figure 3, plate 20. The filaments are usually flattened and matted together, but a few specimens show them to have been slender, cylindrical tubes similar to the filaments on the exopodite of *Marrella* *splendens* (see restorations). The presence of a rudimentary endopodite is suggested on some specimens by an elongate, triangular, light-colored space on the proximal portion of the exopodites as shown by figure 3, plate 20; these light areas may be the outline of a space inside the broad arm of the exopodite, but they usually cross the axis of the arm diagonally; if they do represent the endopodite they were exceedingly delicate and attached by a broad base beside the exopodite in such a manner as to be held almost rigidly in place, and they are always in the fossil state pressed against the proximal section of the exopodite, and they have a silvery sheen so characteristic of the contents of the inside of the limbs of all crustaceans of the Burgess shale preserving the limbs. I do not think that they represent the endopodites, but they are the only suggestion of the latter thus far observed in connection with the abdominal limbs of *Waptia*.

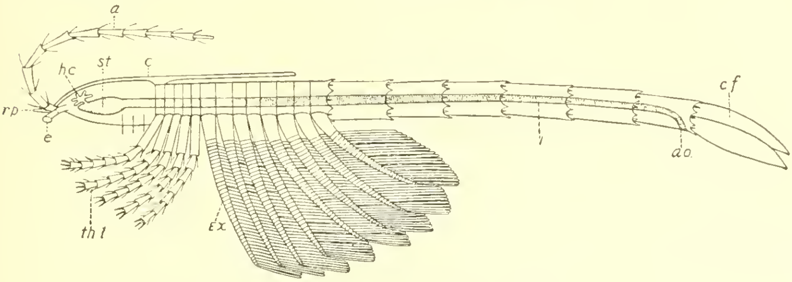

FIG. 7.—*Waptia fieldensis* Walcott.

a, antennae; *a. o.*, anal opening; *c*, carapace; *c. f.*, caudal furca; *e*, eye; *ex*, exopodite; *h. c.*, hepatic caeca; *i*, intestine; *r. p.*, rostral plate; *st*, stomach; *th. l.*, thoracic leg.

(× 3.) Diagrammatic side view of a section of the animal, illustrating the appendages, digestive tract, etc.

Functions of appendages.—The functions of the antennules and antennae were presumably sensory as in recent Malacostracans, as they do not appear to have been modified for any other purpose, and the proximal joint, as far as known, did not function as a manducatory organ.

The mandibles, maxillulae, and maxillae are unknown; the five pairs of thoracic limbs may have been used for crawling on the bottom, but with short joints and spinous distal joint they could not have been very effective; the exopodites of the eight pairs of abdominal limbs served as natatory organs and also as branchiae, the long delicate filaments presenting an extended surface area to the water.

Digestive organs.—What is known of the digestive system of *Waptia* indicates that it was somewhat similar to that of the living

Apus. The elongate globular stomach (*st*), with the small digestive or hepatic glands (*d. gl.*), long simple intestine (*i*) terminating on the last segment at the anus (*an*) all suggest corresponding organs in *Apus,* and it is highly probable that the mouth was ventral and communicated with the stomach by a gullet extending upward and forward. The shell gland (*sh. gl.*) or renal organ is distinctly marked in several specimens and, as far as comparison is possible, is not unlike that of *Apus.*

Observations.—*Waptia* was a pelagic, free and active swimming animal using its abdominal limbs and the broad terminal rami for propulsion. The fact that it is found in association with algae and sponges is explained by the conclusion that the sessile forms of life were detached and drifted into the Burgess pool and deposited along with the pelagic forms that dropped to the bottom of the sea.[1]

The carapace of *Waptia* is much like that of *Hymenocaris* except that it is not separated into two equal parts by a median longitudinal hinge line, and there is no evidence of the presence of an adductor muscle scar on each side as in *Hymenocaris.*

DIAGRAMMATIC RESTORATION OF VENTRAL VIEW OF THE BODY AND APPENDAGES, WITH OUTLINE OF DIGESTIVE ORGANS

Most of the data on which the restoration is based is shown by the specimens illustrated on plates 18, 19 and 20. The form and position of the cephalic appendages are unknown with the exception of the antennae and possibly antennules; the proximal joints of the thoracic and abdominal limbs are outlined on the specimens though their form is not preserved, but otherwise the limbs are fairly well known. The body cavity is outlined by figure 3, plate 18, but it is not included in this diagrammatic figure. The shell glands (*sh. gl.*), stomach, intestine, and hepatic caeca are outlined, as they represent what is known of the digestive organs.

Plesiotypes.—U. S. N. M., Nos. 83948a-e.

WAPTIA CIRCULARIS, new species

Plate 21, fig. 3

A single specimen with a short, rounded carapace was labeled *W. circularis* by Doctor Walcott. As far as the rather poor preservation permits a determination it would seem that otherwise it is similar to *W. fieldensis.*

Holotype.—U. S. N. M., No. 83449.

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[1] Smithsonian Misc. Coll., vol. 67, no. 5, pp. 219, 220, 1919. Idem, no. 6, p. 265, under *Habitat.*

SKANIA, new genus

Description.—Dorsal shield thin, broadly rounded in front and tapering from the postero-lateral angles of the cephalic carapace to the posterior end of the shield.

Cephalic carapace transverse with the postero-lateral angles extended into spines; posterior margin arched forward; frontal margin reflected to form a doublure to which a small elongate labrum is attached. Eyes unknown but indicated by a bright spot on the carapace a short distance outward from the side of the labrum. No traces of facial sutures.

Posterior dorsal shield, elongate and formed of 14 or 15 fused segments with a more or less distinctly marked border. There is a short transverse segment or telson (pygidium) outlined, but whether it is free from the next anterior segment is unknown.

Surface of test apparently smooth.

Dimensions.—This genus is based on a small animal, *S. fragilis*, 5 to 17 mm. in length.

Appendages.—There are indications of antennae, three pairs of cephalic limbs, and a pair of limbs for each segment of the posterior dorsal shield.

Digestive organs.—An intestine extends from the posterior segment forward to the central part of the cephalic carapace where it widens out to form an elongate oval stomach. There are traces of hepatic caeca adjoining the stomach.

Genotype.—*Skania fragilis* Walcott.

Stratigraphic range.—The stratigraphic range is limited to a band of dark siliceous shale about 4 feet in thickness forming a part of the Burgess shale member of the Stephen formation.

Observations.—The generic name is derived from Skana, the name of a glacier in the Mount Robson District, Alberta, Canada.

The specimens representing the species of this genus are small and so thoroughly flattened in the shale that little more than a black film remains. This makes it very difficult to obtain details and also leaves some doubt as to whether the posterior dorsal shield is formed of fused or free segments.[1]

SKANIA FRAGILIS, new species

Plate 21, fig. 1

Description.—General outline irregularly heart-shaped but subject to wide variation owing to distortion by compression.

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[1] At the head of these notes, Doctor Walcott later wrote, "A trilobite, C. D. W."

Dorsal shield.—Owing to its extreme tenuity there is usually little more than a dark film on the shale that has definite outlines, and shining through it are traces of the digestive organs and the ventral limbs. The transverse cephalic carapace recalls that of *Marrella* without the great median spines; it is often incurved at the center of its anterior margin and laterally projects into long backward-curving, spine-like extensions that are so tenuous as to suggest that the cephalic carapace was formed of a delicate membrane.

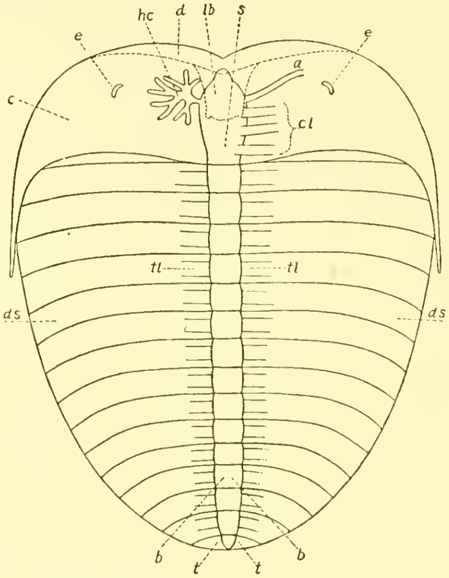

FIG. 8.—*Skania fragilis* Walcott.

(× 7.) Diagrammatic outline of ventral side showing the various parts as interpreted from several specimens. No details of the segments of the posterior dorsal shield are preserved, but the segments are clearly outlined. The intestine is quite definite, also the fact that it contracted at each segment and expanded into a stomach beneath the cephalic carapace. Only the proximal portion of the limbs is outlined, although fragments of the distal portion are preserved on one specimen.

The thoracic portion of the dorsal shield is clearly segmented in two specimens, and traces of segmentation occur in others, but usually there is only a black smear on the shale with the outline of the intestine showing through it. There appear to be 14 or 15 fused segments and possibly a minute terminal segment or telson. None of the 29 specimens in the collection show the outlines of the median lobe, although one has a slight elevation along the line of the intestine.

Labrum.—Traces of a narrow doublure and small labrum have been seen on two specimens; the labrum appears to have been elongate with an outline similar to that of the labrum of *Burgessia.*

Dimensions.—The largest specimen has a length of 17 mm., but the average length is from 5 to 8 mm.

Appendages.—One specimen has several thoracic endopodites out of place on one side, and other specimens show the proximal joint obscurely but sufficiently well to recognize them; another specimen has what may have been slender antennae projecting from beneath the flattened labrum and posterior to it three pairs of slender appendages in which all traces of joints have disappeared; there are also on this specimen several threadlike, silvery lines extending from the central axis out to a margin which indicates that the limbs were long and slender; none of the specimens clearly show the exopodites or any details of the limbs. Specimens of *Marrella* and *Burgessia* often have threadlike, silvery lines representing the limbs, these lines being the pyritized contents of the joints, the test having disappeared in the process of mineralization of the original specimen.

Digestive organs.—The stomach is represented by an enlargement of the anterior portion of the intestine within the cephalic carapace, and the intestine extends back to the last segment; traces of hepatic caeca also occur beneath the cephalic carapace adjacent to the stomach.

Observations.—This very delicate form was placed, when sorting the collections, among specimens of the young of *Marrella splendens,* but it became evident upon close examination that they were quite distinct. They have a dorsal shield resembling that of *Naraoia.* I have examined all the specimens in hopes of finding free segments, but without results. There is no well-defined border about the posterior dorsal shield as in *Naraoia,* but there is a definite margin that is unbroken by the extension of the fused segments beyond it.

The almost complete flattening of all the specimens prevents any comparison with the median lobe of the trilobites, and there is no indication of facial sutures although there are slight traces of eyes on the cephalic shield at about the same place as in *Nathorstia.*[1]

Holotype.—U. S. N. M., No. 83950.

MOLLISONIA Walcott 1912

MOLLISONIA ? RARA Walcott

Plate 21, fig. 4

Mollisonia ? rara Walcott, 1912, Smithsonian Misc. Coll., vol. 57, no. 6, p. 198, pl. 24, figs. 6, 7.

Original description.—"Of this species there are several fragmentary specimens. The species differs from *M. gracilis,* with which it is

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[1] Smithsonian Misc. Coll., vol. 57, no. 6, pl. 28, fig. 2, 1912.

associated, in the character of the thoracic segments and pygidium; also, so far as we can determine from this superficial study, there are seven segments and the pygidium shows distinct segmentation with a denticulated border."

A complete individual was found after the two fragments were described in 1912. The angularity of the shield at the bottom of the specimen as mounted on the plate is characteristic as its essential angles and curves are repeated in all the specimens referred to the species.

Plesiotype.—U. S. N. M., No. 83951.

MARRELLA SPLENDENS Walcott

Plate 22, figs. 1-9

Marrella splendens Walcott, 1912, Smithsonian Misc. Coll., vol. 57, no. 6, p. 193, pl. 25, figs. 1-6, pl. 26, figs. 1-6.

In the preliminary note of 1912 the general form and appearance of the carapace and appendages of *Marrella splendens* were described and illustrated. Since then a large number of specimens have been collected, some of which have added to our information both of the carapace and ventral side.

Exoskeleton.—The exoskeleton with the exception of the carapace is very delicate and formed of a series of 31 segments or somites, to 24 of which a pair of biramous appendages are attached; also a terminal segment of the body forming a minute plate-like telson and five segments of the head indicated by the presence of four pairs of free appendages and one segment incorporated in the body of the carapace; this is indicated by the anterior lateral free spines of the carapace with a pair of sessile eyes. As far as may be determined from the compressed fossil specimens the section of the body segments was broadly oval with a dorsal stergite and a ventral sternite section, the appendages being attached on the lower side on the ventral sternite below the margins of the dorsal stergite.

This does not mean that the eyes necessarily represent the anterior segment but that they represent one segment whatever may have been its original position.

Carapace.—Carapace strong, subquadrangular, and with two large dorsal postero-lateral, spinelike lobes (fig. 9) comparable with the postero-lateral lobes of the carapace of the Apodidae. At each antero-lateral angle a strong, backward-curving spine is attached by a close suture. These spines complement the great dorsal thoracic spines and may be compared with the movable or free cheeks of the trilobite. A narrow median carina or ridge extends the entire length of the lateral spines and the postero-lateral lobes.

Labrum.—The labrum is attached to the strong frontal rim (doublure) of the ventral side of the carapace (fig. 9), and extends back to within a short distance below the posterior median margin of the carapace; its posterior lateral angles are extended into short, spine-like projections and the posterior margin appears to have been provided with two short points. The labrum appears to have covered the anterior portion of the mouth; this is indicated by the proximal end of the protopodite or basal joint of the large mandible and that of the antennae passing beneath it in many specimens (see pl. 22).

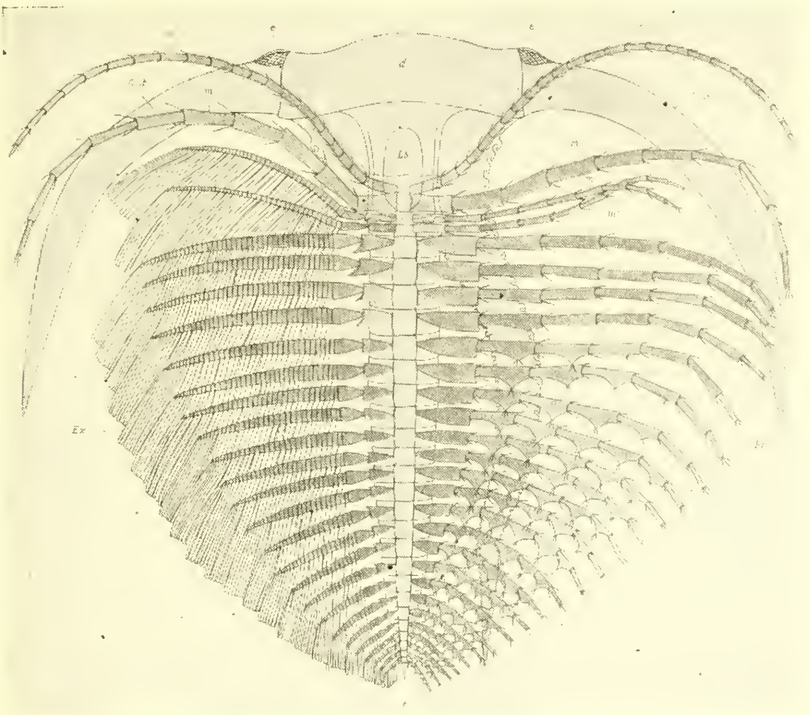

FIG. 9.—*Marrella splendens* Walcott.

Restoration as described in text: *a*, antennae; *c. sp.*, carapace spine; *d*, doublure or reflex of anterior margin of carapace; *e*, eye; *en*, endopodite; *ex*, exopodite; *m*, mandible; *m'*, maxillula; *m''*, maxilla; *t*, telson.

Eyes.—The eyes (fig. 9) have not been seen from the dorsal side of any of the several hundred specimens preserving the carapace, and rarely from the ventral side; this leads to the conclusions (a) that they were located on the lower anterior margin in such a position as to be concealed when the carapace was flattened by compression;

(b) that they were of a very delicate structure and readily destroyed; (c) that when preserved they were likely to be distorted and displaced by compression in the shale and could only be seen from the ventral side of the flattened carapace when they projected beyond the margin and were outlined on the shale. At first I thought that the eyes were situated on the carapace just within the line of its union with the large antero-lateral spines. Later I re-examined all the specimens showing the eyes, and found two that indicated that the visual surface of the eye was on one side of the suture separating the spines from the carapace, and the cap or palpebral lobe on the other, and one that quite clearly indicated that it was attached to the proximal end of the great spines, the latter being equivalent to the free cheeks of the trilobite. The interpretation of this is that the visual surface of the eye was attached to the great spine outside of the suture that outlined the spine from the carapace, and that the cap or palpebral lobe of the elevated visual surface of the eye was attached to the carapace as in the trilobites with elevated eyes and free cheeks.

It is difficult to determine the extent of the elevation of the eye above the carapace, but from its inconspicuous position in the fossil state I strongly suspect that it was only slightly raised and that its field of vision was largely forward and downward; this would be in accord with the needs of a small, active, free-swimming animal that spent little time on the bottom.

Among the trilobites the eye of *Deiphon forbesi* Barrande[1] is at the proximal end of a large genal spine forming the free cheek, and the great eye of *Bohemilla stupenda* Barrande[2] occupies nearly the entire width of the proximal end of the free cheek which is extended into a long strong spine.

Digestive organs.—The intestinal canal extends from the posterior margin of the labrum back to the small, platelike termination of the body; it is contracted a little opposite the line of union of each of the segments (see figs. 6, 7, and 9, pl. 22); anteriorly the intestine widens out between the labrum and carapace to form what may have been the stomach; the narrow canals of the dorsal lobes passed into the space between the carapace and labrum and probably entered the enlarged intestinal canal as did the canals of the antero-lateral spines which appear to pass without interruptions through the close sutures that unite them with the carapace; the canals of the postero-dorsal lobes may represent the shell-glands or excretory organs of the recent Apodidae.

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[1] Syst. Silur. de Boheme, vol. 1, pl. 2B, fig. 4, 1852; suppl., pl. 2, fig. 19, 1872.

[2] Idem, vol. 1, Suppl., pl. 14, fig. 30.

Cephalic appendages.—These consist of antennae, mandibles, simple slender maxillulae, and slender maxillae. The proximal joints of the cephalic appendages are so badly crushed and matted together beneath the labrum or just back of it that it has been very difficult to determine exactly their form and relations to each other, but it is highly probable that they were arranged as in the restoration (text fig. 9).

Antennae.—The antennae are long, slender, and many-jointed, with fine spines at the distal end of each joint. As far as may be determined, the proximal joint was attached to the ventral surface beneath the postero-lateral angle of the labrum just in advance of the mandible. There is no evidence that it served as a jaw or manducatory organ except that in specimens preserving them their inner (proximal) end is in front of and adjoining the large proximal joint of the mandibles (see figs. 3, 6, and 7, pl. 22).

Mandibles.—The mandibles are formed of a strong proximal joint with four short, strong joints followed by five slender, elongate joints (see fig. 9), the latter being almost covered with very fine setae that give a plumose appearance to the appendage as it extends out beyond the great backward curving spines of the carapace. I examined hundreds of specimens before finding a proximal joint with its inner end sufficiently well preserved to suggest the character of its masticatory surface; two specimens indicate that it is as shown in figure 7, plate 22, and in the restoration. There is no evidence as to whether the proximal joint is composed of one long joint or two closely united short joints. The usual location of the mandibles in well preserved specimens is shown by figures 1 and 2, plate 22.

Maxillulae.—These are long, slender, and with about 10 slender joints. They look like thoracic legs (endopodite) but their position and slender joints serve to distinguish them. Portions of them may be seen in figures 1 and 2, plate 22.

Maxillae.—As far as known the maxillae are formed of joints a little longer than those of the maxillula and about the same diameter; both appear to have been slender, rather closely jointed, simple appendages as far as the endopodite was concerned; there is strong evidence that an exopodite was present, similar to those of the exopodites of the trunk appendages, but they have not been seen directly attached to the protopodite; where the parting of the shale is on the plane of the exopodites they are usually present next to the mandible and directly over the position of the maxillulae and maxillae, which suggests strongly that they were present.

The maxillulae and maxillae were so slender that they are usually absent as the result of having been torn off or crushed between the strong mandibles and the thoracic limbs. In figure 1, plate 22, their exopodites are shown on the left side, and on the right side the endopodites of the maxilla with the exopodite of the maxillula, the endopodite of the latter having apparently been pushed under and a little forward of the mandible. Sometimes the endopodite is present but the joints are indistinguishable or only a few can be seen.

Thoracic limbs.—The biramous thoracic limbs appear to be uniform in character from the cephalon to the minute plate-like telson at the posterior end of the body. Each limb is formed of a protopodite, a jointed endopodite, and a jointed fringed exopodite.

Protopodite.[1]—The large protopodite is attached by its inner end to the lower side of the body segment about half way between the ventral median line and the rounded outer side of the body apparently in the same manner as the trunk limbs of *Apus,* except that in the latter there is no evidence that the protopodite served as a gnathobase. The protopodite is elongate, apparently cylindrical at its inner end, and flattened somewhat at the distal end; it is strong, and supports an endopodite and an exopodite. It is usually flattened so as to appear of about the same width throughout its length; a few specimens indicate that it narrowed at its proximal end, essentially as shown in the restoration.

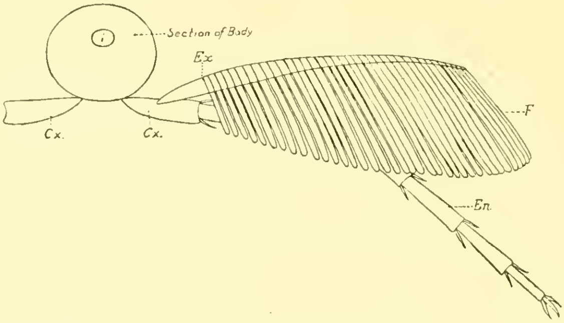

FIG. 10.—Diagrammatic outline of the posterior side of one of the anterior thoracic limbs: *pr*, protopodite; *en*, endopodite; *ex*, exopodite; *f*, filaments of exopodite; *i*, intestine.

This figure indicates the point of attachment of the limb to the body, also approximate position of the intestine.

Endopodites.—The endopodite or leg is formed of six joints. The first five joints of the anterior limbs are rather flat and broad at the

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[1] I find that at many places Doctor Walcott changed "protopodite" to "coxopodite." Whether this term was supposed to have been changed here also I was unable to ascertain.—C. E. RESSER.

sides; narrow and slender on the dorsal and ventral view; short, very fine spines occur at their distal end and along the side of the joints. The slender distal joint is more nearly cylindrical and has a short, strong, slightly curved spine with one or two fine spines beside it extending out from the end of the joint. The anterior legs appear to have been delicate and slender, but usually they have retained their natural position remarkably well. Usually the first joint of the endopodite of the fourth pair of limbs is slightly expanded, and the first and second joints of the fifth to seventh pairs of limbs, and the first five joints of the eighth to twentieth pairs of limbs. The expanded joints vary in degree of expansion from slight enlargement on the fourth limb to where the transverse diameter is considerably greater than the length of the joint. The latter recall the transverse flattened joints of the endopodite of the trilobite *Triarthrus becki.*[1]

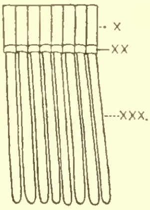

FIG. 11.—Diagrammatic enlargement of a section of the exopodite showing the body and the attached cylindrical filaments.

On some specimens showing the expanded joints the extended portion is very narrow from base to point, and gives the effect of a strong spine projecting from midway of the joint; in other specimens the base is as long as the joint and the apex is obtuse, which is the prevailing form. When in a natural condition the expansion of the joint was undoubtedly on the lower or the ventral side, and the fact that in the fossil state specimens occur with all the expansions pointing forward means only an accident of preservation; some occur with scarcely a trace of the enlarged joint, owing to the fact that the ventral side of the endopodite is buried in the shale, leaving the narrow dorsal side in view; in the restoration (fig. 9) I have outlined the flat, vertical posterior side of the endopodite.

Exopodite.—The exopodite is attached to the protopodite about midway of the length of the latter. It is formed of a long, strong proximal joint to which is attached a long, slender, multi-articulate appendage, each segment of which supports a long, slender, flat

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[1] Smithsonian Misc. Coll., vol. 57, p. 137, pl. 30, fig. 20, 1912.

(formerly round) filament, which is beautifully preserved in some specimens (fig. 8, pl. 22). The fringe of filaments often overlap those of the adjoining exopodite so as to form an imbricating series of fringes the entire length of the body.

An exopodite 3 mm. in length has attached to it 42 filaments that average about 12 to 14 to the millimeter in the proximal portion, and 14 to 16 towards the distal end; they increase gradually in length from the proximal end until on the distal section they may be as long as the entire exopodite. A rusty specimen laid aside as of little value proved on cleaning to have the filaments preserved as long, slender cylinders or tubes (see fig. 8, pl. 22).

Most of the fossil specimens have the fringes extending forward and outward, but when the animal was living they undoubtedly extended outward and backward so as not to impede its forward movement.

As mentioned under *Cephalic appendages,* there is good reason to think that the two posterior oral appendages (maxillulae and maxillae) have in addition to the simple jointed endopodite an exopodite similar in structure to that of the thoracic limbs.

Epipodite.—A single specimen shows what I thought in 1912 to be a large epipodite or branchiae,[1] but which I have now decided to be several of the fringed exopodites pressed down together and more or less macerated in the contents of the body which were squeezed out on that side. It was only after finding a number of examples showing the fringed exopodites arranged in this manner but not pressed into each other that I gave up the view that a large epipodite was present.

Several specimens have been found since 1912 that indicate the presence of a small oval flattened lobe attached to the dorsal side of the protopodite, or it may be to the proximal joint of the exopodite, but it may be that this appearance is caused by the manner in which the protopodite and the segments of the body are matted down together; some of the thin oval bodies, however, are so clearly defined that they suggest the presence of a small epipodite, but I do not consider the evidence sufficient to warrant representing them on the restoration of the thoracic limb.

Functions of appendages.—The proximal joints of the antennae may have assisted in mastication and may have had a sensory function. The proximal joints of the mandibles undoubtedly served in mastication, but whether those of the slender leglike maxillulae and maxillae aided is undetermined, as nothing has been seen of either

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[1] Smithsonian Misc. Coll., vol. 67, pls. 29, 32, 1918.

gnathobasic spines or lobes. It is probable, however, from their position and form they were of service in directing food to the mouth.

The long, flat outer joints of the mandibles may have been used in swimming as an aid to the thoracic limbs.

The endopodite of the biramous trunk appendages probably served both as a natatory and ambulatory leg, although from their delicate distal joints they evidently were little used in walking. The fringed exopodites may have assisted in swimming and they undoubtedly served as gills. The absence of a channel formed of gnathobases on the protopodites of the trunk limbs such as occurs in the Apodidae and Trilobita, and also of any known organ for seizing food, leads to the conclusion that the exopodite may have served to direct a current of water bearing food towards the mouth. The long, strong filaments attached to the segments of the exopodite are comparable with the filaments of the exopodite of the trilobite *Neolenus*,[1] and the remarks on the latter should be read in this connection.

Diagrammatic restoration of the ventral appendages.—This is shown in text figure 9 and presents my interpretation of the arrangement of the appendages. The long body, with its numerous segments, is attached to the carapace in its cephalic region only. The antennae (*a*), mandibles (*m*), maxillulae (*m'*), and maxillae (*m"*) are drawn in from the evidence given by many specimens, no one of which has all the limbs in place; several of the best specimens are illustrated on plate 22. The eyes (*e*) are somewhat theoretically placed, but their general position is known despite the displacement most of them have been subjected to. On the right side the entire series of protopodites and endopodites forming the thoracic limb are represented; the form of the inner end of the protopodite is based on indications afforded by several specimens, although usually the protopodite is crushed flat and appears to be of the same size throughout its length. On the left side the protopodite is cut away so as to show the approximate point of attachment of the proximal end of the exopodite. The latter are drawn from such specimens as are represented on figures 1-9, plate 22, and many others not illustrated. The relative position and form of the exopodite, endopodite and protopodite is shown by text figure 10.

Mode of occurrence.—*Marrella splendens* occurs abundantly in the compact, hard shale but there are few really fine specimens. This free-swimming, delicate little crustacean dropped down on the surface of the bottom and was speedily buried by fine mud settling over it; the mass of gradually hardening mud pressed the rounded body into a

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[1] Smithsonian Misc. Coll., vol. 67, no. 7, p. 370, 1920.

thin film and matted those parts resting on each other together unless there was a thin film of mud between them. When there was such a film of mud, it later hardened into shale and formed a plane of weakness along which the shale parted when, from the action of weathering or of force applied with hammer or chisel, the shale was split open. Sometimes the parting is between the matrix and the ventral or dorsal surface of the specimen, or it may be between the series of fringed exopodites and the endopodites; a number of specimens in the collection show a part of the endopodites with the exopodites above or below them, and again the parting may have been above or below the exopodites on one side of the body and the reverse on the other side (see pl. 22). The structure of the body and the thoracic appendages is very clearly exhibited, but the cephalic appendages, labrum and carapace, are usually so matted together that it is difficult to distinguish the details of structure.

OBSERVATIONS

Marrella and the trilobite.—*Marrella* has several characters in common with the trilobite and others that are dissimilar.

SIMILAR CHARACTERS

1. A cephalic shield supporting a labrum.
2. Sessile eyes on the proximal end of a great spine equivalent to the free cheek of the trilobite.
3. A labrum (hypostoma) with the proximal joints of the cephalic limbs gathered at its posterior end in a manner comparable with that of the trilobite.
4. A pair of biramous limbs for each trunk segment formed of a protopodite, jointed endopodite (leg), and a jointed exopodite, but without any known epipodite.
5. Expansion of the joints of the endopodites on some of the thoracic limbs.

DISSIMILAR CHARACTERS

1. Absence of a thoracic dorsal shield.
2. Almost total absence of an abdominal section or pygidium.
3. Position of proximal joint of antennae.
4. A large third cephalic appendage (mandible).
5. The manner of attachment of the coxopodite of each trunk limb directly by its proximal end to the side of the ventral surface of the body.

6. The coxopodite did not serve as a gnathobase.

1 and 2 are considered to be more primitive characters.

3, 4, 5, and 6 less primitive.

My present conclusion is that *Marrella* is a less primitive form than the Apodidae, and while a more primitive form than the trilobite it is nearer the latter than the Apodidae, and should be grouped near it but not with the Trilobita. At the time of my preliminary examination of the crustaceans then known to me from the Burgess shale I placed *Marrella* and *Nathorstia* as progenitors of the trilobite,[1] but with our present information *Marrella* will be placed with *Burgessia*, *Nathorstia* being left under Trilobita.

COMPARISON WITH CRUSTACEANS

Marrella and the Branchiopoda.—*Marrella*, with its sessile eyes, carapace-like cephalic shield, labrum attached to the doublure, numerous trunk limbs, and the large mandible, suggests the Apodidae, but when we consider the well-developed antennae, large removable spine attached to the cephalic shield, biramous trunk limbs on each body segment consisting of a fully developed endopodite and exopodite, and the absence of caudal rami, the conclusion is that *Marrella* represents a more advanced stage in the evolution of the Crustacea than *Apus* and its allies. The biramous limb of *Marrella*, like that of the trilobite, undoubtedly passed through the foliaceous or multiramous limb stage in its evolution, probably in pre-Cambrian time.

Marrella differs from the Branchiopoda in:

a. Absence of lobed multiramous foliaceous trunk limbs with gnathobases and in the presence of biramous trunk limbs with protopodite, jointed endopodite (leg), and jointed exopodite.

b. Absence of furcal rami.

c. Presence of a pair of biramous limbs on each trunk segment back to the telson.

Marrella includes the following characters of the Branchiopoda:

a. A true carapace arising from a fold of the integument.

b. A labrum attached to the reflected margin or "doublure" of the carapace.

c. A large mandible serving as a jaw in the process of mastication.

Plesiotypes.—U. S. N. M., Nos. 83486a-i.

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[1] Smithsonian Misc. Coll., vol. 57, p. 161, 1912.

HELMETIA Walcott 1918

HELMETIA EXPANSA Walcott

Plate 27

Helmetia expansa Walcott, 1918, Smithsonian Misc. Coll., vol. 68, no. 12, p. 7, fig. 8.

This is another of the species first published in the Smithsonian explorations pamphlet for 1917, and for that reason is here reprinted.

Holotype.—U. S. N. M., No. 83952.

EXPLANATION OF PLATES

PLATE 1

PAGE

Margaretia dorus, new species.................................... 2

FIG. 1. Impression of outer surface.
2. A wider and less well defined specimen. Possibly a mutilated fragment.
3. Impression of surface, on which the elevations apparently were more conical and more numerous, which may indicate another species.
4. Unretouched photograph by reflected light of the typical form. This is again the impression of the outer surface. Compare the elongate elevations with the more conical ones in fig. 3.
5. Unretouched photograph of the holotype.
6. (× 2.) Another, less perfect specimen on which Doctor Walcott apparently laid stress.

PLATE 2

PAGE

Miskoia placida, new species.................................... 4

FIG. 1. The holotype showing the annulations, the teeth around the mouth, and the manner in which the digestive tract seems to run along one side of the body, as it is compressed in the shale.

Redoubtia polypodia Walcott.................................... 3

FIG. 2. A specimen, possibly of a different species, since it has smaller appendages. Parts of a *Hymenocaris?* lie above it.
3. (× 1.5.) Holotype, as illustrated previously.

PLATE 3

PAGE

Wiwaxia corrugata Walcott.................................... 6

FIG. 1. Photograph of a very fine individual retouched to bring out the striae on the scales.

Portalia mira Walcott.................................... 3

FIGS. 2, 3. Counterparts of the holotype. A specimen of *Miskoia* lies nearby.

PLATE 4

PAGE

Canadia spinosa Walcott 4

FIG. 1. (× 1.5.) Specimen having an unusually straight position, with all the spines turned backward and thus crowded together.

2, 3. Natural size and enlarged (× 3) views of a fine complete individual. The enlarged picture has been retouched.

PLATE 5

PAGE

Canadia spinosa Walcott 4

FIGS. 1, 2. Natural size and enlarged (× 4) photographs. The larger one has been retouched.

PLATE 6

PAGE

Canadia spinosa Walcott 4

FIG. 1. (× 2.) Photograph of a well preserved specimen.

2. (× 2.) Unretouched illustration of another specimen whose specific identity Doctor Walcott doubted somewhat.

Canadia sparsa Walcott 5

FIG. 3. (× 2.) Unretouched photograph of this peculiar worm.

Canadia irregularis Walcott 5

FIG. 4. Small, somewhat broken specimen. (See pl. 9, fig. 3, for enlargement.)

5. (× 2.) An unretouched photograph of the lectotype.

6. (× 2.) Coiled specimen doubtfully referable to the species.

PLATE 7

PAGE

Canadia setigera Walcott 5

FIG. 1. (× 2.) Unretouched photograph of a rather complete curled specimen.

4. (× 2.) Unretouched photograph showing the attachment of the setae.

Canadia dubia Walcott 6

FIG. 2. (× 3.) A good illustration of this small form.

Canadia irregularis Walcott 5

FIG. 3. (× 3.) Enlargement of specimen illustrated as fig. 4 on preceding plate.

Plate 8

PAGE

Canadia dubia Walcott 6

Fig. 1. A fairly large specimen.

2. (× 2.) A specimen showing the intestinal tract.

Canadia setigera Walcott 5

Fig. 3. (× 3.) Retouched figure of a specimen showing the bundles of spines particularly well.

Pikaia gracilens Walcott 7

Fig. 4. (× 2.) A wide specimen. The illustration is slightly retouched.

5. (× 2.) Another rather well preserved example.

Plate 9

PAGE

Ottoia minor Walcott 6

Fig. 1. (× 2.) A short form that may have its shape because the mouth parts are retracted.

2. (× 2.) Small specimen, showing intestinal tract, doubtfully referred to the species.

3. (× 2.) Apparently the anterior end of a poorly preserved individual.

4. (× 2.) Another form like fig. 2.

5. (× 2.) A specimen with a peculiar restriction that may be accidental.

6, 7. Retouched photographs of a particularly fine individual. The whole specimen is enlarged somewhat (× 1.5) and the anterior end considerably (× 4).

Canadia dubia Walcott 6

Fig. 8. (× 2.) Unretouched photograph of a small individual.

Canadia simplex, new species 6

Fig. 9. (× 3.) Retouched photograph of the holotype.

Canadia grandis, new species 5

Fig. 10. (× 2.) Retouched figure of the holotype.

Plate 10

PAGE

Selkirkia major (Walcott) 7

Fig. 1. (circa × 3.5.) A large individual, possibly preserving the original proportions of the shell.

2. (circa × 3.5.) Another specimen whose shell is more or less crushed, but with even better preservation of the soft parts.

PLATE 11

PAGE

Aysheaia pedunculata Walcott.................................... 8

FIG. 1. (× 2.) An unusually perfect specimen.

2. Large coiled specimen that Doctor Walcott regarded as possibly representing a different animal, but which may appear odd only because of its unusual attitude.

PLATE 12

PAGE

Leanchoilia superlata Walcott.................................... 8

FIG. 1. (× 2.) Retouched figure of a fragmentary specimen.

2. Natural size unretouched photograph of a well preserved individual.

3. Enlarged, retouched figure of the counterpart of the preceding figure.

PLATE 13

PAGE

Leanchoilia superlata Walcott.................................... 8

FIG. 1. (× 3?). An appendage apparently belonging to this species.

2. An individual flattened out in the horizontal plane, thus giving it an unusual aspect.

Leanchoilia major, new species.................................... 10

FIG. 3. Illustration of the holotype.

Naraoia compacta Walcott.................................... 10

FIG. 4. (× 3.) An unretouched photograph of a good specimen. The appendages are only faintly shown extending beyond the carapace at the rear of the specimen. (See pl. 15, fig. 3.)

PLATE 14

PAGE

Naraoia compacta Walcott.................................... 10

FIG. 1. (× 2.) Dorsal view of a compressed and somewhat distorted specimen, on which the outline of the body trunk is well shown and, on the left side, the ends of 16 exopodites preserving their fine filaments.

2. (× 2.) Dorsal view of a specimen with the carapace shortened nearly one-half by compression. The central portion showing the hepatic glands or caeca is unusually well preserved. The posterior dorsal shield has the outlines of the fused segments and the outer border clearly indicated, and on the left side, where a piece is broken out, two of the exopodites are seen, and at the posterior margin, traces of endopodites.

3. (× 3.) Enlarged view of a specimen with peculiar features along the axis.

Leanchoilia superlata Walcott.................................... 8

FIG. 4. (× 2.) Details of a separate appendage.

5. (× 2.) Another appendage of a different type.

PLATE 15

	PAGE
Naraoia spinifer, new species	15

FIG. 1. (× 2.) Posterior dorsal shield with traces of segmented body and thoracic limbs; a dorsal view of another specimen shows clearly defined exopodites with the slender, distal ends of endopodites projecting from beneath them.

Naraoia compacta Walcott 10

FIG. 2. (× 2.) Smaller, retouched picture of the specimen shown in fig. 4, pl. 13.

3. (× 1.5.) Incomplete individual clearly showing the axis.

Burgessia bella Walcott 15

FIG. 4. (× 3.) Specimen showing the outlines of 10 thoracic legs formed of the six joints of the endopodite and the large protopodite, also the annulated intestine and fragments of the crushed carapace.

5. (× 4.) A dorsal view of a specimen in which the stomach and portion of the intestine as well as the large hepatic tubes are distended so as to be moderately convex. The specimen also shows the position of the antennae and portions of the hepatic caeca.

6. (× 4.) A macerated specimen indicating the position of the eyes, the antennae, a portion of the labrum, the mandibles, the maxillulae, and the maxillae; also the proximal portion of seven pairs of the thoracic limbs, with a fair indication of the point of attachment of the limbs to the body.

7. (× 3.) Another very fine individual.

PLATE 16

	PAGE
Burgessia bella Walcott	15

FIG. 1. (× 2.) Fragmentary specimen indicating structure of limbs. (Possibly oriented incorrectly.)

2. (× 4.) A specimen preserving 10 pairs of thoracic limbs, showing their approximate place of attachment to the body, and also their expanded joints and general form.

The carapace has been crowded back and crushed, but the antennae project from its anterior side in an almost natural position.

3. (× 2.) A badly decayed specimen that shows the manner of attachment of the limbs.

4. (× 4.) Dorsal view of a specimen with the digestive organs beautifully preserved. These include the intestine posterior to the large hepatic tubes, the stomach anterior to the latter, and also the anterior and posterior branches of the main hepatic tubes and the numerous finer hepatic caeca, which occur on both the outer and inner sides of the main branches.

This specimen gives most of the data for the restoration of the digestive organs as shown by text fig. 5.

5. (× 4.) Specimen showing the expanded joints of the endopodites of the cephalic limbs.
6. (× 3.) Partly side view of a crushed and distorted specimen illustrated for the purpose of showing the exopodites that occur near the body, the proximal part of the endopodites with the protopodites having been flaked off from above the exopodites in the specimen; in their natural position the exopodites were probably above and between the endopodites. The outer ends of the long, strong endopodites are well shown in this specimen, although the joints have been obscured. The slender jointed leglike structure associated with the exopodites may be the distal part of the endopodites of the right side.

PLATE 17

PAGE

Burgessia bella Walcott.. 15

FIG. 1. (× 3.) Another specimen preserving mainly the "skeleton."
2. (× 2.) A small individual crushed obliquely.
3. (× 3.) Ventral view of a specimen preserving the reflected anterior margin and labrum, also the antennae, outlines of the inner portions of the cephalic limbs, and more or less distinctly outlined thoracic endopodites with transversely expanded joints. The anal plate is clearly indicated, also the anterior end of the telson.
4. (× 4.) Side view of a crushed specimen preserving on the left lower side the outlines of 10 thoracic legs, on the right side the outlines of four entire lobelike exopodites and the distal end of four posterior to them. The exopodites still show slight traces of fine filaments (?) along the posterior and outer margins.

PLATE 18

PAGE

Burgessia bella Walcott.. 15

FIG. 1. (× 2.) An incomplete specimen showing the manner in which the limbs project beyond the carapace.

Waptia fieldensis Walcott.. 20

FIG. 2. (× 4.) Side view of a flattened specimen preserving six or more cephalic limbs, the limbs from both sides being more or less crushed down together.
3. (× 2.) Specimen showing on the right side a flattened uninjured antennae in its natural form, and on the left side only the outline of the interior of the joints. The latter mode of occurrence is quite common for the antennae and other appendages. This specimen also has the stalked eye preserved on the right side.

4. (× 2.) A few thoracic exopodites in which the flattened filaments are unusually well preserved.
5. (× 4.) Side view of a flattened specimen showing the outlines of body through the carapace, the stalked eye, antennae, four cephalic limbs, and several thoracic limbs.

This specimen is particularly instructive, as it shows the outline of the thoracic limbs from the body to their distal end.

PLATE 19

	PAGE
Waptia fieldensis Walcott	20

FIG. 1. (× 2.) Anterior portion of an individual showing the limbs.
2. (× 2.) Unretouched photograph of a distorted specimen showing the eye particularly well.
3. (× 2.) Dorsal view of the carapace of a specimen showing the outline of the body, also the small rostrum between the the antennae and the eyes.
4. (× 3.) Specimen with details of eyes and antennae.

PLATE 20

	PAGE
Waptia fieldensis Walcott	20

FIG. 1. (× 2.) Posterior portion of specimen preserving the three segments, the anal opening, and the lobed, segmented caudal furca.
2. (× 3.) Anterior portion of a carapace, median rostral plate, antennae, stalked eyes, and a palp on the left side.
3. (× 2.) Side view of a flattened specimen in which a number of the exopodites retain the fringing filaments, some of the latter being gathered in a cluster at the distal ends. This specimen also shows the outlines of elongate triangular, light-colored, shiny places that may indicate the interior of the exopodite or possibly a rudimentary endopodite.

PLATE 21

	PAGE
Skania fragilis Walcott	25

FIG. 1. (× 4.) Specimen showing the flattened intestine and outline of thoracic segments.

Waptia fieldensis Walcott	20

FIG. 2. (× 2.) Dorsal view of a flattened specimen in which the carapace has been removed from over the cephalic area and portion of the thoracic region. The proximal portion of eight thoracic limbs is clearly shown, also of three pairs of cephalic limbs.

Waptia circularis, new species.. 24

Fig. 3. (× 2.) Side view of a flattened specimen illustrating the form of the carapace, one side of which has been crushed upward and backward. The exopodites of the thoracic limbs appear to have the same structure as those of *Waptia fieldensis*.

Mollisonia ? rara Walcott.. 27

Fig. 4. (× 2.) A retouched figure of a most excellent specimen.

Plate 22

PAGE

Marrella splendens Walcott.. 28

Fig. 1. (× 4.) Dorsal view of a specimen showing the mandibles, the antenna on the left side extending down beside the mandible, and the exopodites referred to the maxillae and maxillulae; what may be the endopodite of the maxillulae is shown on the right side below the fringing filaments of the exopodite of the maxilla.

2. (× 4.) In this ventral view the mandibles have been pushed forward so that the mandible and antenna on the right side are in a vertical position and side by side, and the endopodites of the maxilla and maxillula are in advance of their natural position; on the left side two endopodites of thoracic limbs are faintly outlined.

3. (× 4.) Ventral view of a specimen in which the joints of the mandibles have been crowded together and somewhat shortened; the proximal joint on the right side is well exposed by the labrum having been pushed forward; the inner margin of the joint is serrated but not quite as clearly shown as on the specimen represented by fig. 6.

4. (× 4.) The dorsal view of this specimen is illustrated to show the position of the antenna on the right side which is the same as the antenna on the left side in fig. 1, and on both sides in fig. 5; the position of the mandibles is also well shown.

5. (× 4.) Ventral view showing the position of the mandibles beside the labrum, also the exopodites of the maxillae and maxillulae posterior to them; the antennae appear to have been torn away in the crowding forward of the mandibles.

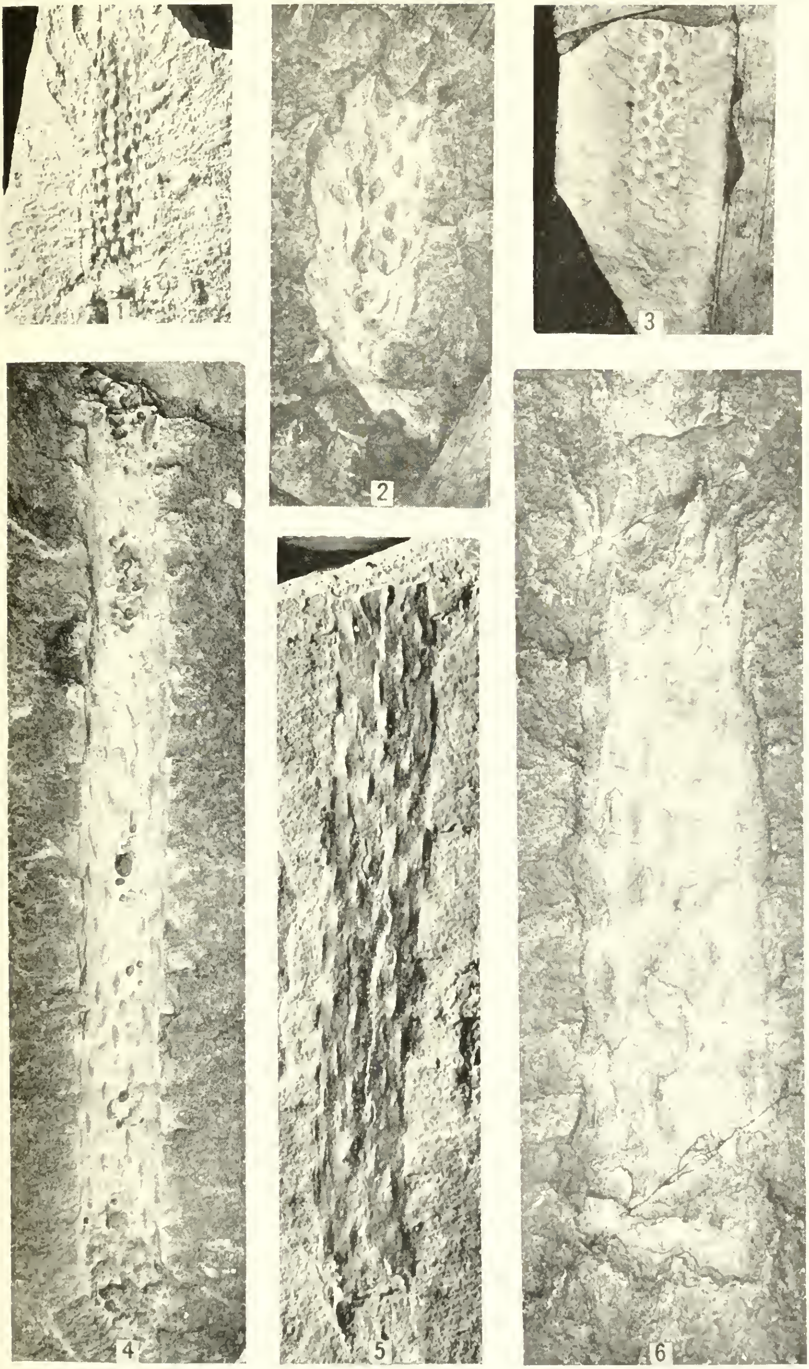
6. (× 4.) Ventral view of a specimen showing the mandibles, the one on the right side preserving the proximal joint with a serrated inner margin. This mandible has been colored white in order to bring it out more clearly in the reproduction; the thoracic exopodites are very clearly shown on both sides, the endopodites having been largely exfoliated.

7. (× 4.) Ventral view of a specimen preserving a complete mandible on the left side, also several endopodites of the thoracic limbs, and on the right side six joints of the mandible and a few imperfect thoracic endopodites, which are exposed on both sides by the exfoliation of the exopodites.

8. (× 6.) Enlargement of the filaments of one of the thoracic exopodites in which the filaments retain their original round, slender tubular form. This is the only specimen among several hundred that I have examined which has escaped flattening by compression. This is due to the pyritization of the filaments of this particular specimen.
9. (× 4.) Ventral view of a specimen illustrated to show what appears to be a small oval flattened lobe attached to the dorsal side of a protopodite or it may be to the proximal joint of the exopodite; a number of the thoracic exopodites with the filaments projecting forward occur on both sides, also fragments of the large postero-lateral spines of the carapace which lie above the exopodite of the thoracic limbs.

PLATE 23

PAGE
Helmetia expansa Walcott.. 38
Photograph of the holotype.



Burgess Shale Fossils

For explanation see page 38.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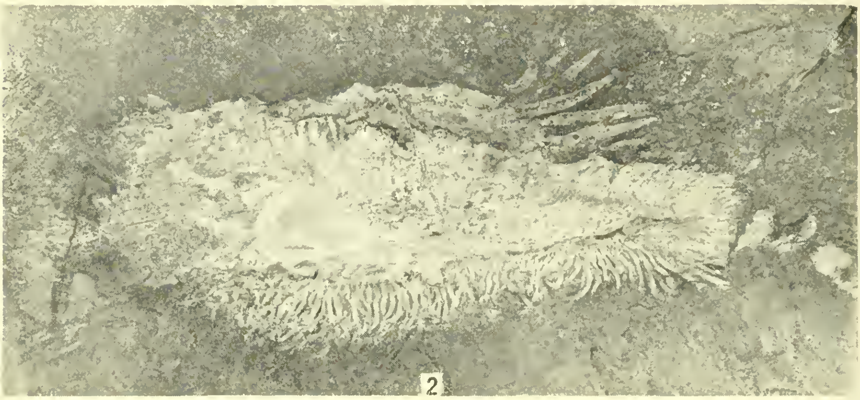
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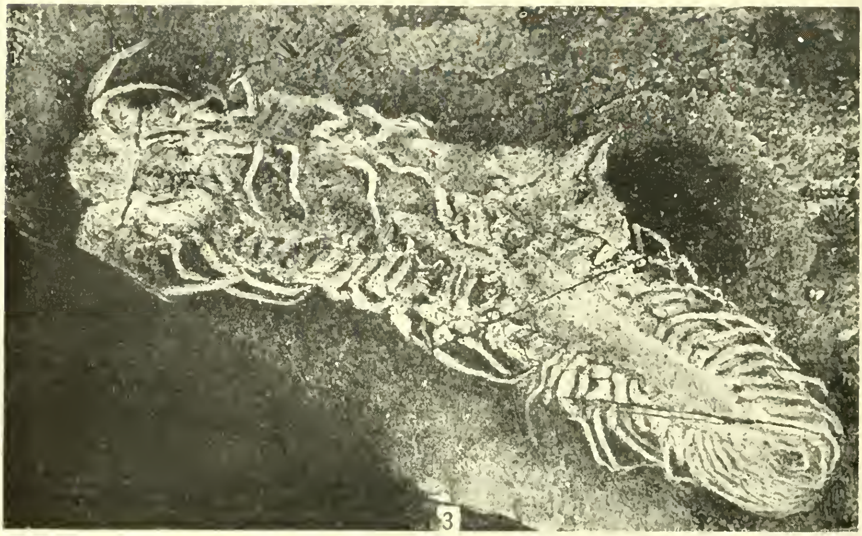
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Burgess Shale Fossils

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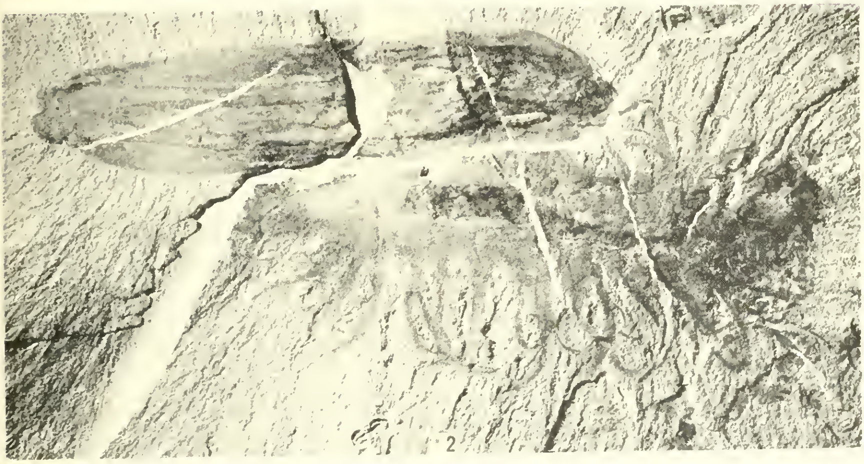

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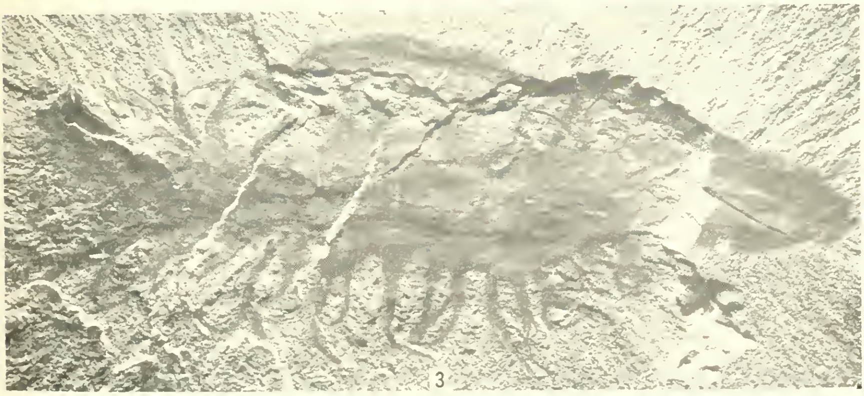

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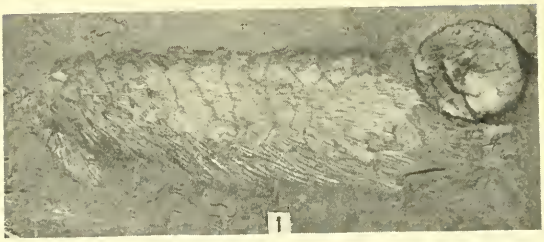

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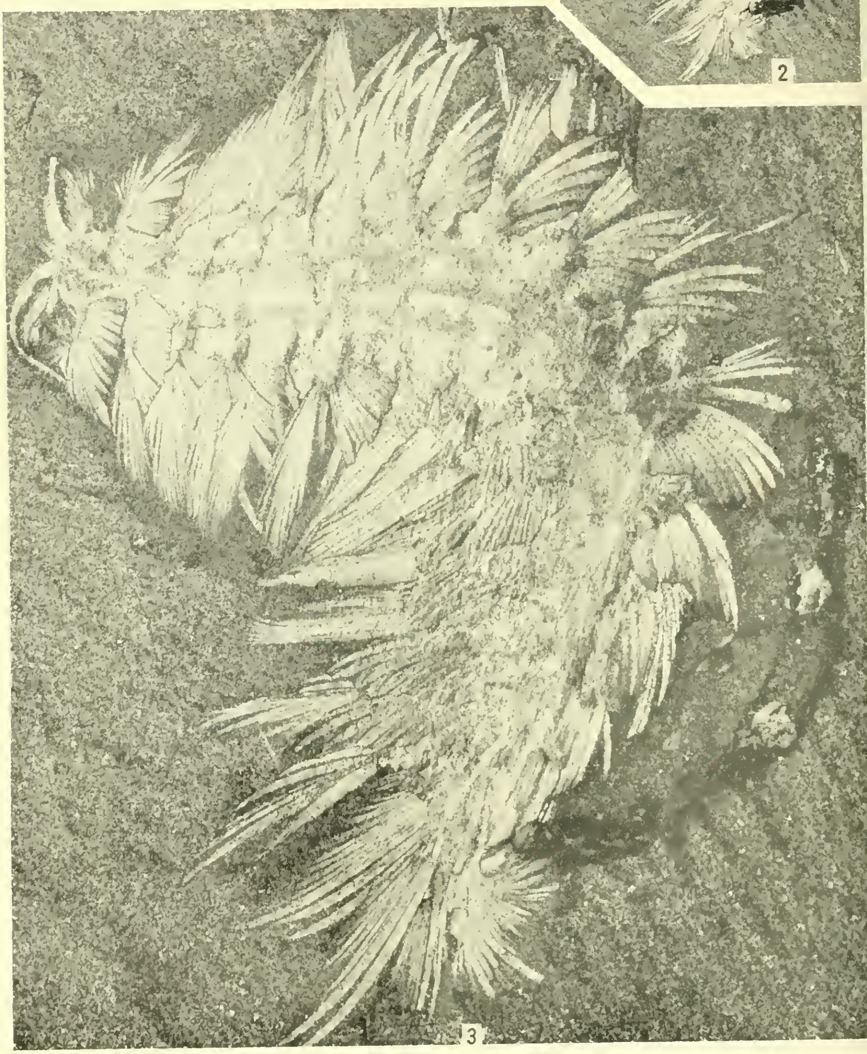

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FOR EXPLANATION SEE PAGE 39.

Burgess Shale Fossils

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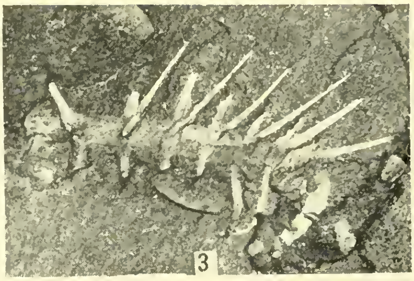
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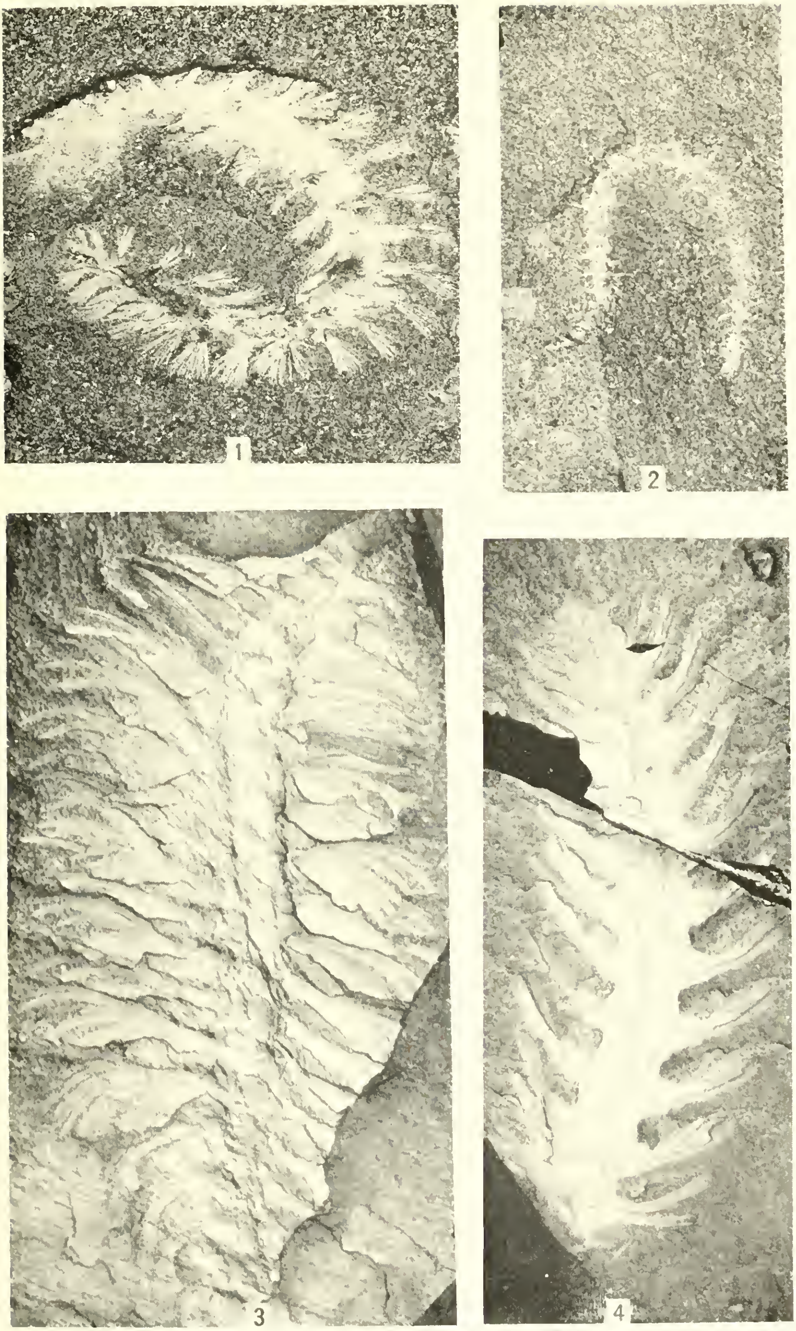

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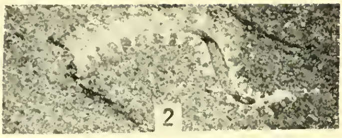
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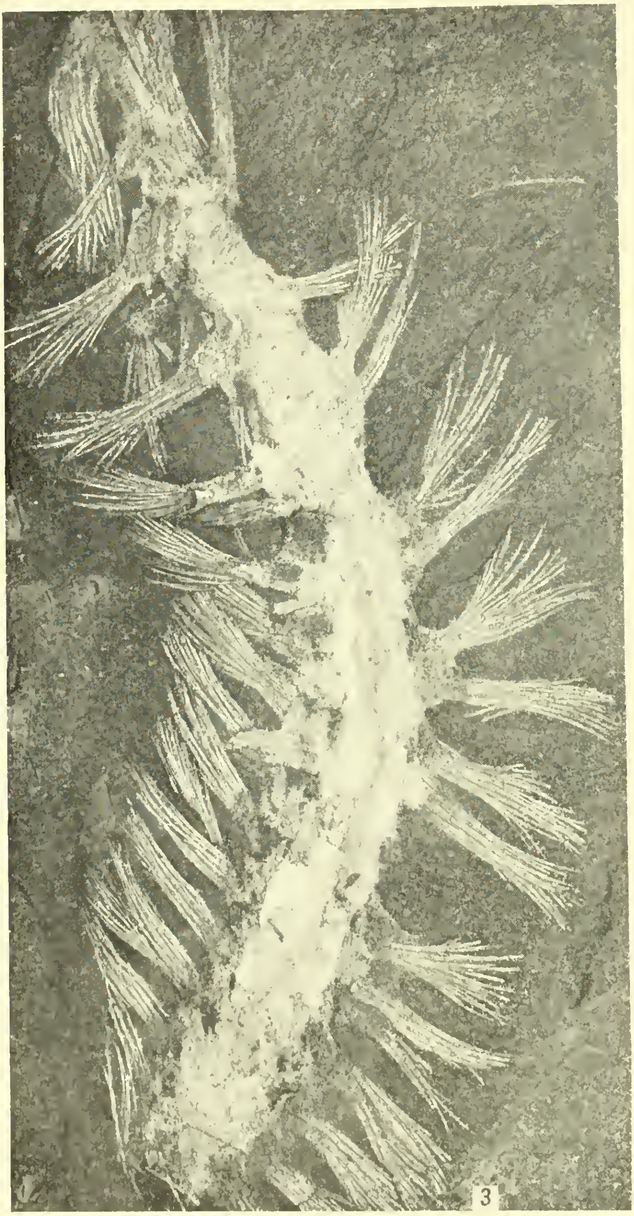
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Burgess Shale Fossils

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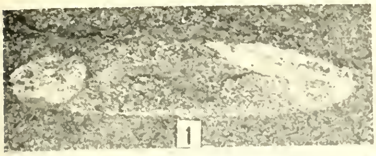
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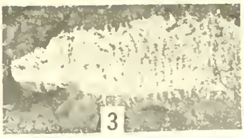
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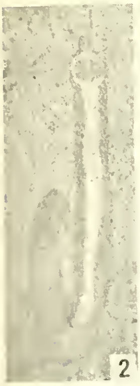
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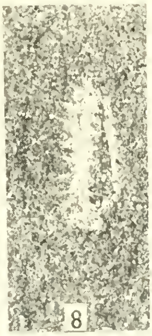
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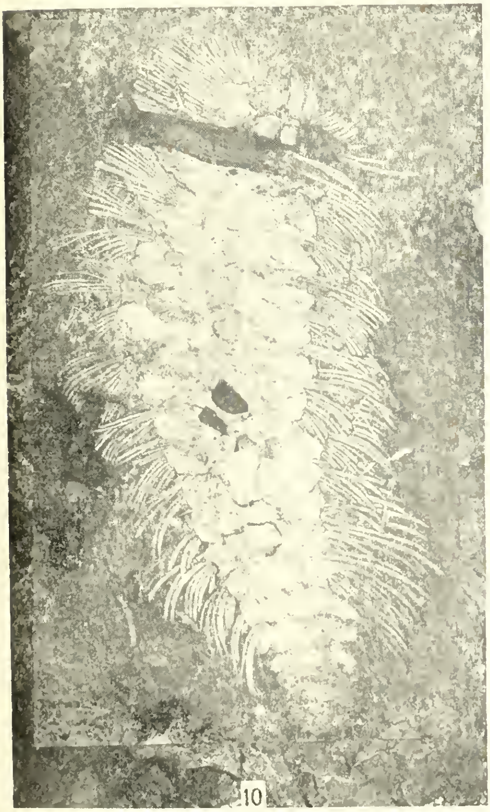
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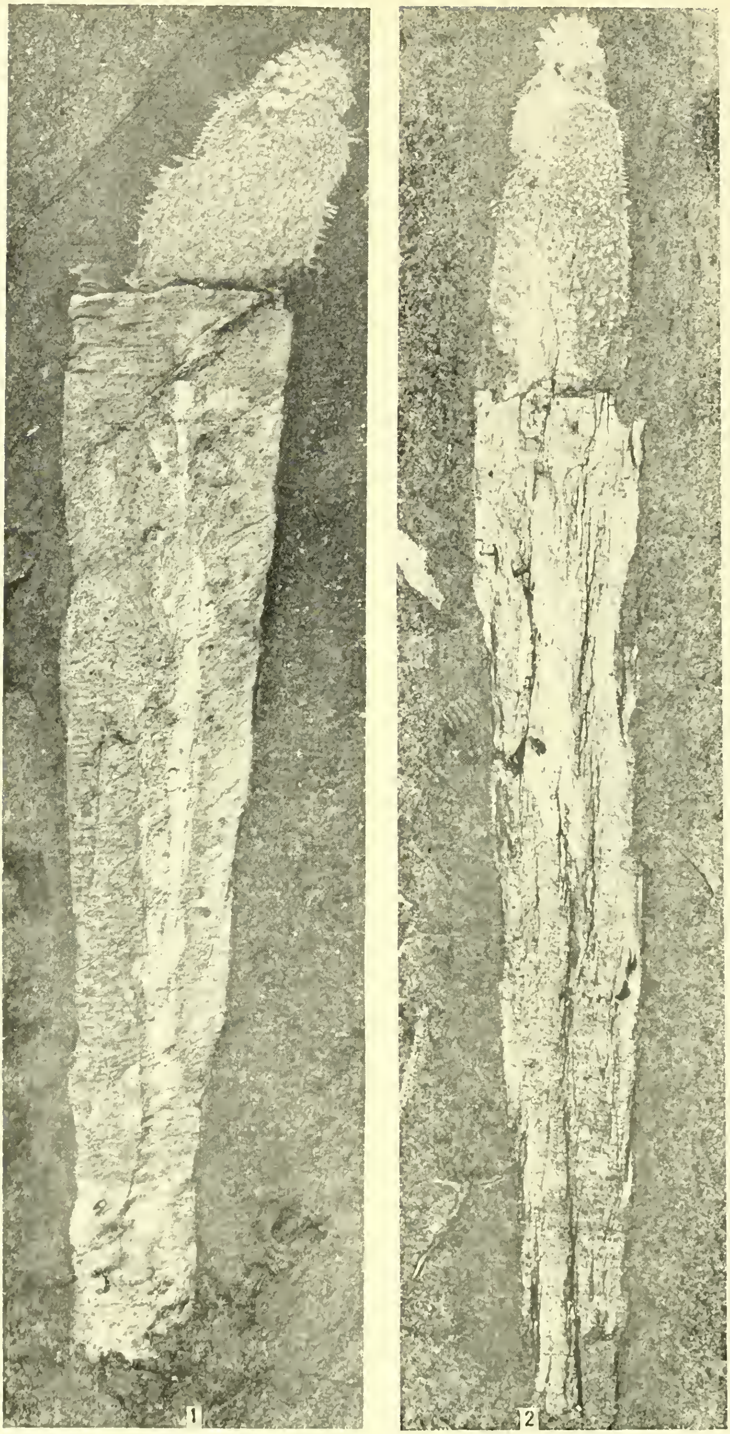

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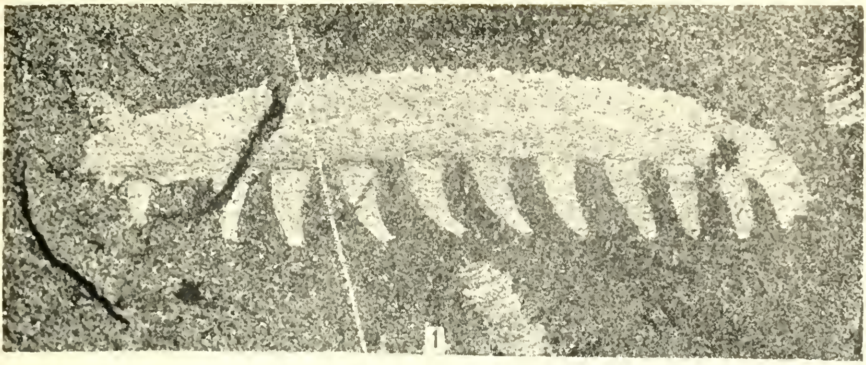

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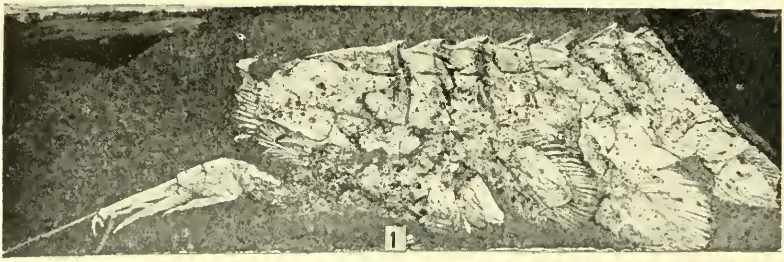

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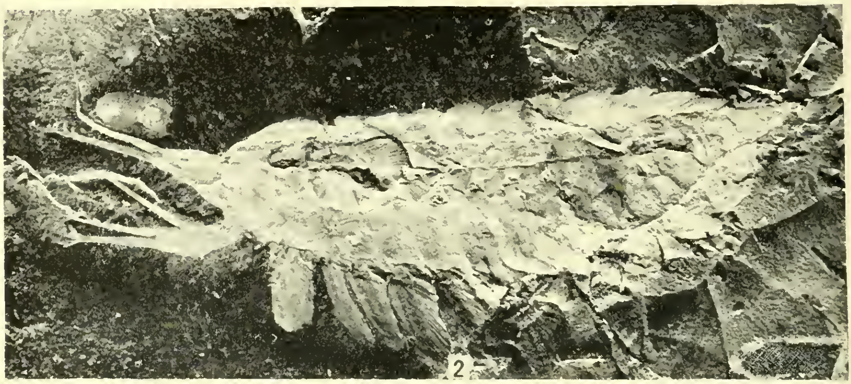

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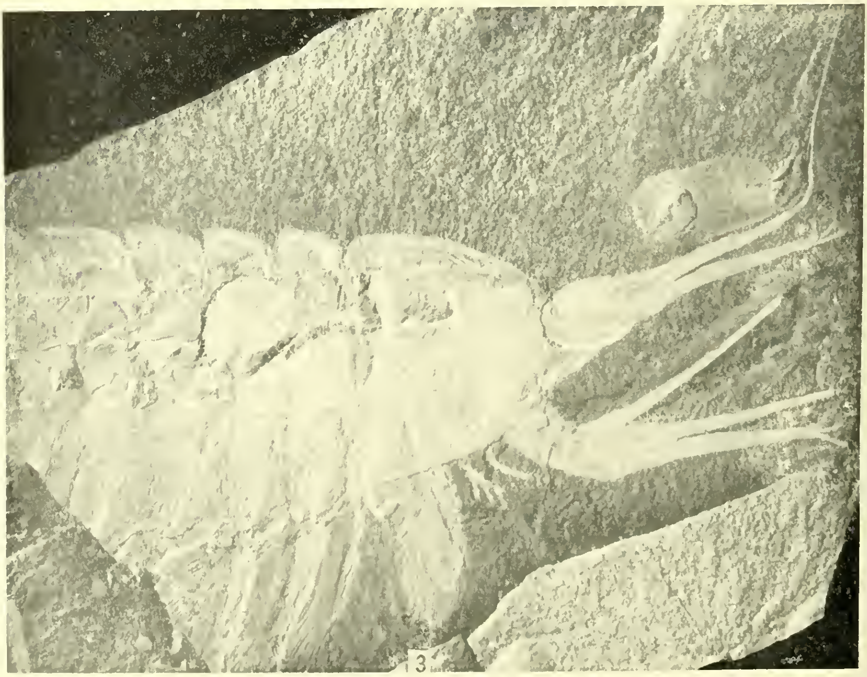

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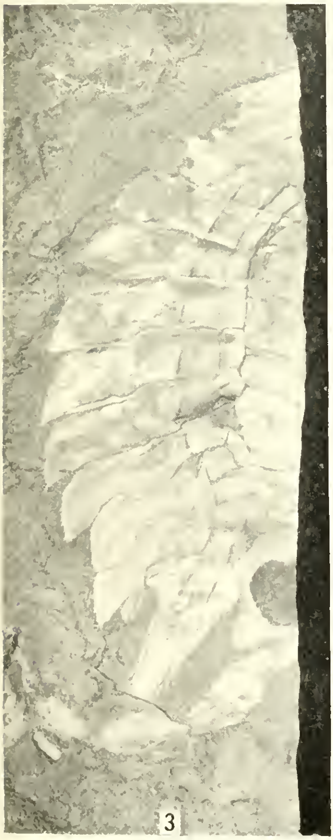
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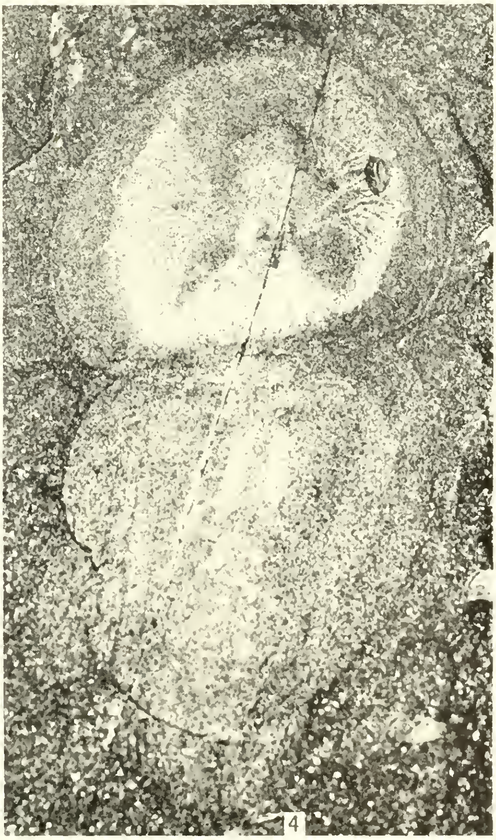
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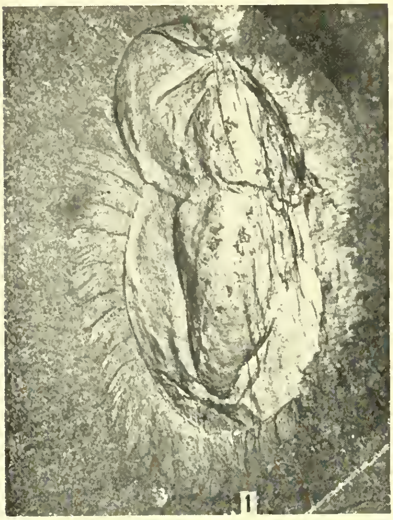
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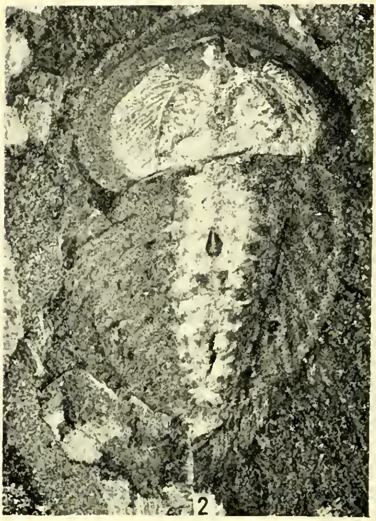
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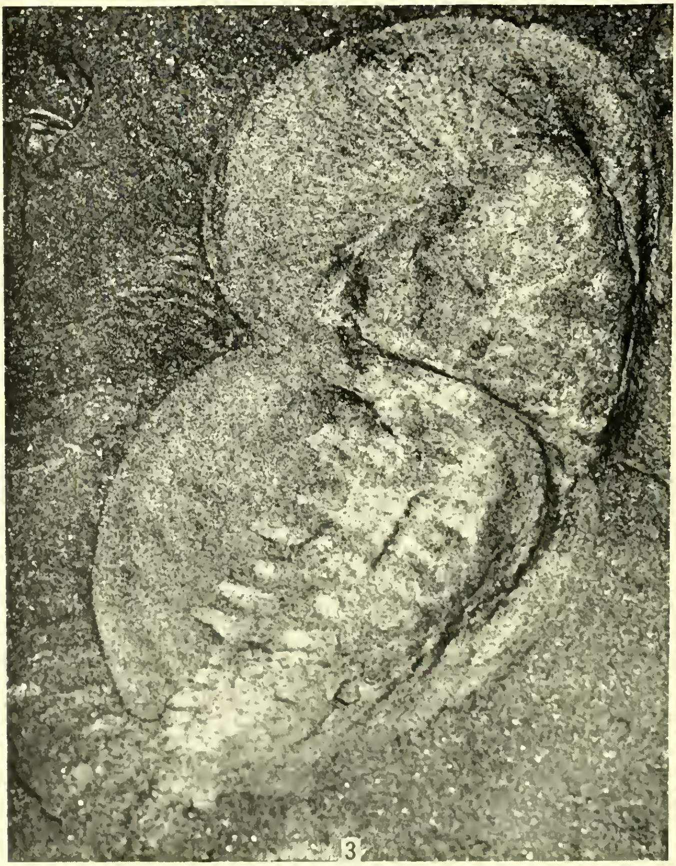
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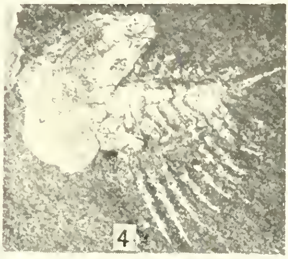
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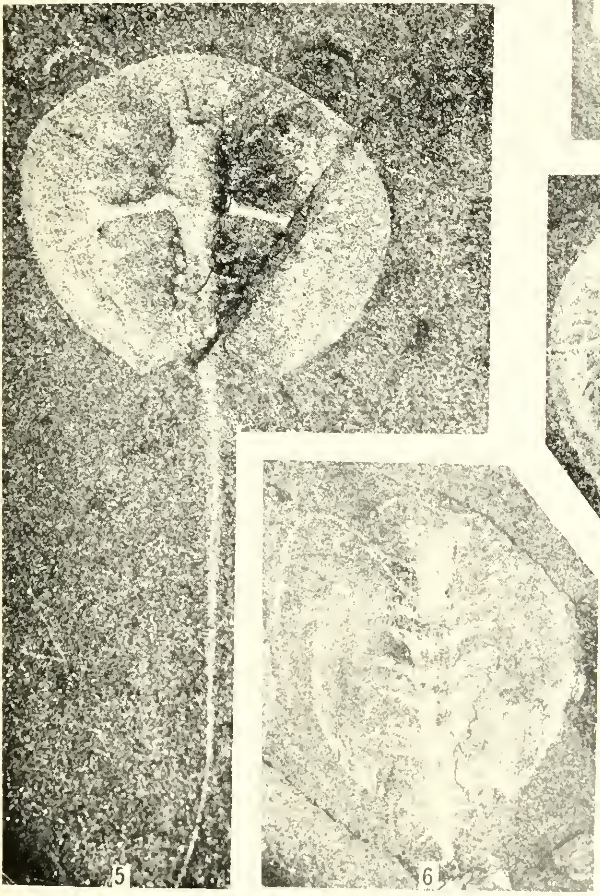
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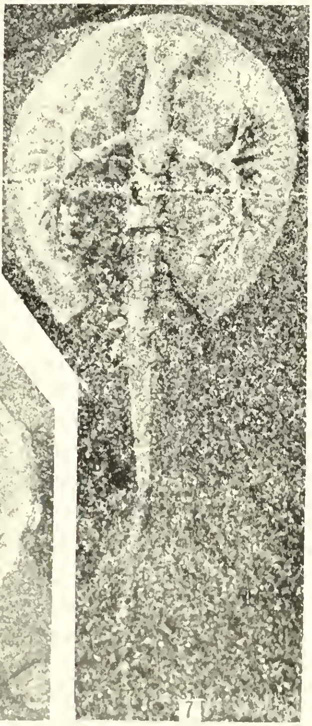
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Burgess Shale Fossils

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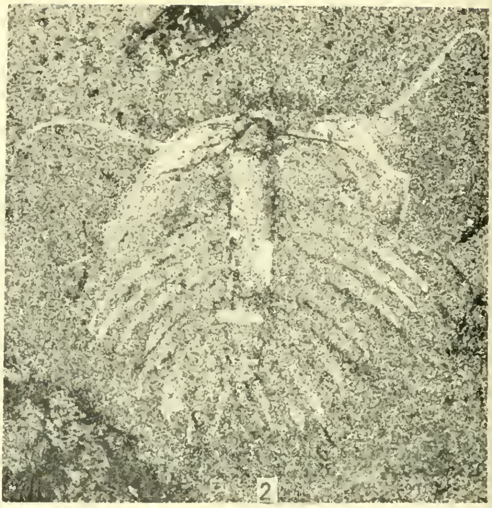
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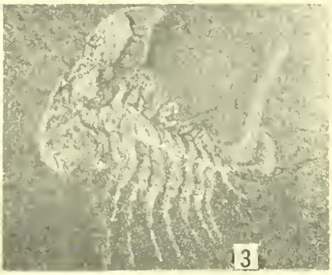
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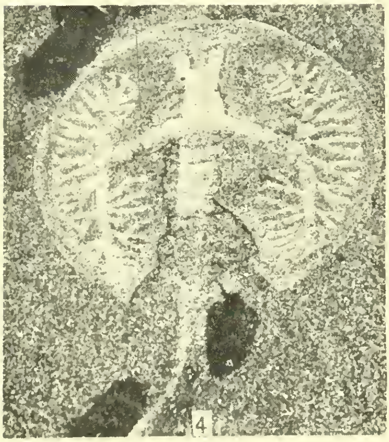
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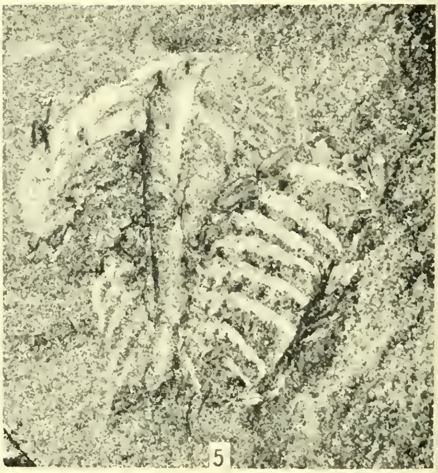
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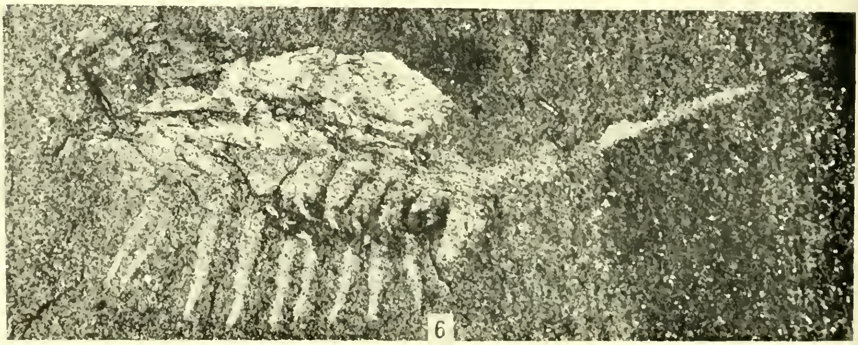
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Burgess Shale Fossils

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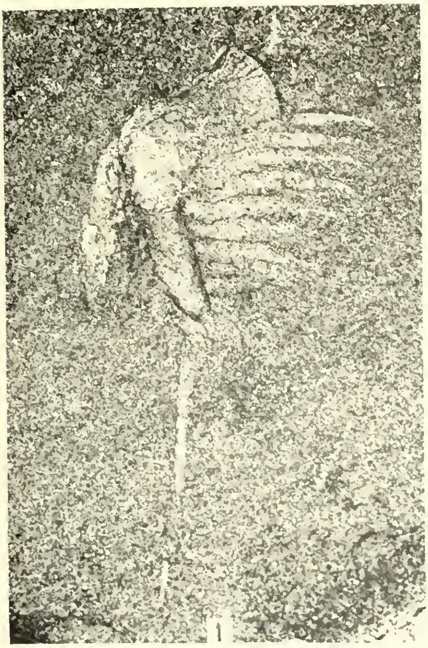
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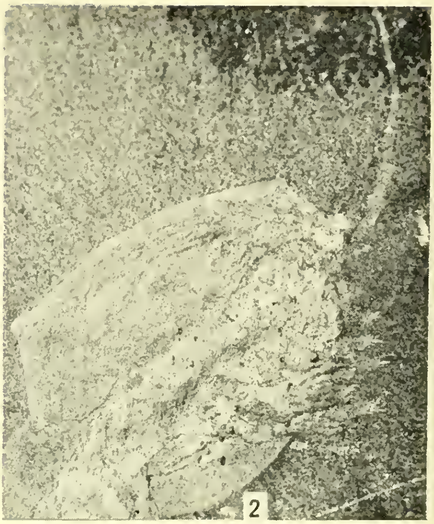
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Burgess Shale Fossils

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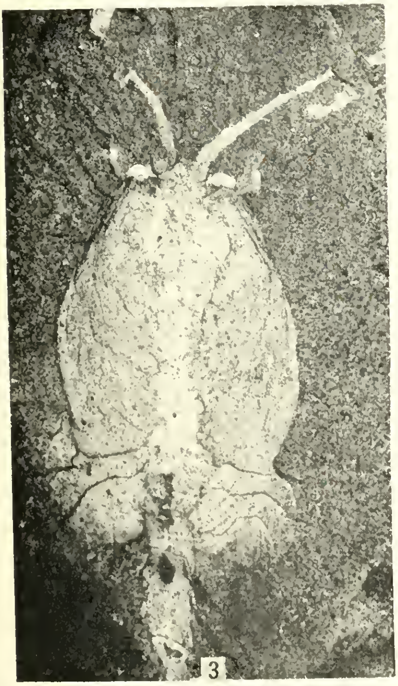
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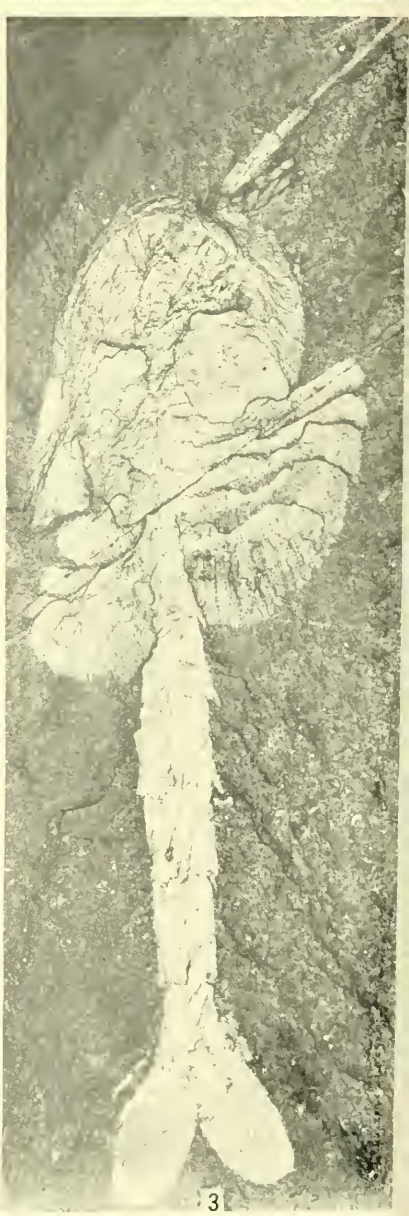
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Burgess Shale Fossils

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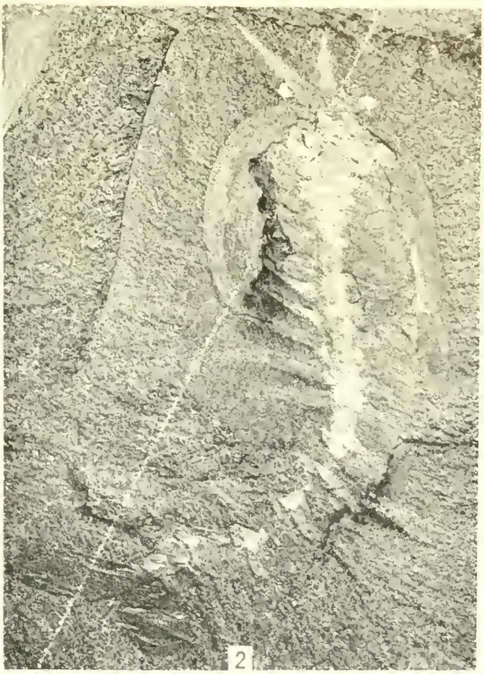
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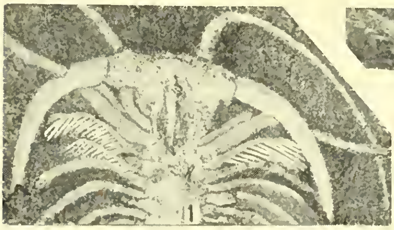
BURGESS SHALE FOSSILS

FOR EXPLANATION SEE PAGE 44.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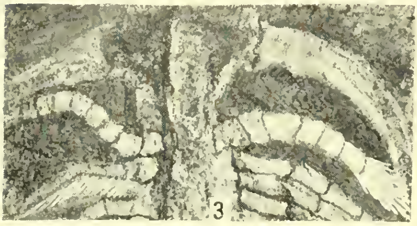
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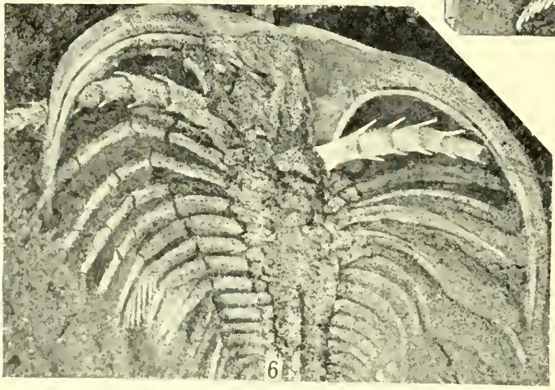
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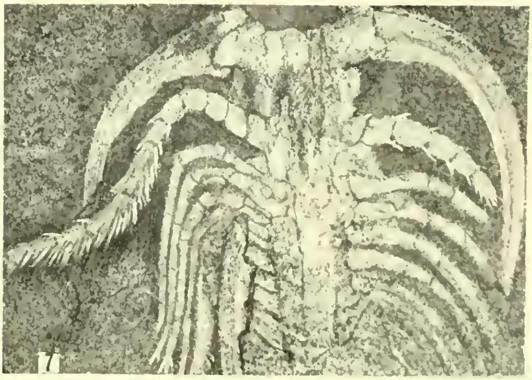
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Burgess Shale Fossils

For explanation see page 45.

BURGESS SHALE FOSSILS

FOR EXPLANATION SEE PAGE 46.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 85, NUMBER 4

MEXICAN MOSSES COLLECTED BY BROTHER ARSÈNE BROUARD—III

BY
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MEXICAN MOSSES COLLECTED BY BROTHER ARSÈNE BROUARD—III

By I. THÉRIOT

FONTAINE LA MALLET, FRANCE

With the present paper the study of Brother Arsène's mosses comes to an end. In addition to this collection a rather large number of species collected by Brother Amable in 1926-27 are included. These last are from the Valley of Mexico and adjacent regions. Together the two collections comprise about 300 species, among which 18 had not been found previously in Mexico, and 44 are entirely new. Brother Arsène's and Brother Amable's explorations have thus enriched the bryological flora of Mexico by more than 60 species. These valiant botanists are deserving of great praise and also of thanks from all those who are interested in bryology. Referring to the figures given by Cardot[1] the Mexican flora now includes, with the Arsène and Amable contributions, about 700 species of mosses. We are therefore well above the 400 species enumerated in the Prodrome of Bescherelle.

It remains now for me to fulfill the very agreeable duty of expressing my gratitude to Brother Arsène and Edwin B. Bartram, who have assumed with such kindness the task of translating my French text into English, and to the Smithsonian Institution for publishing my studies.

The two previous parts were published in the Smithsonian Miscellaneous Collections as follows: Vol. 78, no. 2, pp. 1-29, June 15, 1926; vol. 81, no. 1, pp. 1-26, August 15, 1928. In the introduction to the first of these there will be found a list of localities in the states of Michoacán and Puebla from which specimens are cited; this will prove useful also for the present and final contribution.

DITRICHACEAE (continued)

DISTICHIUM CAPILLACEUM (Sw.) Bry. Eur.

Valle de México: Desierto (*Bro. Amable* 1500).

Very probably new to Mexico.

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[1] Rev. Bryol. 38: 97. 1911; 40: 33. 1913.

BRYOXIPHIACEAE

BRYOXIPHIUM MEXICANUM Besch. Journ. de Bot. 6: 180. 1892

Eustichium norvegicum Schimp. in Besch. Prodr. Bryol. Mex. 29. 1871.

Valle de México: Desierto (*Bro. Amable* 1629).

DICRANACEAE (continued)

CAMPYLOPUS (Eucampylopus) ANGUSTI-ALATUS Thér., sp. nov.

Distr. Federal: Río Frío, alt. 3,000 meters (*Bro. Amable* 1724).

Habitu, colore, rete foliorum *C. Pittieri* R. S. W. sat similis, sed differt: caulibus elongatis usque 6 cm., foliis magis concavis, angustis (basi 0.5 mm.), acumine angustiore, cellulis laminae minus incrassatis, costa angustiore (0.36 mm.).

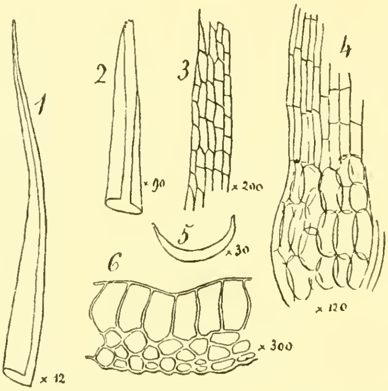

FIG. 1.—*Campylopus angusti-alatus* Thér. 1, leaf; 2, acumen; 3, lamina cells in the upper third; 4, alar and suprabasal cells; 5, cross-section of a leaf near the base; 6, cross-section of costa.

In size this species suggests *C. Apollinairei* Thér.,[1] from Colombia, but may be distinguished from it by the leaves, which are erect-appressed when dry, little or not flexuous, shorter and only half as wide, very narrow toward the base (8 to 10 rows of cells), and by the non-incrassate cells of the lamina.

CAMPYLOPUS DESTRUCTILIS (C. M.) Jaeg.

Dicranum destructile C. M. Bot. Zeit. 17: 220. 1859.
Campylopus Arsenei Thér. Smithsonian Misc. Coll. 78^2: 5. 1926.

Having seen from the Berlin Museum the types of *C. Chrismari* (C. M.) and *C. destructilis* (C. M.), both Mexican species, I have

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[1] Archiv. Bot. 2: 187. 1928.

come to the conclusion that they are distinct, the first belonging to the subgenus *Eucampylopus,* the second to the subgenus *Pseudocampylopus;* furthermore, that *C. Arsenei* Thér. does not differ from the latter.

CAMPYLOPUS (Eucampylopus) SAINT-PIERREI Thér., sp. nov.

Hidalgo: El Chico, on rocks, alt. 2,600 meters, leg. Marius Saint-Pierre (*Bro. Amable* 1589).

Sterilis. Caespites densi. Caulis 2-3 cm. altus, simplex vel parce ramosus, inferne radiculosus, basi terra obrutus, dense foliosus. Folia sicca erecta, parum flexuosa, humida erecto-patula, lanceolata, longissime subulata, canaliculata, marginibus integris, apice denticulatis, 5-6 mm. longa, 0.7 mm. lata; costa basi 0.3 mm., breviter excurrente, dorso superne sulcata, haud lamellosa; auriculis distinctis, valde excavatis, cellulis alaribus numerosis, minutis, vesiculosis, rete suprabasilari chlorophylloso, cellulis marginalibus (3-4) linearibus, hyalinis, sequentibus quadratis, internis rectangularibus, parietibus incrassatis, sinuatis; cellulis laminae rhomboidalibus valde incrassatis, juxtamarginalibus minutis, juxtacostalibus sensim majoribus.

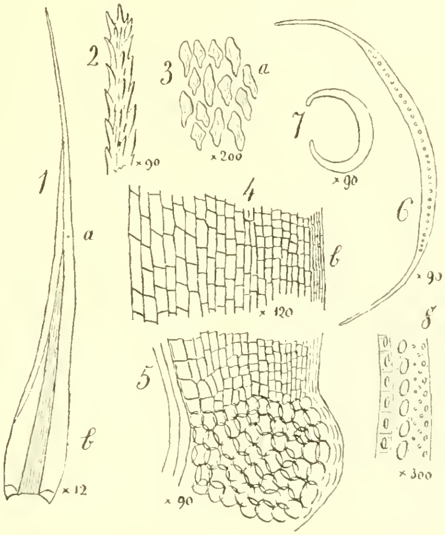

FIG. 2.—*Campylopus Saint-Pierrei* Thér. 1, leaf; 2, acumen; 3, upper cells at *a*; 4, suprabasal cells toward *b*; 5, alar cells; 6, cross-section of leaf near the base; 7, section from the acumen; 8, cross-section of costa near the base.

At first sight a cross-section of the costa seems to indicate the subgenus *Palinocraspis.* Under a moderate magnification this section appears as a thin opaque slice, in which is seen only the median arc of eurocysts covered on both sides by cells with a small lumen.

But, using a higher magnification for the same section, one notices that the ventral surface is formed of a unique layer of cells with very thick walls showing a lumen like a " cat-eye " (not punctiform). These cells, which are not stereids, remind one exactly of those found in *C. matarensis* Besch., from La Réunion Island. Like the last named species, *C. Saint-Pierrei* belongs to the group " C.b."[1]

Another peculiarity is that the comal leaves often end in a rather long hair point, which is discolored or subhyaline, recalling to mind that of the group Trichophylli.

POTTIACEAE

MOLENDOA OBTUSIFOLIA Broth. & Par. in Card. Rev. Bryol. 40: 36. 1913

Puebla: Hacienda Alamos (4631, 4697); Río Alseseca (574). Vera Cruz; Córdoba (10978). Distr. Federal: Mixcoac (9432, 9434, 9462, 9465, 9466, 9468). Valle de México (*Bro. Amable*): Desierto (1244); San Juanico (1261).

The leaves of this species show a peculiarity which has not yet been pointed out: the margins of the acumen are a little thickened by the bistratose marginal cells, such as may be seen in some other species of the family Pottiaceae.

MOLENDOA OBTUSIFOLIA Broth. & Par. var. **INCRASSATA** Thér., var. nov.

Puebla: Hacienda Batán (5007 p. p.), associated with *Trichostomopsis crispifolia* Card.

Caulis 1 cm. altus. Folia breviora latioraque, 1 mm. × 0.25 mm.; rete opaco, cellulis incrassatis, costa 50 μ.

Here the thickening of the cell walls is more accentuated than in the type form: toward the apex the lamina is composed of 2 layers of cells throughout, while in the middle the thickening is confined to 2 or 3 rows of marginal cells.

ANOECTANGIUM LIEBMANNI Schimp. in Besch. Prodr. Bryol. Mex. 15. 1871

Morelia: Jesús del Monte (7965).

ANOECTANGIUM COMPACTUM Schwaegr. Suppl. 1: 36, pl. 11. 1811

Puebla: (4800).

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[1] E. & P. Nat. Pflanzenfam. ed. 2, 10: 187. 1924.

ANOECTANGIUM APICULATUM Schimp. in Besch. Prodr. Bryol. Mex. 16. 1871

Puebla: Hacienda Alamos (4770). Morelia: Cerro San Miguel (5042). Valle de México: Puente de la Venta (*Bro. Amable* 1388).

ANOECTANGIUM EUCHLORON (Schwaegr.) Mitt. Musc. Austr. Amer. 176. 1869

Morelia: Loma del Zapote (7508).

ANOECTANGIUM CONDENSATUM Schimp. in Besch. Prodr. Bryol. Mex. 16. 1871

Valle de México (*Bro. Amable*): Contreras (1483); Desierto (1627).

HYMENOSTOMUM (Kleioweisia) SEMIDIAPHANUM Thér., sp. nov.

Morelia: Cerro San Miguel, on earth (5040).

Dioicum? fl. masc. haud vidi. Tenellum; caulis 1 mm. altus, paucifoliatus. Folia sicca crispula, madida patula, inferiora minuta, caetera sensim majora, oblonga-lanceolata, breviter acuminata, acuta, concava, superne canaliculata, marginibus integerrimis, valde involutis, folia media 1 mm. longa, 0.3 mm. lata; costa basi 40 μ, percurrente vel breviter excurrente; rete basilari in dimidio inferiore hyalino, cellulis rectangularibus, parietibus tenuibus, cellulis laminae opacis, densissime

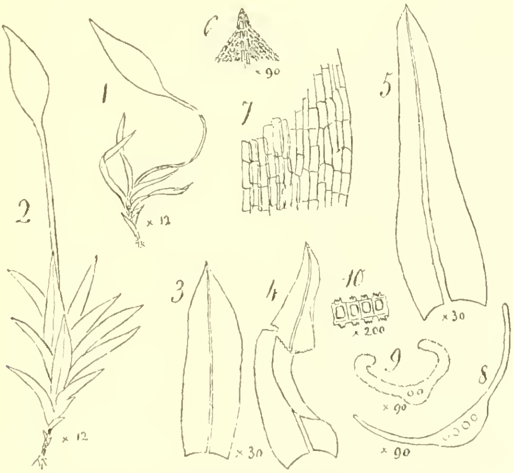

Fig. 3.—*Hymenostomum semidiaphanum* Thér. 1, entire plant, dry; 2, moist plant; 3, 4, 5, leaves; 6, acumen; 7, basal cells; 8, cross-section of leaf toward the base; 9, cross-section of acumen; 10, fragment of cross-section from acumen.

papillosis, papillis elatis, diam. 6 μ. Pedicellus 3 mm. longus, pallidus, siccus valde arcuatus, humidus erectus; calyptra cucullata, dimidium partem capsulae obtegens; capsula oblonga, clausa; operculum haud secedens, e basi conicum oblique rostratum; sporae papillosae, 18-20 μ.

Easily distinguished from the other species of the subgenus *Kleioweisia* by the length of the pedicels.

HYMENOSTOMUM MEXICANUM Card. Rev. Bryol. 36: 70. 1909

Puebla: Road to Cholula (4849). Valle de México: Tenayuca (*Bro. Amable* 1380).

These plants conform closely to Cardot's type except in the inflorescence. The type specimen has a paroicous inflorescence (teste Cardot); here it is autoicous (male flower on a short pedicel under the female flower). However, I do not think it is wise to base a new species on this difference alone; it seems more logical, in my opinion, to conclude that in *H. mexicanum* the inflorescence is variable, occasionally paroicous but more often autoicous, as is normal among the species of the genus *Hymenostomum*.

GYMNOSTOMUM CALCAREUM Bryol. Germ. 1: 153, pl. 10, f. 15. 1823

Valle de México: Morales (*Bro. Amable* 1595), c. fr.

This species is new to Mexico.

GYROWEISIA OBTUSIFOLIA (Hampe) Broth. in E. & P., Nat. Pflanzenfam. 1^3: 389. 1902

Puebla: Cerro Guadalupe (666); Hacienda Alamos (4634). Morelia: Loma del Zapote (7507).

The leaves of this species are identical as to form and areolation with those of *Husnotiella revoluta*. But this is the only likeness, the leaves of *G. obtusifolia* being exactly plane on the margin and having the costa half as narrow, not dilated at the apex.

GYROWEISIA PAPILLOSA Thér., sp. nov.

Morelia: (4927); Loma Santa María (7887).

Pusilla, caulis vix 1 mm. Folia erecto-appressa, parum crispula, difficile emollita, oblonga vel oblongo-lanceolata, summo late obtusa, valde concava, integerrima, marginibus planis, costa basi 30 μ, superne dilatata, sub apicem evanescente, cellulis basilaribus hyalinis, rectangularibus, cellulis mediis et superioribus quadrato-hexagonis, chlorophyllosis, papillosis, 8-10 μ, parietibus tenuibus. Pedicellus pallidus, erectus, 8-10 mm. longus; capsula oblonga, erecta, basi attenuata; operculum conico-rostratum; annulus latus, peristomium sub orificio insertum, dentes papillosi.

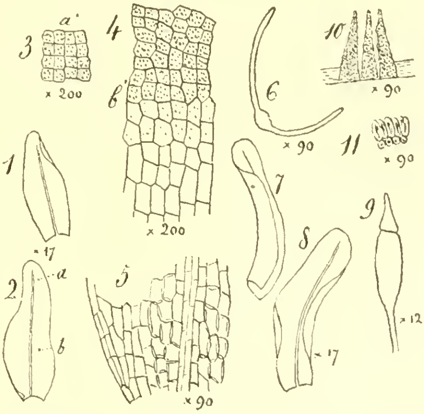

FIG. 4.—*Gyroweisia papillosa* Thér. 1, 2, leaves; 3, cells in upper part at *a*; 4, middle cells near *b*; 5, basal cells; 6, cross-section of a leaf; 7, 8, perichaetial leaves; 9, capsule; 10, fragment of peristome; 11, annulus.

Differs from *G. obtusifolia* by the very unequal, narrower leaves, whose cells are more chlorophyllose and papillose, also by the capsule with a broader annulus.

HUSNOTIELLA REVOLUTA Card. Rev. Bryol. 36: 71. 1909

Puebla: Guadalupe (662, 671, 800); Hacienda Santa Bárbara (4519, 4520, 4595 p. p.). Morelia: (4922, 7653); Andameo (4829, 4841, 4842, 4845). Distr. Federal: Mixcoac (9441, 9447, 9475 p. p., 9483). Valle de México (*Bro. Amable*): Desierto (1249); San Juanico (1227); Penon (1255); San Borja (1259).

Forma **ELATA** Thér., form. nov.—Stems longer, up to 10 to 15 mm., green above, discolored below. Leaves dimorphous, the lower short, oval as in the type, those of the young shoots elongated, almost twice as long as the lower stem leaves. Valle de México: Contreras (*Bro. Amable* 1333).

HUSNOTIELLA REVOLUTA Card. var. **PALMERI** (Card.) Thér., comb. nov.

Husnotiella Palmeri Card. Rev. Bryol. 37: 121. 1910.

Puebla: (698); Rancho Santa Bárbara (4594b). Morelia: Loma Santa María (7880, 4902). Distr. Federal: Mixcoac (9471, 9475 p. p., 9490).

In reducing *H. Palmeri* Card. to a mere variety, following my own observations, I feel in perfect agreement with Mr. R. S. Williams and also with Cardot himself.[1]

HUSNOTIELLA TORQUESCENS (Card.) Bartr. Bryologist 29: 45. 1926

Didymodon torquescens Card. Rev. Bryol. 36: 83. 1909.

Morelia: (7652); Bosque San Pedro (4577, 4583); La Huerta (7967); Loma Santa María (4913, 7882, 7886).

These specimens differ slightly from the type in being green, not glaucous, above; but the agreement is complete in so far as the fruit and the form and structure of the leaves are concerned.

HYMENOSTYLIUM CURVIROSTRE (Ehrh.) Lindb.

Puebla: Boca del Monte (4737); Hacienda Batán, with var. *scabrum* Lindb. (4960); Esperanza (7976).

HYMENOSTYLIUM INCURVANS (Schimp.) Broth. in E. & P. Nat. Pflanzenfam. 1^3: 389. 1902

Gymnostomum incurvans Schimp. in Besch. Prodr. Bryol. Mex. 15. 1871.

Puebla: Esperanza (4740). Valle de México: Desierto (*Bro. Amable* 1500 p. p.).

For want of good capsules the determination remains uncertain. The male and female flowers are lateral, an abnormal character for the genus *Hymenostylium*. This fact is, however, not unique; I have previously mentioned a similar case in connection with *H. curvirostre*.[2]

TRICHOSTOMUM CLINTONI C. M. Linnaea 38: 636. 1874

Morelia: Jesús del Monte (7613 p. p.); Loma Santa María (7860, 7874); Campanario (7643).

TRICHOSTOMUM INVOLVENS Card. Rev. Bryol. 40: 34. 1913

Puebla: Cerro Guadalupe (674, 802); Rancho Guadalupe (4612).

E. G. Paris distributed as *T. lamprothecium* C. M. a moss collected by Bro. Arsène at Puebla which is very different from this species and should be referred to *T. involvens*.

TRICHOSTOMUM CHLOROPHYLLUM C. M. var. BREVIFOLIUM Thér., var. nov.

Puebla: (4994, 4995).

Folia breviora latioraque.

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[1] Rev. Bryol. 40: 34. 1913.

[2] Bull. Acad. Internat. Geogr. Bot. 11: 319. 1902.

TIMMIELLA SUBANOMALA (Besch.) Broth. in E. & P. Nat. Pflanzenfam. 1^3: 392. 1902

Trichostomum subanomalum Besch. Prod. Bryol. Mex. 33. 1871.

Puebla: Hacienda Alamos (582, 4513, 4635, 4769); Finca Guadalupe (730). Morelia: Campanario (4773, 7523); Loma Santa María (4907). Distr. Federal: Mixcoac (9448). Valle de México (*Bro. Amable*): Desierto (1215, 1251, 1271); Río Frío (1711). Hidalgo: El Chico (1579).

TIMMIELLA ANOMALA (Bry. Eur.) Limpr. Laubm. Deutschl. 1: 590. 1888

Valle de México: Tenango (*Bro. Amable* 1686).

This species, which grows also in California, Arizona, Louisiana, and Florida, has not previously been recorded from Mexico. The specimens are identical with the European moss.

T. subanomala is very close to *T. anomala*, and to my mind seems to be only a subspecies or a species of secondary rank. It differs from *T. anomala* by the position of the male flowers, the form of the acumen (which is more gradually narrowed and more acute), and by the much broader costa, up to two and a half times as wide.

TRICHOSTOMOPSIS CRISPIFOLIA Card. Rev. Bryol. 36: 74. 1909

Puebla: Rancho Santa Bárbara (4593, 4594a, 4595, 4599); Rancho Posadas (4807). Morelia: Cerro Azul (4934, 4936). Valle de México (*Bro. Amable*): San Jerónimo (1593); Tenango (1688).

Forma **CRASSIRETIS** Thér., form. nov.—Cellulae laminae valde incrassatae.—Puebla: Hacienda Batán (5007 p. p.).

TRIQUETRELLA FERRUGINEA (Schimp.) Thér., comb. nov.

Barbula ferruginea Schimp. in Besch. Prodr. Bryol. Mex. 37. 1871.

San Cristóbal (*F. Müller*), original specimen. Puebla: Boca del Monte (*Purpus*, in hb. Cardot), (*Arsène* 4726); Esperanza (4742). Valle de México: Desierto (*Bro. Amable* 1419).

The leaves are triquetrous, squarrose-spreading when moist; the areolation and papillae suggest the genus *Leptodontium*. I found in no. 4726 a single capsule. The fruit of this species not being known, I describe it:

Folia perichaetialia erecta, vaginantia; pedicellus flavidus, 1 cm. altus; capsula parum inclinata, oblongo-cylindrica; operculum oblique rostratum.

LEPTODONTIUM ANGUSTINERVE Thér., sp. nov.

Puebla: Esperanza (4741; 4743).

Sterile. Caespites sat densi, intense virides. Caulis 4-5 cm. longus, simplex vel parce ramosus, laxe foliosus. Folia sicca erecta, parum patula, flexuosa, madida patula, oblongo-lanceolata, sensim acuminata, acuta, carinata, decurrentia, marginibus integerrimis, in medio reflexis, 1.2 mm. longa, 0.3 mm. lata; costa basi 45 μ, percurrente, dorso papillosa; cellulis laminae quadrato-hexagonis, incrassatis, 12 × 10 μ, papillosis, papillis 1-2, elatis, obtusis, cellulis apicalibus laevibus, cellulis basilaribus rectangularibus, incrassatis, laevibus.

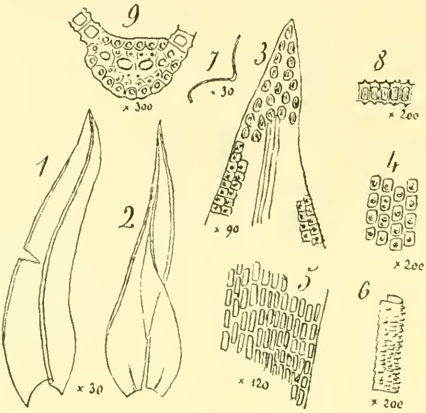

Fig. 5.—*Leptodontium angustinerve* Thér. 1, 2, cauline leaves; 3, acumen; 4, middle cells; 5, basal cells; 6, papillae from the dorsal side; 7, cross-section near the lower third of leaf; 8, 9, fragments of 7.

This species is rather close to *L. filescens* Hampe, but is distinguished by the narrow acute leaves, the narrow costa, the incrassate cells with only 1 or 2 large papillae, the smooth apical cells, and the more compact basal areolation.

LEPTODONTIUM ARSENEI Thér., sp. nov.

Morelia: Cerro San Miguel (5073).

Sterile. Caespites sat densi, compacti, fusco-virides. Caulis 4-5 cm. altus, dense radiculosus, regulariter foliosus. Folia sicca crispula, humida patulo-squarrosa, vaginantia, e basi erecta, breviter oblonga, superne dilatata, sat abrupte in acumen angustum, canaliculatum, subobtusum contracta, marginibus integris, in medio folii revolutis, 1.3 mm. longa, 0.5 mm. lata; costa basi 70 μ, percurrente, dorso papillosa, cellulis laminae opacis, vix distinctis, quadratis, 7-8 μ, dense et tenuiter papillosis, cellulis basilaribus juxtamarginalibus linearibus, laevibus, hyalinis, internis rectangularibus, papillosis, paulum chlòrophyllosis.

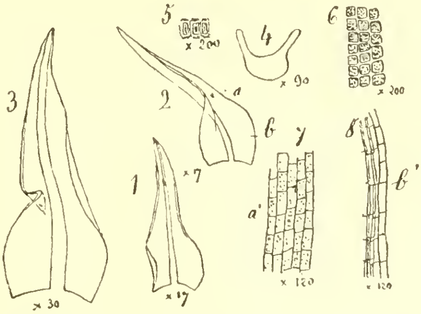

Fig. 6.—*Leptodontium Arsenei* Thér. 1, 2, 3, cauline leaves; 4, cross-section in the acumen; 5, fragment of 4; 6, upper cells; 7, cells in the upper part of leaf base toward *a*; 8, marginal cells of leaf base at *b*.

This species also belongs to the group of *L. filescens*. It may be separated from it by the more elongated stems, by the leaves with a short sheathing base, by the narrower acumen (subobtuse and not apiculate), and the smaller median cells.

LEPTODONTIUM FILESCENS (Hampe) Mitt. Musc. Austr. Amer. 50. 1869

Valle de México: Desierto, upon bark associated with *Rozea stricta* Besch. (*Bro. Amable* 1444).

A Colombian species, new to Mexico.

LEPTODONTIUM SQUARROSUM (Hook.) Par. Ind. Bryol. 732. 1896

Holomitrium serratum (Schimp.) C. M. Syn. 2: 587. 1851.

Valle de México (*Bro. Amable*): Desierto (1431); Río Frio (1396).

The last plant is a form with strongly undulate leaves.

LEPTODONTIUM EXASPERATUM Card. Rev. Bryol. 36: 74. 1909

Valle de México: Río Frío (*Bro. Amable* 1690).

LEPTODONTIUM sp.

Valle de México (*Bro. Amable*): Puenta de la Venta (1391); Desierto (1439 p. p.).

The present species, which unquestionably is new, was recognized as such independently by my friend Edwin B. Bartram, who will shortly publish a description.

TORTULA SUBNIGRA Mitt. Musc. Austr. Amer. 164. 1869

The position of this moss has remained uncertain until now. Jaeger classified it as a *Barbula*. Brotherus[1] thought that perhaps it was a *Didymodon*. Lastly, J. Cardot, who saw its capsules in good condition, verified the absence of a peristome and asked[2] if it might not be convenient to separate Mitten's species from true *Tortula* to constitute the type of a new subgenus.

Mr. Bartram and myself think that we must go further. Transverse sections of the leaves show that the costa possesses the structure of the Trichostomoideae and not of the Pottioideae. Another peculiar fact is that the lamina is composed of two layers of cells, except at the margin. These noteworthy characters, in addition to that presented by the sporophyte, justify the creation of a new genus. We are happy to dedicate this Mexican genus to our eminent friend J. Cardot, whose last and precious works contributed so much to a better understanding of the bryological flora of Mexico, and who has enriched it with such a large number of new species.

NEOCARDOTIA Thér. & Bartr., gen. nov.

Caulis erectus. Folia sicca crispata, humore patulo-squarrosa, carinata, acuta, marginibus inferne revolutis, superne serratis ; rete opaco, bistratoso ; cellulis basilaribus linearibus, laevibus, hyalinis, caeteris minutis, dense papillosis ; costa breviter excurrente, in sectione transversali e strato medio cellulis eurycystis et stereidis ventralibus et dorsalibus composita. Folia perichaetialia perlonga, erecta, vaginantia ; capsula erecta, cylindrica, symmetrica, gymnostoma, annulata ; operculum breviter conicum, cellulis recte seriatis ; sporae laeves.

The affinities of the genus *Neocardotia* are with the genus *Leptodontium,* as much through the habit of the plant as by its serrated cauline leaves and strongly sheathing perichaetial leaves, 2 to 3 times larger than the stem leaves.

A single species:

NEOCARDOTIA SUBNIGRA (Mitt.) Thér. & Bartr., comb. nov.

Tortula subnigra Mitt. Musc. Austr. Amer. 164. 1869.

Caespites nigrescenti-virides ; caulis 2-4 cm. altus. Folia 3.5-4 mm. longa, 1 mm. lata ; costa basi 60-80 μ, dorso rugulosa ; cellulis laminae 6-7 μ, paulum incrassatis, papillis minutis, obtusis ; pedicellus 1 cm.

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[1] E. & P. Nat. Pflanzenfam. 1^3: 405. 1902 ; ed. 2, 10: 273. 1924.

[2] Rev. Bryol. 38: 101. 1911.

longus, sporae diam. 12-18 μ.—Often mixed with other mosses, and almost always with *Braunia secunda.*

Mexico: Loc. class. (*Humboldt*); La Cima (*Barnes & Land* 373 p. p.). Valle de México (*Bro. Amable*): Salazar (1294, 1716); Contreras (1470). Hidalgo: Mineral del Chico (*Orcutt* 6841). Arizona: Santa Rita Mts. (*Bartram* 813).

The plant from Arizona shows some differences as compared with the Mexican plant, slight differences it is true, but worthy of mention; it is a little more slender, the leaves are more shortly acuminate, and their cells less regularly bistratose.

HYOPHILA DENTATA Card. Rev. Bryol. 40: 36. 1913

Morelia: (7896).

HYOPHILA MEXICANA Thér., sp. nov.

Valle de México: Tizapán, on earth (*Bro. Amable* 1613 p. p.).

Sterilis. Caulis perbrevis; folia 2 mm. longa, 0.6 mm. lata, marginibus integerrimis, planis, superne paulum involutis; cellulis laminae hexagonis, papillosis, parietibus tenuibus, diam. 6-7 μ, costa latissima, 90-100 μ, in mucronem brevem acutum excurrente.

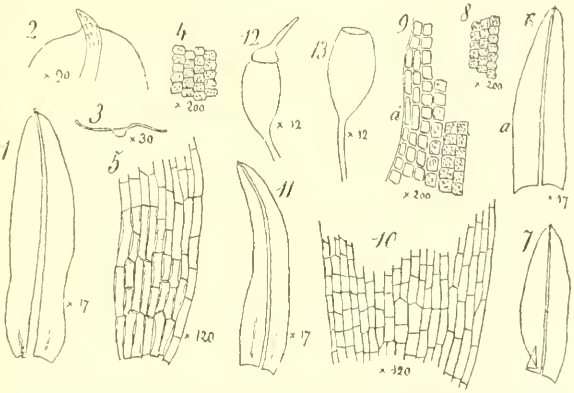

FIG. 7.—*Hyophila mexicana* Thér. 1, leaf; 2, acumen; 3, cross-section toward the middle; 4, median cells; 5, basal cells. *Hyophila subangustifolia* Thér. 6, 7, cauline leaves; 8, median cells; 9, marginal cells toward *a*; 10, basal cells; 11, perichaetial leaf; 12, 13, capsules.

In form, size, and areolation of the leaves this species may be compared with *H. Beschcrellei* C. M. It differs in the very short stems and perfectly entire leaves, and in the hyaline basal cells, with thin, soft walls. These last characters distinguish our species from *H. fragilis* Card.

HYOPHILA SUBANGUSTIFOLIA Thér., sp. nov.

Valle de México: Tizapán, on earth, associated with the preceding species and other mosses (*Bro. Amable* 1613 p. p.).

Dioica. Caespites incohaerentes laxiusculi, virides. Caulis perbrevis, 2-3 mm. altus. Folia sicca crispula, humida erecto-patentia, 1.3-1.6 mm. longa, 0.40—0.45 mm. lata, oblongo-lanceolata, obtusa, breviter mucronata, marginibus planis, integris, superne parum involutis; costa 60 μ lata, breviter excedente, dorso laevi; cellulis basilaribus hyalinis, ad costam elongate rectangulis, ad marginem brevioribus, superioribus minutis, quadratis vel hexagonis, papillosis, obscuris, diam. 7-8 μ. Pedicellus erectus, 4 mm. longus; capsula oblonga, gymnostoma, annulata; operculum oblique et longe rostratum, capsulam subaequans; sporae papillosae, diam. 18 μ. Flos masculus ignotus.

I can find no better comparison for this than *H. angustifolia* Par. & Ren., from Madagascar. It differs from the latter in its shorter stems, oblong-lanceolate leaves (wider, scarcely involute above, and not cucullate at the apex), more compact areolation, and longer operculum.

WEISIOPSIS STENOCARPA Thér., sp. nov.

Valle de México: Desierto (*Bro. Amable* 1205 p. p.). Growing as isolated stems among other mosses, such as *Didymodon oeneus* and *Campylium hispidulum* var. *Sommerfeltii*.

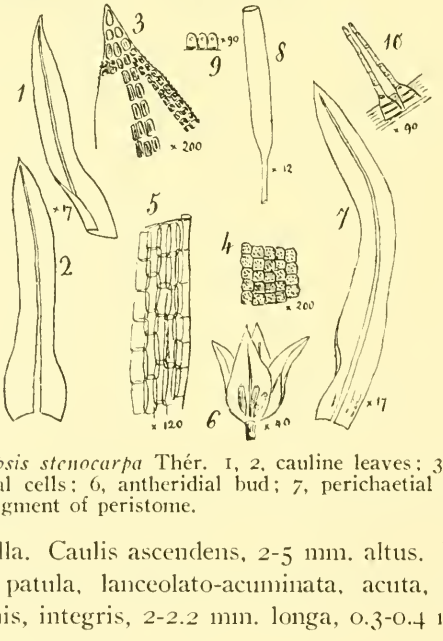

FIG. 8.—*Weisiopsis stenocarpa* Thér. 1, 2, cauline leaves; 3, acumen; 4, median cells; 5, basal cells; 6, antheridial bud; 7, perichaetial leaf; 8, capsule; 9, annulus; 10, fragment of peristome.

Autoica, pusilla. Caulis ascendens, 2-5 mm. altus. Folia sicca crispula, humore patula, lanceolato-acuminata, acuta, basi plicatula, marginibus planis, integris, 2-2.2 mm. longa, 0.3-0.4 mm. lata, costa basi 60 μ, percurrente vel breviter excedente; rete opaco, papilloso, papillis densis, minutis, cellulis quadrato-hexagonis, 8-9 μ, cellulis basilaribus laxioribus, hyalinis, rectangularibus. Folia perichaetialia longiora (3 mm.); pedicellus erectus, pallidus, 5-6 mm. longus; capsula angustissime cylindrica 1.5 mm. longa, 0.26 mm. crassa, annulata, peristomium sub ore insertum, dentes lineares, integri, tenuiter papillosi; sporae laeves, 12 μ crassae. Calyptra? Operculum?

Comparable to *W. stomatodonta* (Card.) Broth. in form and size of capsule, but very different in its autoicous inflorescence, longer, more narrowly acuminate leaves (with margins not involute), looser basal areolation, and entire peristome teeth.

Furthermore, does Cardot's species, which has the peristome teeth divided into two branches, really belong to the genus *Weisiopsis?*

DIDYMODON (Erythrophyllum) PATENTIFOLIUS Thér., sp. nov.

Valle de México: Xoquiapán (*Bro. Amable* 1676); Mixcoac (*Arsène* 9442).

Dioicus, tenellus, obscure viridis. Caulis erectus, simplex, vix 2 mm. altus. Folia sicca crispula-patula, humida patentia, carinato-concava, lanceolato-ligulata, acuta, marginibus anguste revolutis, integris, 1.5-1.6 mm. longa, 0.3 mm. lata; costa papillosa, basi 60 μ crassa, percurrente; cellulis laminae hexagonis, chlorophyllosis, obscuris, papillosis, 8-9 μ, basilaribus laxis, hyalinis, teneris, oblongo-hexagonis, vel rectangularibus. Folia perichaetialia similia sed majora,

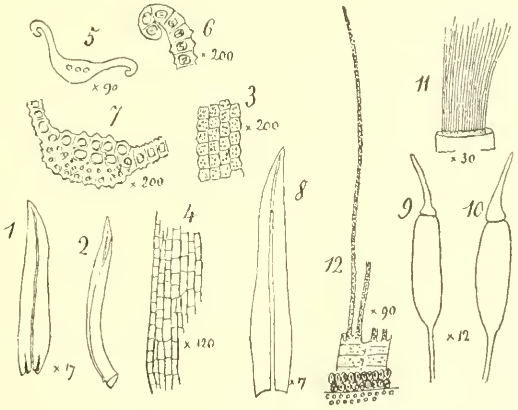

FIG. 9.—*Didymodon patentifolius* Thér. 1, 2, cauline leaves; 3, median cells; 4, basal cells; 5, 6, cross-sections in acumen; 7, cross-section of costa near base; 8, perichaetial leaf; 9, dry capsule; 10, moist capsule; 11, peristome; 12, fragment of peristome.

haud vaginata; pedicellus purpureus, erectus, 10-12 mm. longus; capsula oblonga (2 mm. longa c. operculo), annulata, peristomii dentes e membrana basilari humillima erecti (0.6 mm. alti), fere usque ad basin in 2 crura filiformia papillosa divisi; sporae laeves, 12-15 μ; operculum conico-rostratum.

Distinguished at a glance from *D. oeneus* by its small size. The leaf margin is so closely revolute that at first sight the border seems to be thickened and formed of two layers of cells.

DIDYMODON OENEUS (C. M.) Schimp. in Besch. Prodr. Bryol. Mex. 28. 1871

Trichostomum Oeneum C. M. Syn. 2: 628. 1851.

Puebla: Esperanza (4802). Valle de México: Desierto (*Bro. Amable* 1205 p. p., 1417).

DIDYMODON CAMPYLOCARPUS (C. M.) Broth. in E. & P. Nat. Pflanzenfam. 1^3: 405. 1902

Trichostomum campylocarpum C. M. Syn. 2: 628. 1851.

Valle de México: Desierto (*Bro. Amable* 1248).

DIDYMODON INCRASSATO-LIMBATUS Card. Rev. Bryol. 36: 81. 1909

Morelia: (7914); Rincón (4567); Loma Santa María (4886); Cerro San Miguel (5085). Valle de México: Tlalpan (*Bro. Amable* 1348, 1349).

According to these specimens the peristome teeth are a little twisted, and not exactly straight. Furthermore, the cells of the operculum are arranged in oblique rows, a character which is also found in Pringle's no. 10588. No. 4567, from Rincón, is a form with acute leaves whose margins are less strongly thickened.

DIDYMODON FUSCO-VIRIDIS Card. Rev. Bryol. 36: 83. 1909

Valle de México: San Juanico (*Bro. Amable* 1264).

DIDYMODON PUSILLUS Card. Rev. Bryol. 36: 82. 1909

Valle de México (*Bro. Amable*): Desierto (1207 p. p., 1331, 1615); Río Frío (1746); Xoquiapán (1752).

A robust form, the stems tall, up to 2 cm., leaves wider at the base, margins plane or slightly reflexed. These plants seem to mark a transition toward the last preceding species.

DIDYMODON DIAPHANOBASIS Card. Rev. Bryol. 37: 125. 1910

Valle de México (*Bro. Amable*): Contadero (1363); Río Frío (1704).

DIDYMODON MEXICANUS Besch. Prodr. Bryol. Mex. 28. 1871

Puebla: Hacienda Alamos (4764). Valle de México: San Juanico (*Bro. Amable* 1322, 1332).

DACTYLHYMENIUM PRINGLEI (E. G. Britt.) Card. Rev. Bryol. 36: 72. 1909

Puebla: (9493); Rancho Santa Bárbara (4598, 4811).

These specimens represent a form with less papillose leaves and a nearly smooth costa.

BARBULA BESCHERELLEI Sauerb.

Puebla: Cerro Guadalupe (686a, 799). Morelia: Punguato (5048); Campanario (7564); Cerro San Miguel (5087). Tlaxcala: (613). Valle de México: Desierto, Contadero (*Bro. Amable*).

BARBULA BESCHERELLEI Sauerb. var. **CRASSINERVIA** Thér., var. nov.

Distr. Federal: Mixcoac (9470, 9473).

Folia basi cordata, sat abrupte contracta, costa lata, 90 μ; folia perichaetialia late ovata vel oblonga, breviter acuminata; capsula anguste cylindrica.

BARBULA BESCHERELLEI Sauerb. var. **STENOCARPA** Card.

Valle de México: Xoquiapán (*Bro. Amable* 1749).

BARBULA ALTISETA Card. Rev. Bryol. 36: 83. 1909

Tlaxcala: (621, 720).

A robust form, the stems longer and the leaves less strongly revolute than usual.

BARBULA GRACILIFORMIS Schimp. in Besch. Prodr. Bryol. Mex. 35. 1871

Puebla: Cerro Guadalupe (668, 669, 680, 801). Distr. Federal: Mixcoac (9460, 9461). Tlaxcala: Acuitlapilco (725).

Nos. 680 and 801 are more robust forms.

BARBULA GRACILESCENS Schimp. in Besch. Prodr. Bryol. Mex. 34. 1871

Puebla: (600). Morelia: (7946, 7948); Bosque San Pedro (4577 p. p., 4578, 4581, 4925, 4926); Loma Santa María (4888, 4904); Jesús del Monte (7622). Distr. Federal: Mixcoac (9431, 9435, 9454, 9456, 9458, 9469, 9480).

Barbula altiseta Card., *B. graciliformis* Schimp., and *B. gracilescens* Schimp. are very closely allied species, especially the last two.

According to authentic specimens *B. gracilescens* is distinguished from *B. graciliformis* by its flexuose leaves when dry (not stiff and subimbricated), often narrower, with the acumen a little longer and thinner. I have not detected any differences in areolation, costa, or recurvature of the leaf margins. And inasmuch as I have found forms that could not be definitely connected with either species, I am much inclined to believe that these so-called species are in reality but forms of a single one.

BARBULA TERETIUSCULA Schimp. in C. M. Syn. 1: 614. 1849

Puebla: (907); Fort de Lorette (4622). Morelia: Loma Santa María (7864 p. p.).

BARBULA SUBTERETIUSCULA Card. Rev. Bryol. 36: 85. 1909

Puebla: Rancho Posadas (4808).

BARBULA BOURGEANA Besch. Rev. Bryol. 36: 35. 1909

Puebla: (4996); Río San Francisco (4999); Hacienda Alamos (4637).

BARBULA ORIZABENSIS C. M. Linnaea 40: 638. 1876

Puebla: Hacienda Alamos (578); Cerro Guadalupe (4616); Rancho Guadalupe (4590 p. p.). Distr. Federal: Mixcoac (9464, 9467).

All of these plants are sterile but are identical with the type, which I have been able to examine.

The author compares this species with *B. spiralis* Schimp. It is distinguished, he says, by its less twisted leaves and its cylindrical capsule. These characters are rather intangible and valueless to one who has seen a series of specimens of *B. spiralis*. Happily other important and obvious characters are available: In *B. orizabensis* the margins of the leaves are merely reflexed and not revolute; they are plane at the apex, the costa is thinner and not widened in the acumen, and finally the areolation is chlorophyllose and papillose almost to the base. These characters establish the true position of *B. orizabensis* by the side of *B. unguiculata* and not of *B. spiralis*.

I have noticed in all my specimens, as well as in Pringle's no. 10574, the presence of abundant moniliform propagula in the leaf axils.

BARBULA SPIRALIS Schimp. in C. M. Syn. 1: 622. 1849

Puebla: (892); Mayorazgo (4673, 5975); Cerro Guadalupe (655, 663, 675, 681, 690, 691, 692, 693, 4619, 4620); Rancho Guadalupe (728, 4591, 4602 p. p., 4604 p. p., 4607, 4609 p. p.); Río Alseseca (701); Malinche (6003). Distr. Federal: Tlaquecomeca (9478); Mixcoac (9446, 9447, 9449, 9482). Tlaxcala: Acuitlapilco (741, 742). Morelia: Campanario (7922); Andameo (4830, 4843, 4844); Cuincho (5082); Cerro Azul (5053); Loma del Zapote (7509). Valle de México (*Bro. Amable*): San Juanico (1231, 1262); Texcoco (1287); Guadalupe (1228); Peñon de los Baños (1256).

Of all the mosses known to Mexico this species seems to be the most common.

BARBULA EHRENBERGII (Lor.) Fleisch. var. **MEXICANA** Thér., var. nov.

Nuevo Leon: Monterrey (*Bro. Abbon* 10969).

A forma typica differt foliis valde revolutis.

BARBULA (Hydrogonium) **RUBRICAULIS** Thér., sp. nov.

Nuevo Leon: Monterrey (*Bro. Abbon* 10968).

Sterilis. Caespites densi, glauco-virides. Caulis erectus, simplex, ruber, 1.5-2 cm. altus, basi terra obrutus, laxe foliosus. Folia sicca erecto-flexuosa, madida erecta, paulum patula, oblongo-ligulata, subobtusa, concava, decurrentia, marginibus integris, planis vel uno latere parce reflexis; costa basi 60-70 μ, apicem attingente, rete chlo

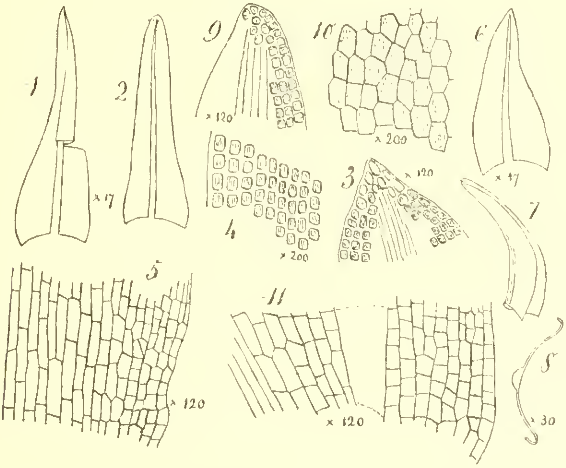

FIG. 10.—*Barbula rubricaulis* Thér. 1, 2, leaves; 3, acumen; 4, median and marginal cells; 5, basal cells. *Barbula Abbonii* Thér. 6, 7, leaves; 8, cross-section of leaf; 9, acumen; 10, median cells; 11, basal cells.

rophylloso, cellulis subquadratis, 10×8 μ, laevibus, parietibus incrassatis, rete basilari laxiore, cellulis juxtacostalibus rectangularibus, hyalinis, margines versus quadratis vel breviter rectangularibus. Caetera desunt.

In color of the stems and in form, size, and areolation of the leaves *B. rubricaulis* is very close to *B. dialytrichoides* Thér., from China, differing only in its nearly smooth areolation. I have not seen the fruit.

BARBULA (Hydrogonium) ABBONII Thér., sp. nov.

Nuevo Leon: Monterrey (*Bro. Abbon* 10970).

A *B. rubricauli* proximo differt: caule viride, foliis siccis valde patulis, humidis subsquarrosis, brevioribus, 1.4 mm. longis, 0.60-0.65 mm. latis, costa latiora, 90-100 μ crassa, cellulis mediis majoribus, 15-20 μ × 10-15 μ.

The leaves show the median areolation of *B. Ehrenbergiana* var. *mexicana* and the basal areolation of *B. rubricaulis;* the leaf margins are narrowly revolute three-fourths of the way up from the base.

BARBULA (Streblotrichum) CALCAREA Thér., sp. nov.

Morelia: Loma Santa María, on calcareous rocks (4891). Valle de México: Desierto (*Bro. Amable* 1620).

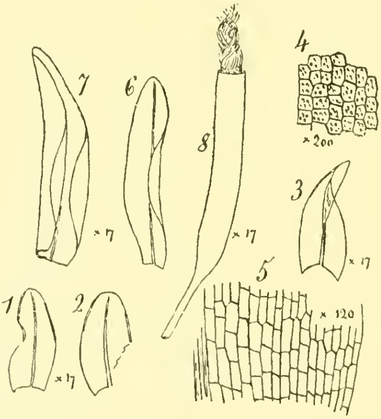

FIG. 11.—*Barbula calcarea* Thér. 1, 2, 3, cauline leaves; 4, median cells; 5, basal cells; 6, 7, perichaetial leaves; 8, deoperculate capsule.

Pusilla. Caulis gracilis, simplex, 3-5 cm. altus, laxe foliosus. Folia mollia, sicca appressa, humida patula, elliptica vel oblonga, late rotundata, decurrentia, marginibus integerrimis, inferne planis, superne valde revolutis, 0.9 mm. longa, 0.4 mm. lata; costa basi 60 μ, continua, dorso papillosa; cellulis mediis opacis, indistinctis, dense papillosis, diam. 10-12 μ, superioribus minoribus, rete basilari laxiore, pellucido, cellulis rectangularibus, chlorophyllosis, plus minus papillosis, infimis laevibus. Folia perichaetialia pauca, intima 2 duplo longiora, convoluta, longe vaginantia, apice lingulata, obtusa; pedicellus tenuis, pallido-luteus, 7-8 mm. longus; capsula (immatura) minuta, anguste-cylindrica; operculum rostratum. Caetera ignota.

By its slender habit, its loosely foliate stems, and leaves revolute in the upper two-thirds, the present species is immediately distinguished from *B. hypselostegia* Card. and *B. Muenchii* Card., both of which also have obtuse leaves.

BARBULA (Streblotrichum) STENOTHECA Thér., sp. nov.

Valle de México; Río Frío, on earth (*Bro. Amable* 1726).

Dioica. Caespites sat densi, obscuro-virides. Caulis erectus, flexuosus, gracilis, remote foliosus, 10-15 mm. altus. Folia sicca incurvato-crispata, madida patula, oblongo-lanceolata, subobtusa, breviter apiculata, marginibus integris, usque ad apicem revolutis, 2 mm. longa, 0.6 mm. lata, costa valida, basi 60 μ crassa, dorso laevi, breviter ex-

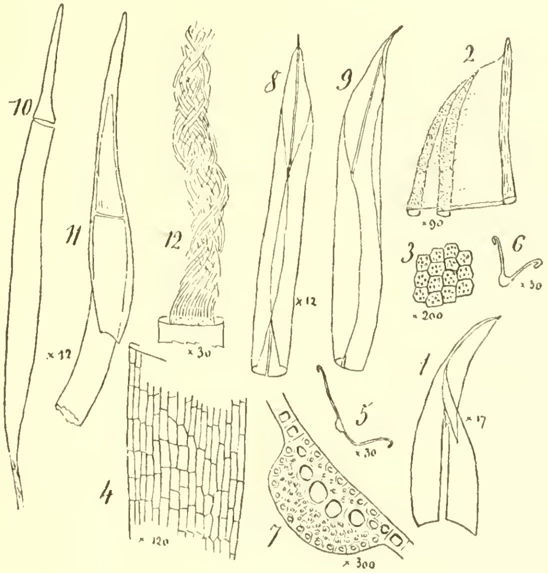

FIG. 12.—*Barbula stenotheca* Thér. 1, cauline leaf; 2, acumen; 3, median leaf cells; 4, basal cells; 5, 6, cross-sections of leaf; 7, cross-section of costa near base; 8, 9, perichaetial leaves; 10, dry capsule; 11, calyptra; 12, peristome.

currente; rete opaco, cellulis hexagonis, 10 μ, parietibus tenuibus, dense et minute papillosis, cellulis inferioribus rectangularibus, pellucidis, laevibus, parietibus firmis. Folia perichaetialia numerosa, externa patulo-subsquarrosa, intima convoluta, longe vaginantia, decolorata, longissima, 4 mm. longa, obtusiuscula, apiculata; pedicellus ruber, 15 mm. longus; capsula erecta, angustissime cylindrica vel arcuato-cylindrica, 4 mm. longa, 0.4 mm. crassa; calyptra $\frac{1}{4}$ partem capsulae obtegens; operculum longe conicum, 1.3 mm. longum; annulus simplex; peristomium elatum, 1 mm. altum, dentibus valde contortis, membrana basilari brevi; sporae laeves, 8-9 μ.

Differs widely from the other Mexican species of the section *Streblotrichum* in size and habit, and especially in the dimensions of the capsule.

MORINIA EHRENBERGIANA (C. M.) Thér., comb. nov.

Barbula Ehrenbergiana C. M. Syn. 1: 636. 1849.
Barbula trichostomoides Besch. Prodr. Bryol. Mex. 38. 1871.
Morinia trichostomoides Card. Rev. Bryol. 37: 124. 1910.

Valle de México: Desierto, on earth (*Bro. Amable* 1240).

While studying this specimen I recognized, by a happy chance, its identity with *Barbula Ehrenbergiana* C. M. and with *Morinia trichostomoides* (Besch.) Card. The name established by Müller has priority, hence the above new combination.

ALOINA CALCEOLIFOLIA (Spruce) Broth. in E. & P. Nat. Pflanzenfam. 1^3: 428. 1902

Puebla: (704); Mayorazgo (4672).

ALOINELLA CATENULA Card. Rev. Bryol. 36: 76. 1909

Valle de México (*Bro. Amable*): Desierto (1207 p. p., 1217 p. p.); Salazar (1296 p. p.).

Terrestrial, in isolated bits, always associated with other mosses.

TORTULA PARVA Card. var. LATIFOLIA Thér., var. nov.

Puebla: (4509); Rancho Santa Bárbara (4593, 4600); Hacienda Alamos (4720). Morelia: Cerro Azul (4933). Valle de México: Cartridge Factory (*Bro. Amable* 1459 p. p.).

A forma typica differt statura robustiore, foliis longioribus et duplo latioribus, 1.2-1.8 mm. × 0.6-0.8 mm.

TORTULA AMPHIDIACEA (C. M.) Broth. in E. & P. Nat. Pflanzenfam. 1^3: 424. 1902

Barbula? amphidiacea C. M. Linnaea 38: 639. 1874.

Puebla: Rancho Santa Bárbara (4810 p. p.). Morelia: Parc San Pedro, c. fr. (4587); Cerro Azul (4932). Valle de México: Contadero (*Bro. Amable* 1300, 1308 p. p., 1360).

The plant from San Pedro bears capsules. The fruit being unknown, I describe it: Pedicel short, 6-7 mm., almost hidden by the long and numerous innovations; capsule oblong-cylindrical. All the capsules are old and have neither operculum nor peristome.

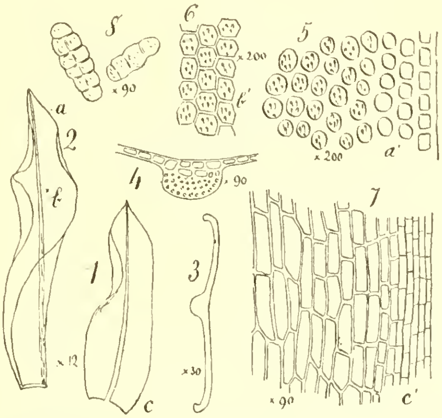

FIG. 13.—*Tortula amphidiacea*. 1, 2, stem leaves; 3, cross-section of a leaf; 4, the same, costa; 5, upper marginal cells toward *a*; 6, median cells; 7, basal cells; 8, propagulae.

The species is well characterized in other particulars: The leaf is acute and entire, more or less marginate at the base with several rows of narrow cells, the lamina with differentiated, incrassate and smooth cells; the costa is percurrent or short-excurrent; the stems bear oblong propagula.

TORTULA RIPICOLA Thér., sp. nov.

Valle de México: Morales, on earth, bank of a small stream, associated with *Fissidens tortilis* Hampe & C. M. (*Bro. Amable* 1596 p. p.).

Sterilis, pusilla. Caulis inferne denudatus, superne rosulato-foliosus, 0.5-1 cm. altus, in axillis foliorum propagula numerosa, fusca, sphaerica gerens. Folia sicca paulum crispula, humore patula, ovato-lanceolata, obtusa vel raro subacuta, breviter mucronata, marginibus integerrimis, toto ambitu revolutis, 1.5 mm. longa, 0.6-0.7 mm. lata; rete opaco, dense et minute papilloso; cellulis quadrato-hexagonis, chlorophyllosis, haud incrassatis, diam. 6 μ, basilaribus paucis, hyalinis, laevibus, breviter rectangularibus, costa basi 60 μ, dorso minute papillosa, in mucronem brevem excedente, structura in sectione transversali ut in genere.

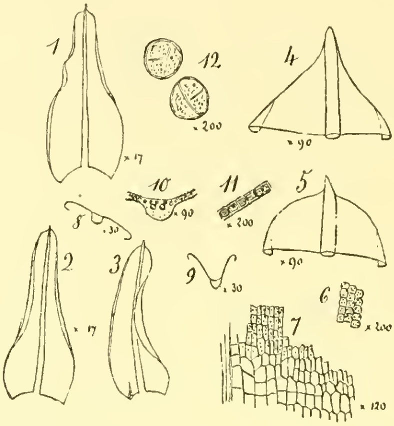

Fig. 14.—*Tortula ripicola* Thér. 1, 2, 3, leaves; 4, 5, acumens; 6, median leaf cells; 7, basal cells; 8, 9, 10, 11, cross-sections of a leaf; 12, propagulae.

Group of *T. papillosa* Wils. Well characterized by its small size, its leaves broadened at base, revolute all around and short-mucronate, and its very compact areolation.

TORTULA FRAGILIS (Tayl.) Mitt. Musc. Austr. Amer. 172. 1869

Tortula confusa Card. Rev. Bryol. 36: 87. 1909.
Tortula Pringlei Card. Rev. Bryol. 36: 87. 1909.

Puebla: (4510); Esperanza (4940). Distr. Federal: Tlalpam (9494).

For the synonymy of this species the reader is referred to a recent note by Mr. E. B. Bartram.[1] While studying Bro. Arsène's collection I also formed a clear idea that Cardot's two species could not be maintained, as the author himself apparently suspected.

TORTULA OBTUSISSIMA (C. M.) Mitt. Musc. Austr. Amer. 174. 1869

Puebla: Cerro Guadalupe (667, 673). Tlaxcala: (606). Valle de México (*Bro. Amable*): San Juanico (1232); Tenayuca (1376); Xoquiapán (1675).

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[1] Bryologist 29: 53. 1926.

TORTULA OBTUSISSIMA (C. M.) Mitt. var. CONNECTENS (Card.) Thér., comb. nov.

Tortula connectens Card. Rev. Bryol. 36: 87. 1909.

Puebla: Fort Guadalupe (4621). Morelia: Cerro Azul (4531). Distr. Federal: Mixcoac (9485).

The characters indicated to separate *T. connectens* from *T. obtusissima* do not appear constant, and I combine the two species.

GRIMMIACEAE (continued)

GRIMMIA INVOLUCRATA Card. Rev. Bryol. 36: 105. 1909

Valle de México (*Bro. Amable*): Tlalpam, c. fr. (1448); Zacatenco, ster. (1352).

GRIMMIA PRAETERMISSA Card. Rev. Bryol. 36: 105. 1909

Valle de México (*Bro. Amable*): Río Frío, on rocks (1401 p. p., 1681).

The capsule is sometimes pale and scarcely exserted, sometimes brown, longer-pedicellate, and well exserted.

GRIMMIA CALIFORNICA Sull. in U. S. Rep. Expl. Miss. Pacif. 4: 187, pl. 4. 1856

Valle de México (*Bro. Amable*): Río Frío, intimately mixed with the preceding species (1401 p. p.); Llano Grande, alt. 3,700 meters (1724, 1734).

GRIMMIA PULLA Card. Rev. Bryol. 36: 106. 1909

Valle de México: Contreras, on rocks (*Bro. Amable*).

The plants are fruited, but the over-ripe capsules have lost their peristomes. Sporophyte pseudo-lateral, because of the 1-3 rather elongated innovations borne under the male flower; pedicel 2-2.5 mm. long, suberect when dry, arcuate when moist; capsule oblong, strongly furrowed.

SPLACHNACEAE

TAYLORIA (Eutayloria) TORTELLOIDES Thér., sp. nov.

Hidalgo: El Chico, 2,600 meters (*Bro. Amable* 1587 p. p.). Growing as isolated stems among other mosses, especially with *Bryum Ehrenbergianum*.

Dioica? Flos masculus ignotus. Caulis brevis, vix 1 cm. altus, simplex vel parce ramosus, inferne denudatus, radiculosus, paucifoliatus, apice rosulato-foliosus. Folia sicca valde crispata, nitida, humore patentia, oblongo-spathulata, e basi contracta, decurrentia, apice rotundata, apiculata, apiculo brevi, obliquo, marginibus planis, inferne paulum reflexis, integris vel remote et obtuse denticulatis, 3 mm. longa, 2 mm. lata; costa basi 120 μ, raptim attenuata, sub apicem evanescente, in sectione transversali ut in genere; cellulis mediis hexagonis, chlorophyllosis, parietibus tenuibus, 60 × 30 μ, marginalibus (2-3 ser.) elongatis, inanis, cellulis basilaribus rectangularibus, parce chlorophyllosis. Folia perichaetialia similia, intima minora; pedicellus erectus, perbrevis, 1.5 mm. longus, laevis, pallidus; capsula subcylindrica, brevicollis, 2 mm. longa; operculum obtuse conicum, columella inclusa, peristomii 16 dentes liberi, opaci, dense papillosi, 0.4 mm. longi; sporae laeves, 15-18 μ crassae. Calyptra?

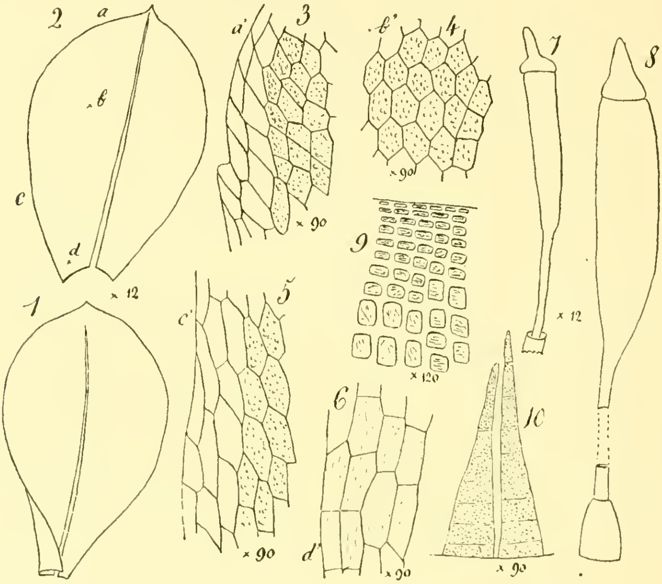

FIG. 15.—*Tayloria tortelloides* Thér. 1, lower leaf; 2, comal leaf; 3, upper cells at *a*; 4, median cells at *b*; 5, marginal cells toward *c*; 6, basal cells; 7, young dry capsule; 8, moist capsule; 9, wall of capsule orifice; 10, fragment of peristome.

The extremely short pedicel and the entire leaves, rounded apiculate, broadly spatulate, and shrivelled when dry (like some *Tortula*), readily distinguish this plant from the other species of the subgenus *Eutayloria*.

BRYACEAE (continued)

MIELICHHOFERIA SAINT-PIERREI Thér., sp. nov.

Valle de México: Lerma; leg. *Marius Saint Pierre* (*Bro. Amable* 1685).

Paroica, laxiuscula caespitosa, tenella, viridis. Caulis julaceus, 2-3 mm. altus, ramis erectis, vix 5 mm. longis. Folia caulina conferta, imbricata, ovato vel oblongo-lanceolata, acuminata, acuta, 0.8-1.2 mm. longa, 0.4-0.5 mm. lata, marginibus parce et anguste reflexis, superne remote denticulatis vel sinuolatis, costa basi 30-36 μ crassa, subpercurrente, rete membranaceo, cellulis elongate rhomboideis, 60-70 μ × 12 μ, marginibus angustioribus, basilaribus rectangularibus; folia ramea angustiora, marginibus erectis. Folia perichaetialia caulinis similia; pedicellus erectus, 8-12 mm. longus; capsula inclinata vel subhorizontalis, symmetrica, oblongo-cylindrica, collo attenuato instructa; annulus latus; peristomium simplex, membrana basilari subnulla, processus angusti, 10 μ lati, granulosi haud appendiculati; sporae sublaeves, 12-15 μ; operculum convexum, mamillatum.

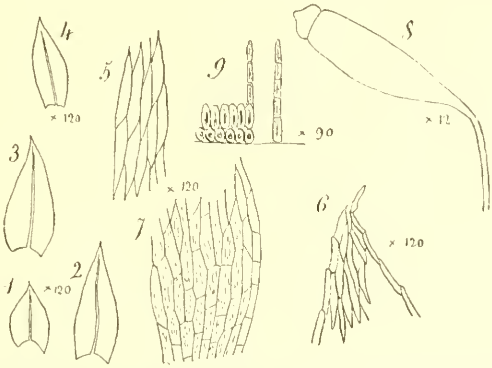

FIG. 16.—*Mielichhoferia Saint-Pierrei* Thér. 1, 2, 3, stem leaves; 4, leaf from an innovation; 5, median cells; 6, apical cells; 7, basal cells; 8, moist capsule; 9, fragment of peristome and annulus.

LEPTOBRYUM PYRIFORME (L.) Wils.

Valle de México: Tlalpam (*Bro. Amable* 1246 p. p.).

EPIPTERYGIUM MEXICANUM (Besch.) Broth.

Valle de México (*Bro. Amable*): Puente de la Venta (1400); Santa Rosa (1513); Desierto (1642).

EPIPTERYGIUM MEXICANUM (Besch.) Broth. var. ANGUSTIRETE Thér., var. nov.

Valle de México: Contreras (*Bro. Amable* 1659).

Folia angustiora, cellulis chlorophyllosis, angustioribus.

MNIOBRYUM INTEGRUM (Card.) Broth. in E. & P. Nat. Pflanzenfam. ed. 2, 10: 363. 1924

Webera integra Card. Rev. Bryol. 40: 11. 1913.

Valle de México: Contreras (*Bro. Amable* 1478).

WEBERA SPECTABILIS (C. M.) Jaeg.

Webera cylindrica (Mont.) Schimp. in Besch. Prodr. Bryol. Mex. 52. 1871.

I have received from Bro. Amable rather numerous collections of *Webera* of the present relationship, but frankly, I have not succeeded in distinguishing *W. cylindrica* from *W. spectabilis*. The characters I had considered distinctive are rarely combined on the same plant and all of them show a rather wide variability, as, for instance, in the width of the leaf, the recurvature of the margin, the width of the costa and of the cells, and the length of the capsule. My conclusion is that we must unite the two species. *Webera spectabilis* has priority.

WEBERA PSEUDO-BARBULA Thér., sp. nov.

Valle de México (*Bro. Amable*): Desierto (1630, 1643); Contreras (1658); Lerma (1684).—In all these localities the plants grow in company with *Anomobryum filiforme* var. *mexicanum*, a remarkable fact of association.

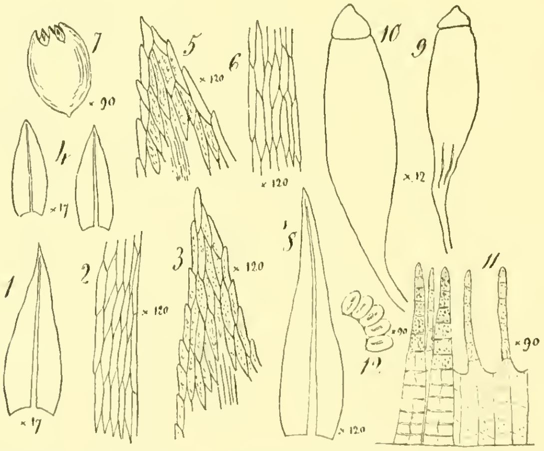

FIG. 17.—*Webera pseudo-Barbula* Thér. 1, stem leaf; 2, marginal and median cells; 3, apical cells; 4, leaves of innovations; 5, apical cells of 4; 6, marginal and median cells of 4; 7, propagula; 8, perichaetial leaf; 9, dry capsule; 10, moist capsule; 11, peristome (fragment); 12, fragment of annulus.

Dioica. Caespites laxi, virides. Caulis brevis, 5 mm. longus, superne innovationibus elongatis, 10-15 mm. longis, in axillis foliorum superiorum propagula fusca, numerosa, subglobosa gerens. Folia sicca erecta, parum flexuosa, humore erecto-patula, ovato-acuminata, 1.2-1.5 mm. longa, 0.5 mm. lata, marginibus planis, interdum anguste revolutis, elimbatis, integerrimis, apice denticulatis; costa basi 60 μ, sensim attenuata, ante apicem evanescente; cellulis anguste rhomboideis, chlorophyllosis, 70-90 μ × 8-9 μ, ad marginem angustioribus; folia innovationis similia sed minora. Folia perichaetialia longiora, ovato-lanceolata, acuminata, intima anguste lanceolata, tenui-acuminata, marginibus revolutis, costa percurrente; pedicellus flexuosus, 20-25 mm. altus; capsula suberecta vel inclinata, oblonga collo breviore attenuata; operculum convexum, mamillatum; annulus latus; exostomii dentes pallidi, haud marginati, dorso inferne laeves, superne papillosi, 0.27 mm. alti, membrana ad $\frac{1}{3}$ dentium producta, processus lineares, fugaces, cilia rudimentaria; sporae diam. 12-15 μ.

Very close to *W. didymodontia* (Mitt.) Broth., which is distinguished at a glance by its globular capsule.

BRACHYMENIUM (Dicranobryum) SAINT-PIERREI Thér., sp. nov.

Valle de México: Contreras, on earth; leg. *Marius Saint-Pierre* (*Bro. Amable* 1338 p. p.).

Dioicum. Caulis brevis, 2-3 mm. altus, inferne denudatus, innovationibus numerosis, clavatis. Folia sicca appressa, oblonga, breviter

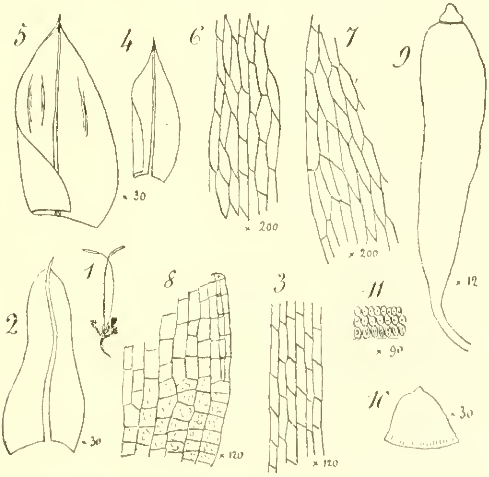

FIG. 18.—*Brachymenium Saint-Pierrei* Thér. 1, plant at natural size; 2, stem leaf; 3, median cells; 4, lower leaf of innovation; 5, upper leaf of innovation; 6, median cells; 7, marginal cells; 8, basal cells; 9, moist capsule; 10, operculum; 11, fragment of annulus.

acuminata, mucronata, elimbata, marginibus integris, planis; costa flexuosa, basi 40 μ, breviter excurrente, cellulis longe hexagonis, 36-60 $\mu \times 10 \mu$, basilaribus quadratis; folia innovationis inferiora minuta, caetera sensim majora, valde concava, apice congesta. Folia perichaetialia majora, deltoidea; pedicellus pertenuis, flexuosus, 12-15 mm. longus; capsula suberecta vel horizontalis, microstoma, oblongo-cylindrica, collo longo attenuata; annulus latus; operculum conico-convexum, mamillatum; peristomium externum normale, 0.32 mm. altum, internum? (capsulae immaturae); sporae laeves, 18 μ crassae.

In the size and form of its capsule this species recalls *B. rubricarpum* (Besch.). It differs in its leaves, which are of another form, short-mucronate, with the hair-point not spreading when dry, in its areolation, the median cells of which are a little shorter and the marginal cells not differentiated, and in its paler capsule.

BRYUM BOTTERII C. M. Linnaea 38: 622. 1874

Valle de México (*Bro. Amable*): Desierto (1619, 1633, 1637); Río Frío (1709); Salazar (1714); Llano Grande, 3,700 meters (1736).

BARTRAMIACEAE (continued)

BARTRAMIA ITHYPHYLLA (Hall.) Brid.

Valle de México: Río Frío (*Bro. Amable* 1405, 1407 p. p.).

This species is new to Mexico.

BARTRAMIA THRAUSTA Schimp.; C. M., Nuov. Giorn. Bot. Ital. 4: 41. 1897

Valle de México: On rocks (*Bro. Amable* 1502 p. p., 1503 p. p.).

An interesting discovery. This species belongs to the South American flora and was known previously only from Bolivia and Argentina. Unfortunately I found only two specimens, these among tufts of *Anacolia intertexta*.

BARTRAMIDULA MEXICANA Schimp. in Besch. Prodr. Bryol. Mex. 58. 1871

Valle de México: Desierto (*Bro. Amable* 1624).

PTYCHOMITRIACEAE

PTYCHOMITRIUM LEPIDOMITRIUM Schimp. in Besch. Prodr. Bryol. Mex. 41. 1871

Valle de México (*Bro. Amable*): Contreras (1443, 1469); Salazar (1719).

HEDWIGIACEAE (continued)

HEDWIGIDIUM IMBERBE (Sm.) Bry. Eur.

Valle de México: Salazar, on trunks of trees (*Bro. Amable* 1294 p. p.).

A new genus for Mexico, also, I believe, for all of North America. This number (1294) was made up of a close intermixture of four species, two of them predominant: *Hedwigidium imberbe* and *Neocardotia subnigra;* the two others, *Hedwigia albicans* var. *viridis* and *Braunia secunda,* were represented by a few plants only.

It was an easy matter to separate *Neocardotia subnigra* and *Hedwigia albicans,* but quite another thing with regard to *Braunia secunda,* whose presence I did not even suspect. If some fruiting plants had not been present this species would have been overlooked, its size and appearance being so similar to those of *Hedwigidium imberbe.*

It is rather unusual to find, associated in such a manner, two species that are indistinguishable either to the naked eye or by the use of a hand lens except by their fruit; and it is even more unusual to be unable to find morphological and anatomical characters by which to separate them. The form and size of the leaves, recurvature of the borders, plication of the lamina, and areolation, all are identical. I do not know of another example of such an association and such a similarity.

AMBLYSTEGIACEAE

CAMPYLIUM CHRYSOPHYLLUM (Brid.) Bryhn, Explor. 61. 1893

Hypnum chrysophyllum Brid. Musc. Rec. **2**^{2}: 84. *pl. 2.* 1801.

Morelia: Loma Santa María (7870).

CAMPYLIUM HISPIDULUM (Brid.) Mitt. var. SOMMERFELTII (Myrin) Lindb. Musc. Scand. 38. 1879

Puebla: Rancho Guadalupe (4602). Morelia: Cerro Azul (4561); Loma Santa María (5103, 5105, 7859 p. p.); Campanario (7462 p. p.). Valle de México (*Bro. Amable*): Desierto (1222 p. p., 1238, 1432); Contreras (1462, 1490).

AMBLYSTEGIUM SERPENS (L.) Bry. Eur.

Distr. Federal: Tlalpam (9493).

This species seems to be new to Mexico.

AMBLYSTEGIUM VARIUM (Hedw.) Lindb. var. ARSENEI (Par. & Broth.) Thér., var. nov.

Amblystegium Arsenei Par. & Broth., Ms.

Puebla: Río San Francisco (5004). Valle de México: Tlalpam (*Bro. Amable* 1453).

I had previously received this plant from E. G. Paris under the name *A. Arsenei* Par. & Broth., sp. nov., likewise from Río San Francisco. Indeed, at first sight it would appear different from *A. varium* in several respects: (1) Its narrower leaves; (2) its greatly developed perichaetium, the perichaetial leaves being almost 4 times longer than the cauline leaves; (3) the capsule not arcuate when dry.

These characters, however, fade out to some extent upon close examination: (1) In *A. varium* the form of the leaves is very variable; (2) if specimens of *A. varium* are found with an inconspicuous perichaetium and short perichaetial leaves, there are others whose perichaetium is as well developed as in *A. Arsenei;* (3) there remains only the character afforded by the form of the capsule. This last is not sufficient to justify the recognition of a species.

AMBLYSTEGIUM ORTHOCLADUM (Beauv.) Jaeg.

Puebla: Finca Guadalupe (737); Hacienda Alamos (4723, 4725). Morelia: Bosque San Pedro (4569).

The last plant, probably half submerged, is a form with greatly elongated stems and branches and a thicker nerve (60 μ).

AMBLYSTEGIUM RADICALE (Beauv.) Mitt. Musc. Austr. Amer. 569. 1869

Puebla: Hacienda Batán (934); Río San Francisco (5000).

Plants sterile, the determination only probable. The plant from Río San Francisco has the stems and branches laxly foliate and the larger leaves widely spreading, either dry or moist.

AMBLYSTEGIUM JURATZKANUM Schimp.

Valle de México: Tlalpam (*Bro. Amable* 1346 p. p.).

The nerve extends well into the apex of the leaf. This is almost the only difference I could find, as compared with the preceding plants identified as *A. radicale*.

AMBLYSTEGIUM HYGROPHILUM (Jur.) Schimp.

Puebla: Hacienda Batán (5008).

A new species for Mexico.

HYGROHYPNUM PALUSTRE (Huds.) Loesk.

Puebla: San Felipe (4504, 4505).

This species was not known previously from Mexico.

DREPANOCLADUS EXANNULATUS (Gümb.) Warnst. var. MEXICANUS (Mitt.) Card. Rev. Bryol. 37: 54. 1910

Puebla: Hacienda Batán (4961). Querétaro: Cienaga de la Cañada (11002).

The var. *mexicanus* seems close to var. *pinnatus* (Boul.), from which it may be distinguished by its almost entire leaves, with thinner costae. The most conspicuous character of this variety consists in the very marked apical prominence of the cells. It is, perhaps, the first time this peculiarity has been noted in connection with *D. exannulatus*.

PLATYHYPNIDIUM SUBRUSCIFORME (C. M.) Fleisch. Laubm. Fl. Jav. 4: 1537. 1922

Hypnum subrusciforme C. M. Linnaea 38: 658. 1874.
Rhynchostegium malacocladum Card. Rev. Bryol. 37: 71. 1910.

Puebla: (699); banks of Alseseca (700); Cerro Guadalupe (676); Hacienda Alamos (4626, 4629, 4761). Valle de México (*Bro. Amable*): Morales (1597); Tenango (1687).

I have noticed the variability of this species with regard to the form of the acumen and of the capsule.

PLATYHYPNIDIUM PRINGLEI (Card.) Broth. in E. & P. Nat. Pflanzenfam. ed. 2, 11: 347. 1925

Rhynchostegium Pringlei Card. Rev. Bryol. 37: 70. 1910.

Puebla: Hacienda Alamos (4628, 4769 p. p.); Hacienda Batán (5006). Morelia: Parc San Pedro (4589); Andameo (4822); Campanario (7534); Loma Santa María (4908, 4910).

PLATYHYPNIDIUM OBTUSIFOLIUM (Besch.) Broth. in E. & P. Nat. Pflanzenfam. ed. 2, 11: 347. 1925.

Rhynchostegium obtusifolium Besch. in Card. Rev. Bryol. 37: 71. 1910.

Morelia: Cerro San Miguel (4870, 5041, 5071); Campanario (7631); Loma Santa María (4890, 4917). Distr. Federal: Tlalpam (9492).

PLATYHYPNIDIUM OBTUSIFOLIUM (Besch.) Broth. var. SUBACUTUM Thér., var. nov.

Leaves subacute and contracted at the apex.

Valle de México: Tlalpam, in water (*Bro. Amable* 1450, 1452).

BRACHYTHECIACEAE

PLEUROPUS BONPLANDII (Hook.) Broth. in E. & P. Nat. Planzenfam. 1^3: 1136. 1908

Leskea Bonplandii Hook. in Kunth Syn. Pl. Aequin. 1: 61. 1822-28.

Puebla: Esperanza (4745, 4754). Valle de México (*Bro. Amable*): Desierto (1438); Santa Rosa (1504). Hidalgo: El Chico (1580).

BRACHYTHECIUM

I must confess that the study of the Mexican specimens belonging to the genus *Brachythecium* has been an extremely laborious task: The sterility of many of them on the one hand and, on the other, the difficulty if not the impossibility of obtaining, for the sake of comparison, good and complete specimens of the types, are among the more important contributory causes.

I studied nearly 60 numbered specimens and drew almost all of them. They belong, excepting five or six, to the sections Acuminata and Salebrosa. Now except for *B. salebrosum* (Hoffm.) and *B. laxireticulatum* Card., the Mexican species of this group are very difficult to identify. For one specimen that agrees with the type there are many others which combine characters common to several species and which one hesitates to attribute to one rather than the other. Hence I gave three different names in succession to the same specimen without being entirely satisfied with any of them. My conclusions are as follows:

(1) Several of my determinations remain uncertain; they are merely probable.

(2) Some of the Mexican species are very polymorphous, like our *B. rutabulum,* and their forms have been taken for new species. Therefore one must not be surprised to find indeterminable specimens which in turn seem like new species.

It will be a task for future bryologists, those who will have the privilege of studying the flora *in situ,* to weigh these variable species and to make, with a thorough knowledge of the facts, whatever reductions are necessary.

BRACHYTHECIUM TENUINERVE Card. Rev. Bryol. 37: 65. 1910

Puebla: Xuehitl, near Esperanza (7988). A form which by its laxer areolation marks a tendency toward *B. lanceolifolium* Card. Valle de México (*Bro. Amable*): Contreras (1221, 1483); Desierto (1618); Salazar (1717); Llano Grande (1738). This is a form with very elongate branches.

BRACHYTHECIUM ALBULUM Besch. in Card. Rev. Bryol. 37: 66. 1910

Morelia: Bosque San Pedro (4582).

I have seen only a very incomplete specimen of the type. The present specimen seems to differ from it by the longer and more slender acumen of the leaves.

BRACHYTHECIUM LANCEOLIFOLIUM Card. Rev. Bryol. 37: 66. 1910

Puebla: Cerro Guadalupe (796); Hacienda Alamos (4760); Río San Francisco (5003). Morelia: Loma Santa María (5089). Distr. Federal: Mixcoac (9453). Valle de México (*Bro. Amable*): Santa Teresa (1339); Contadero (1364); Tizapán (1612).

BRACHYTHECIUM LANCEOLIFOLIUM Card. var. GRACILE Card. Rev. Bryol. 37: 66. 1910

Puebla: Hacienda Batán (935); Hacienda Alamos (4799). Morelia: Campanario (7452).

BRACHYTHECIUM CLADONEURON (C. M.) Par. Ind. Bryol. 132. 1894

Hypnum cladoneuron C. M. Linnaea 38: 652. 1874.

Puebla: Hacienda Alamos (4696).

BRACHYTHECIUM COMTIFOLIUM (C. M.) Jaeg.

Hypnum comtifolium C. M. Linnaea 38: 653. 1874.

Valle de México: Desierto (*Bro. Amable* 1238).

BRACHYTHECIUM TROCHALOBASIS C. M. Bull. Herb. Boiss. 5: 238. 1897

Puebla: Esperanza (4729). Morelia: Cascade de Coincho (4713); Carindapaz (7951); Santa Clara (4886).

BRACHYTHECIUM FLEXIVENTROSUM (C. M.) Jaeg.

Hypnum flexiventrosum C. M. Linnaea 38: 653. 1874.

Morelia: Cerro San Miguel (7546); Campanario (7940); Cerro Azul (4532, 4541, 4554, 4788). Distr. Federal: Tlalpam (9498). Valle de México (*Bro. Amable*): Desierto (1222 p. p.); San Juanico (1261).

Several of these specimens oscillate between this species and the preceding one. In their long and slender acumen and flexuose costa they tend toward *B. flexiventrosum;* but the habit, the short nerve, and the short pedicel (1 cm. or less) bring them nearer to *B. trochalobasis.* I am not far from believing that these two species should be united into one.

BRACHYTHECIUM SERICEOLUM Card. Rev. Bryol. 37: 66. 1910

Puebla: (4997); Hacienda Batán (4975).

BRACHYTHECIUM FLEXINERVE Card. Rev. Bryol. 37: 67. 1910

Puebla: (4862); Hacienda Santa Bárbara (740). Tlaxcala: (4855).

BRACHYTHECIUM ALBO-FLAVENS Card. Rev. Bryol. 37: 68. 1910

Puebla: Rancho Guadalupe (4614); Esperanza (4666). Morelia: Campanario (7537, 7566); Cerro Azul (4530).

BRACHYTHECIUM ALBO-VIRIDE Besch. in Card. Rev. Bryol. 37: 69. 1910

Puebla: Boca del Monte (4674). Morelia: Campanario (7539).

I recognize in these specimens most of the characters attributed to *B. albo-viride:* the green color of the tufts, the laxly foliate branches, the lanceolate leaves strongly excavate at the base, long-acuminate, with a costa reaching to two-thirds and even three-fourths of the leaf; but I have not noticed that the stems are more slender and the branches more tenuous than in *B. albo-flavens.*

BRACHYTHECIUM LAXIRETICULATUM Card. Rev. Bryol. 37: 67. 1910

Valle de México: Desierto (*Bro. Amable* 1412).

BRACHYTHECIUM ACUTUM (Mitt.) Sull. Icon. Musc. Suppl. 99. *pl. 75.* 1874

Pueblo: Río San Francisco (5001 p. p.); sterile plant.

BRACHYTHECIUM SALEBROSUM (Hoffm.) Bry. Eur.

Puebla: Esperanza (4515, 4664, 4690).

BRACHYTHECIUM SALEBROSUM var. **POLYOICUM** Thér., var. nov.

Synoicous and unisexual flowers, male and female, on the same stem.

Puebla: Hacienda Batán (4937).

I combine this curious form with *B. salebrosum* on account of its characters as a whole. It is much nearer to it than to the known synoicous or polyoicous species *B. acutum, B. conostomum,* and *B. Mildeanum.*

BRACHYTHECIUM INTEGRIFOLIUM Thér., sp. nov.

Distr. Federal: Tlalpam (9499).

Sterile. Caulis repens, radiculosus, sat regulariter pinnatus, ramis inaequalibus, 3-4 mm., usque 10 mm. longis, patulis, attenuatis. Folia caulina sicca et humida erecto-appressa, e basi decurrente latissime cordato-ovalia in acumen longiusculum, patulum, acutum sat subito constricta, haud plicata, marginibus planis, integerrimis, 1.6-1.7 mm. longa, 0.8-0.9 mm. lata, costa ad $\frac{2}{3}$ evanida; rete pellucido, chlorophylloso, cellulis linearibus, parietibus tenuibus, $35\text{-}45\,\mu \times 5\text{-}6\,\mu$, cellulis basilaribus et alaribus laxioribus, breviter rectangularibus. Folia ramea minora, secunda, subfalcata, 1 mm. × 0.5 mm. Caetera ignota.

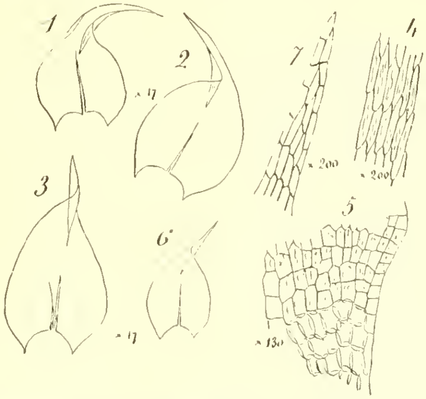

FIG. 19.—*Brachythecium integrifolium* Thér. 1, 2, 3, stem leaves; 4, median cells; 5, basal and alar cells; 6, branch leaves; 7, acumen.

In size and habit like *B. hylocomioides* Card., but that species has denticulate non-falciform leaves and looser areolation. It suggests also *B. reflexum* Starke, but is easily distinguished by its entire leaves, with the nerve reaching only to the base of the acumen.

BRACHYTHECIUM CORBIEREI Card. Rev. Bryol. 38: 42. 1911

Valle de México (*Bro. Amable*): Desierto (1222 p. p., 1441); Río Frío (1692, 1703, 1706); Contadero (1307).

The last number (1307) represents a form with long, flexuose stems, irregularly ramose, with long, slender, almost flagelliform branches.

BRACHYTHECIUM PLUMOSUM (Sw.) Bry. Eur.

Puebla: Huejotzingo (4856). Morelia: Loma Santa María (4896). Valle de México (*Bro. Amable*): Desierto (1245, 1616, 1640); Contreras (1668). Hidalgo: El Chico (1586).

Of the material listed no. 1668 may be classified as var. *sublaevipes* Card.,[1] because the pedicel is scarcely papillose at the top; under a strong magnification one can see only separated, depressed, low papillae. In this specimen a single costa is the exception; most of the leaves have a double nerve of very variable length, sometimes very short. The Bryologia Europaea indicates that this case is not of rare occurrence.

BRACHYTHECIUM HASTIFOLIUM Card. Rev. Bryol. 37: 69. 1910

This species is not mentioned by Brotherus in his treatment of *Brachythecium* in the second edition of Die natürlichen Pflanzenfamilien, but I am inclined to think that it is the one cited in the genus *Heterophyllum* under the combination *H. hastifolium* (Card.) Fleisch.

Cardot says, "Costa ad $\frac{2}{3}$ evanida." How can this character agree with the genus *Heterophyllum,* which has "Rippe sehr kurz oder fehlend?" How could a moss which a bryologist of the standing of Cardot affirms to belong to the genus *Brachythecium* have at the same time the characters of the family Brachytheciaceae and those common to the genus *Heterophyllum* of the family Sematophyllaceae?

I have endeavored to solve this puzzle. An examination of no. 10474 of Pringle's exsiccata brought the answer to me. The specimen in my collection labelled *Brachythecium hastifolium* Card. is not this species, but *Heterophyllum affine* (Hook.) Fleisch. Now if one turns to the original description, where Cardot discusses Pringle's no. 10474, which he considers as a form of his *Brachythecium hastifolium,* the inference is clear that Pringle distributed under this same number (10474) two different species—the form just mentioned and *Heterophyllum affine.* I take no pride in this discovery, but I cannot understand why such an expert and conscientious bryologist as Fleischer failed to find the clue and thus allowed himself to be misled into giving full confidence to a specimen which did not agree with the original description and was distributed by a collector who was not a bryologist.

My conclusions are: First, that *Heterophyllum hastifolium* (Card.) Fleisch. is a myth, and that this combination must disappear from nomenclature; secondly, that the binomial, *Brachythecium hastifolium* Card., which applies to one of the best characterized species of the subgenus *Salebrosium,* ought to take again its place.

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[1] Rev. Bryol. 37: 70. 1910.

RHYNCHOSTEGIUM SAINT-PIERREI Thér., sp. nov.

Valle de México: Contadero, on bark; leg. *Marius Saint-Pierre* (*Bro. Amable* 1298).

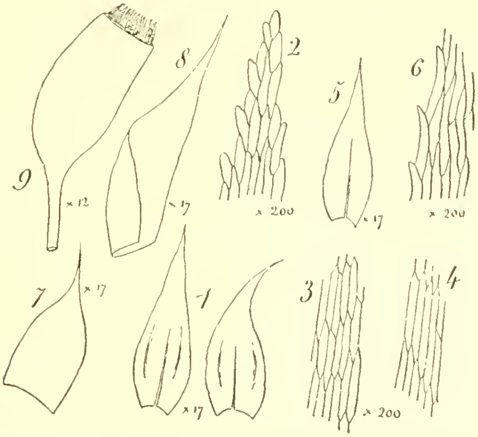

FIG. 20.—*Rhynchostegium Saint-Pierrei* Thér. 1, stem leaves; 2, apical cells; 3, upper cells; 4, median cells; 5, branch leaf; 6, marginal cells; 7, 8, perichaetial leaves; 9, moist capsule.

Rh. leptomerocarpo (C. M.) sat simile, sed differt colore smaragdo-viridi, caulibus gracilibus, laxe foliosis, foliis siccis valde patulis, duplo angustioribus (1.7 mm. × 0.5 mm.), tenuiter acuminatis, paulum decurrentibus, rete densiore (cellulis mediis 90-120 $\mu \times 6 \mu$), foliis perichaetialibus duplo majoribus, pedicellis longioribus (2 cm. longis).

RHYNCHOSTEGIUM HUITOMALCONUM (C. M.) Besch. Prodr. Bryol. Mex. 107. 1871

Hypnum huitomalconum C. M. Syn. 2: 248. 1850.

Morelia: Cascade de Coincho (4712a); Andameo (4827). Valle de México: Tlalpam (*Bro. Amable*).

RHYNCHOSTEGIUM LEPTOMEROCARPUM (C. M.) Besch. Prodr. Bryol. Mex. 107. 1871

Hypnum leptomerocarpum C. M. Syn. 2: 354. 1850.

Puebla: Hacienda Alamos (586). Morelia: Loma Santa María (4868, 4894, 5062). Distr. Federal: Tlalpam (9430a); Cuajimalpa (9487, 9489). Valle de México (*Bro. Amable*): Santa Rosa (1515); Contadero (1315).

RHYNCHOSTEGIELLA ARSENEI Thér., sp. nov.

Puebla: Hacienda Santa Bárbara, on sandy ground (739).

Sterile. Caespites lutescenti-virides, nitidi. Caulis repens, gracilis, laxe foliosus, ramosus, parce radiculosus, paraphyllis raris; ramis erectis, brevibus, 2-3 mm. longis, sat confertis, sat dense foliosis. Folia caulina et ramea sicca erecto-patula, humida patentia, anguste lanceolata-acuminata, acuta, decurrentia, marginibus planis, toto ambitu minute denticulatis, 0.6-0.7 mm. × 0.2 mm.; costa basi 30 μ percurrente; rete opaco, cellulis linearibus, 36-40 μ × 6 μ, basilaribus sat distinctis, marginalibus subquadratis (2-3 ser.), subhyalinis.

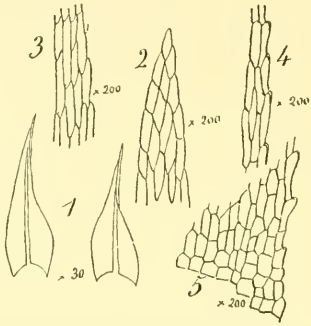

FIG. 21.—*Rhynchostegiella Arsenei* Thér. 1, stem leaves; 2, apical cells; 3, median cells; 4, marginal cells; 5, basal cells.

This species can be compared only with *R. Jacquini* (Garov.) Limpr. and *R. Teesdalii* (Sm.) Limpr. It is distinct from both by its leaves denticulate all around and from the first species also by its larger branch leaves, differentiated basal areolation, and more densely foliate branches; from the second species by its acute, decurrent leaves.

EURHYNCHIUM SUBSTRIATUM Thér., sp. nov.

Valle de México: Llano Grande, alt. 3,700 meters, on rocks (*Bro. Amable* 1735).

E. striato (Schreb.) simillimum differt: statura graciliore, ramis brevioribus, foliis minus profunde sulcatis, caulinis angustius decurrentibus, rete basilari praecipue ad angulos densiore, foliis rameis margine dentibus brevioribus.

I segregate this plant from *E. striatum,* because, in addition to the characters enumerated above, the European species is absolutely unknown throughout the American continent and it is therefore hardly possible to consider the moss from Llano Grande as a local form.

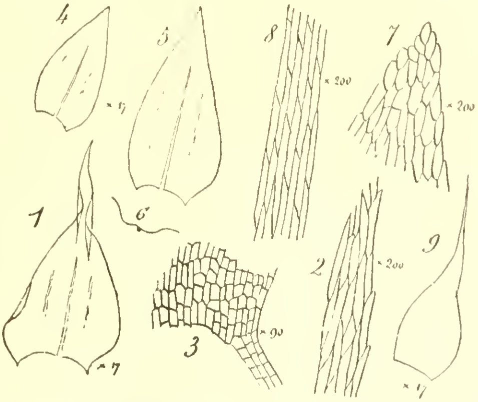

FIG. 22.—*Eurhynchium substriatum* Thér. 1, stem leaf; 2, median and marginal cells; 3, basal cells; 4, 5, branch leaves; 6, cross-section of branch leaf; 7, apical cells; 8, median cells; 9, perichaetial leaf.

EURHYNCHIUM STOKESII (Turn.) Bry. Eur.

Puebla: Boca del Monte (4738); a form with stems less densely branched, elongate, and laxly foliate. Valle de México: Contreras (*Bro. Amable* 1518).

ENTODONTACEAE (continued)

PTERIGYNANDRUM FILIFORME (Timm.) Hedw. var. MEXICANUM Thér., var. nov.

Folia valde secunda, latiora (0.5 mm.), cellulis apice parum prominulis, costa gemella usque ad $\frac{1}{3}$ folii producta.

Valle de México: Santa Rosa (*Bro. Amable* 1503). Hidalgo: Mineral del Chico (*Orcutt* 6649).

The typical form of this species has not yet been found in Mexico.

ROZEA STRICTA Besch. Prodr. Bryol. Mex. 100. 1871

Valle de México (*Bro. Amable*): Desierto (1418, 1425, 1444); Llano Grande (1731).

ENTODON JAMESONII (Tayl.) Mitt. Musc. Austr. Amer. 525. 1869

Morelia: Cerro Azul (4779). Valle de México (*Bro. Amable*): Desierto (1245); Contadero (1311).

ENTODON ABBREVIATUS (Bry. Eur.) Jaeg.

Valle de México (*Bro. Amable*): Contadero (1302, 1305); San Rafael (1280).

The pedicel is very variable in length. In the same tuft I have seen pedicels 3 mm. long and others up to 9 mm. long.

ENTODON ABBREVIATUS (Bry. Eur.) Jaeg. var. TURGESCENS Thér., var. nov.

Caules et rami turgidi, folia 2.2 mm. × 1.3 mm., valde concava, cochleariformia, rete laxiore, cellulis mediis 70-90 μ × 9 μ.

Valle de México: Contadero (*Bro. Amable* 1362).

The facies of this variety is very different from the usual forms of *E. abbreviatus*. In its leaves and their areolation it comes close to Pringle's no. 15226, identified by Cardot as *E. brevipes* (Schimp.).

SEMATOPHYLLACEAE

RHAPHIDORRHYNCHIUM OBLIQUEROSTRATUM (Mitt.) Broth. in E. & P. Nat. Pflanzenfam. ed. 2, 11: 428. 1925

Sematophyllum obliquerostratum Mitt. Musc. Austr. Amer. 472. 1869.

Morelia: Campanario (7926, 7941).

RHAPHIDORRHYNCHIUM DECUMBENS (Wils.) Broth. in E. & P. Nat. Pflanzenfam. ed. 2, 11: 427. 1925

Hypnum decumbens Wils. (Ms.); *Sematophyllum decumbens* Mitt. Musc. Austr. Amer. 488. 1869.

Valle de México: Desierto (*Bro. Amable* 1439).

SEMATOPHYLLUM CAESPITOSUM (Sw.) Mitt. Musc. Austr. Amer. 479. 1869

Morelia: (7893, 7909, 7912); Cerro Azul (4784); Campanario (7515, 7516, 7520, 7537, 7550, 7552, 7557, 7935).

SEMATOPHYLLUM CAESPITOSUM (Sw.) Mitt. var. LATICUSPIDATUM (Card.) Thér., comb. nov.

Rhaphidostegium caespitosum var. *laticuspidatum* Card. Rev. Bryol. 40: 39. 1913.

Morelia: (7890, 7916); Campanario (7642).

SEMATOPHYLLUM HAMPEI (Besch.) Broth. in E. & P. Nat. Pflanzenfam. ed. 2, 11: 433. 1925

Rhynchostegium Hampei Besch. Prodr. Bryol. Mex. 105. 1871.

Morelia: Campanario (7518).

HYPNACEAE (continued)

STEREODON FALCATUS (Schimp.) Fleisch. in E. & P. Nat. Pflanzenfam. ed. 2, 11: 452. 1925

Stereodon subfalcatus (Schimp.) Fleisch. in E. & P. Nat. Pflanzenfam. ed. 2, 11: 452. 1925.

Further observations have convinced me that in these two species of Schimper's there is only a single specific type.[1]

New localities: Valle de México (*Bro. Amable*): Desierto (1219, 1221); Acopilco (1201); Salazar (1236).

HYPNUM AMABILE (Mitt.) Broth. in E. & P. Nat. Pflanzenfam. ed. 2, 11: 454. 1925

Ectropothecium amabile Mitt. Musc. Austr. Amer. 513. 1869.

Puebla: (4945, 4947, 4948, 4949, 4951, 4953, 4956, 4959). Distr. Federal: San Angel (9479).

ISOPTERYGIUM CYLINDRICARPUM Card. Rev. Bryol. 37: 56. 1910

Valle de México: Desierto (*Bro. Amable* 1247, 1623).

TAXIPHYLLUM PLANISSIMUM (Mitt.) Broth. in E. & P. Nat. Pflanzenfam. ed. 2, 11: 462. 1925

Isopterygium planissimum Mitt. Musc. Austr. Amer. 498. 1869.

Puebla: Hacienda Alamos (584). Distr. Federal: Tlalpam (10999).

ISOPTERYGIUM PLANISSIMUM Mitt. var. LAXIRETE Thér., var. nov.

A forma typica differt: rete laxiore, cellulis diam. 8-9 μ.

Morelia: Loma Santa María (4877).

VESICULARIA VESICULARIS (Schwaegr.) Broth. in E. & P. Nat. Pflanzenfam. 1³: 1094. 1908

Hypnum vesiculare Schwaegr. Suppl. 2²: *pl. 199.* 1827.

Nuevo León: Monterrey (*Bro. Abbon* 10969).

MICROTHAMNIUM THELISTEGUM (C. M.) Mitt. Musc. Austr. Amer. 504. 1869

Hypnum thelistegum C. M. Syn. 2: 269. 1850.

Morelia: Campanario (7924).

Sterile, the determination uncertain. The cauline leaves are sharply dentate and the branch leaves secund.

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[1] See, Smithsonian Misc. Coll. 78²: 28. 1926.

MICROTHAMNIUM SUBTHELISTEGUM (Card.) Broth. in E. & P. Nat. Pflanzenfam. ed. 2, 11: 471. 1925

Mittenothamnium subthelistegum Card. Rev. Bryol. 37: 55. 1910.

Morelia: Jesús del Monte (7608a).

HYLOCOMIACEAE

LEPTOHYMENIUM EHRENBERGIANUM (C. M.) Fleisch. in sched.

Hypnum Ehrenbergianum C. M. Bot. Zeit. 14: 408. 1856.
Hylocomium Ehrenbergianum Besch. Prodr. Bryol. Mex. 111. 1871.

Vera Cruz: Jalapa (7998).

POLYTRICHACEAE (continued)

POGONATUM BESCHERELLEI Hampe in Besch. Prodr. Bryol. Mex. 63. 1871

Valle de México: Salazar, alt. 3,100 meters (*Bro. Amable* 1715).

POLYTRICHUM ALPINIFORME Card. Rev. Bryol. 37: 6. 1910

Valle de México (*Bro. Amable*): Contreras (1667); Xoquiapán (1750).

The last plant, which is in fruit, affords an opportunity to complete the description:

Folia perichaetialia numerosa (12-15), remota, longe et late vaginantia (vagina 4-5 mm. longa, 0.2 mm. lata), in acumen angustum abrupte contracta, humida patulo-squarrosa. Pedicellus 20 mm. altus; capsula minuta, oblonga, laevis; calyptra angusta, elongata, 6-7 mm., parce pilosa. Caetera ignota (capsulae immaturae).

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 85, NUMBER 4 (ADDENDUM)

INDEX TO PAPERS BY I. THÉRIOT ON MEXICAN MOSSES COLLECTED BY BROTHER ARSÈNE BROUARD PUBLISHED BY THE SMITHSONIAN INSTITUTION[1]

INDEX

[Synonyms in italic. Page numbers of principal entries in heavy-faced type.]

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[1] Part I, Smithsonian Misc. Coll., vol. 78, no. 2, June 15, 1926.
Part II, idem, vol. 81, no. 1, August 15, 1928.
Part III, idem, vol. 85, no. 4, August 25, 1931.

ERRATUM.

Part III, page 43 (Smiths. Misc. Coll. 85, no. 4)—For **Isopterygium planissimum** Mitt. var. **laxirete** Thér., var. nov., substitute **Taxiphyllum planissimum** (Mitt.) Broth. var. **laxirete** Thér., var. nov.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 85, NUMBER 5

INFRA-RED ABSORPTION BANDS OF HYDROGEN CYANIDE IN GAS AND LIQUID

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INTRODUCTION

The absorption spectrum of hydrogen cyanide in gas phase in the region from 3μ to 15μ was investigated originally by W. Burmeister,[1] and more recently at higher resolution by E. F. Barker.[2] These investigations have shown the presence of a strong doublet at 14μ, weaker bands at 7μ, 4.7μ, and 3.6μ, with another very strong band at 3.04μ. Whereas the frequency relations supported the view earlier held that the 7μ, 4.7μ, and 3.6μ bands were respectively second, third, and fourth harmonics of a fundamental at 14μ, the intensity of the 4.7μ band led Barker to question this interpretation and to suggest that very likely a new fundamental was present at approximately the same wave-length as the third harmonic. The 3.6μ band is thus more likely to be a combination of the new fundamental at 4.7μ, with the lower frequency vibration.

The band occurring at 3.04μ is recognized as another fundamental. The bands at 14μ and 7μ are clearly of the doublet character. Molecular moments of inertia are readily calculated from these data. From Burmeister's curves for the 14μ band, yielding an apparent separation of maxima of 37.5 cm.$^{-1}$, one calculates a moment of inertia of 33×10^{-40} g. cm.^{2} If, however, the relatively large slit-width at which this work was carried out is taken into account, estimates may be made as to the degree of overlapping, and more probable positions of the two components of the doublets may be plotted from the composite curve. On this basis a larger separation is obtained, of the order of 50 cm.$^{-1}$. The 7μ band was investigated by Barker at sufficiently high resolution so that no such correction needs to be made.

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[1] Verh. Deutsche Phys. Ges., vol. 15, p. 589, 1913.

[2] Phys. Rev., vol. 23, p. 200, 1924.

Because of some uncertainty as to the exact intensity values, however, the form of the curve introduces some uncertainty in the determination of the separation of the maxima. In view of this, and of the inadequate resolution of Burmeister's apparatus, Barker's calculation of 13.2×10^{-40} g. cm.^{2} for the moment of inertia, based on the separation of 58 cm.$^{-1}$, is perhaps in as good agreement as could be expected with the corrected value of Burmeister. As the band occurring at 4.7μ is certainly composite, no great significance can be attached to calculations of moments of inertia involving data on this band.

Recently, R. M. Badger and J. L. Binder[1] have carried out a photographic investigation of the absorption spectrum in the near infra-red of hydrogen cyanide vapor in a 280 cm. absorption cell. They have observed two bands in this region occurring at $\lambda 7912$ and $\lambda 8563$, respectively. In these bands they have been able to resolve the fine structure attributed to rotation in the molecules. On the basis of their measurements, they interpret each of the bands as composed of a P and R branch. From this rotational structure they are able to compute an accurate moment of inertia of 18.79×10^{-40} g. cm.^{2} This calculation is in a reasonable agreement with the values based on doublet separation for the 14μ and 7μ bands. The absence of a Q branch is in harmony with the observations of a clearly doublet character of both the latter bands. In regard to the apparent central maxima in the bands occurring at 4.7μ and 3.6μ the question naturally arises as to the possible presence of a Q branch. It should be borne in mind, however, that these may readily be explained as due to overlapping.

Assuming three fundamental frequencies corresponding to the bands at 14μ, 4.7μ, and 3.04μ, which have been designated respectively as δ, ν_2 and ν_1, Badger and Binder have interpreted the near infra-red bands as $3\nu_1 + \nu_2$ for the band at $\lambda 8563$ and as $4\nu_1$ for the band at $\lambda 7912$. Because of the absence of a Q branch, they have assumed a linear arrangement of atoms, and on the basis of three fundamental frequencies, offered an interpretation of the three fundamental modes of vibration corresponding to these fundamental frequencies. From an analysis of probable atomic distances of separation, they have come to the conclusion that the molecule must be hydrogen cyanide rather than hydrogen isonitrile (HNC).

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[1] Phys. Rev., vol. 37, p. 800, 1931.

EXPERIMENTAL RESULTS

The results to be presented here were obtained with an automatic recording apparatus yielding high resolution and possessing certain novel features. An earlier self-recording instrument of high resolution was set up at the University of California by F. S. Brackett, yielding on effective slit-width of 10 Å. A similar instrument, but one with considerably greater aperture, was constructed by E. D. McAlister at the University of Oregon, yielding an effective slit-width of 6 Å. The instrument used in the present investigation at the Fixed Nitrogen Laboratory is of approximately the same aperture, though of considerably greater focal length, and yields the same effective resolution.

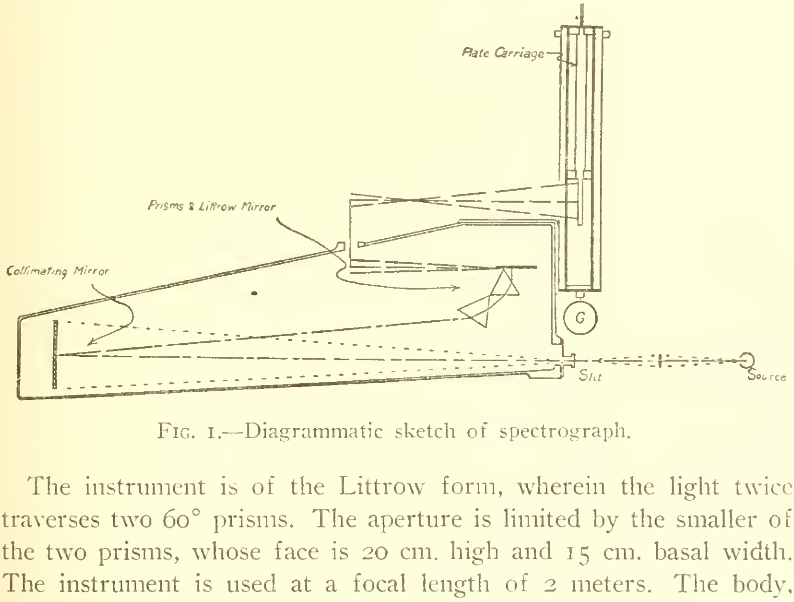

Fig. 1.—Diagrammatic sketch of spectrograph.

The instrument is of the Littrow form, wherein the light twice traverses two 60° prisms. The aperture is limited by the smaller of the two prisms, whose face is 20 cm. high and 15 cm. basal width. The instrument is used at a focal length of 2 meters. The body, a large casting, may be sufficiently evacuated to remove atmospheric absorption. Wave length variation is accomplished by rotation of the plane mirror, which is coupled with the motion of the photographic plate by a lever system. The use of a mechanical lever system with a variable pivot permits a wide range of variation of relative motion of the plate carriage to the angular rotation of the mirror, giving practically any desired spread of spectrum. This improved mechanical system, together with the use of photographic plates instead of film or paper, gives a much greater reproducibility of spectrum and accuracy of wave length than heretofore obtained. The calibration was effected with mercury arc spectra and water vapor bands, the observed wave lengths being consistent with grating measurements within ±2 Å.

The thermocouple used is a modification of the type of single junction vacuum thermocouple described by Brackett and McAlister.[1] The source of continuous radiation is a tungsten ribbon filament, using 16 amperes current at 6 volts and working at an approximate temperature of 2900° K.

INVESTIGATION OF LIQUID HYDROGEN CYANIDE

In the present investigation, the absorption spectrum of hydrogen cyanide in liquid phase has been studied with cell thicknesses of 1 mm., 1 cm., 5 cm., and 30 cm.

The liquid hydrogen cyanide was obtained through the courtesy of W. B. Wood of the Plant Quarantine and Control Administration of the Department of Agriculture. This product had quite a perceptible odor of hydrogen sulfide. The original sample containing about 1500 cc. was distilled over P_2O_5, primarily to remove any water, but a considerable quantity of sulfur was precipitated, as was expected from the presence of hydrogen sulfide. The second 500 cc. fraction was taken as an experimental sample. A drop of it did not affect lead acetate paper. This purification was made possible through the courtesy of Drs. G. E. Hilbert and L. B. Howard of the Fixed Nitrogen Research Laboratory.

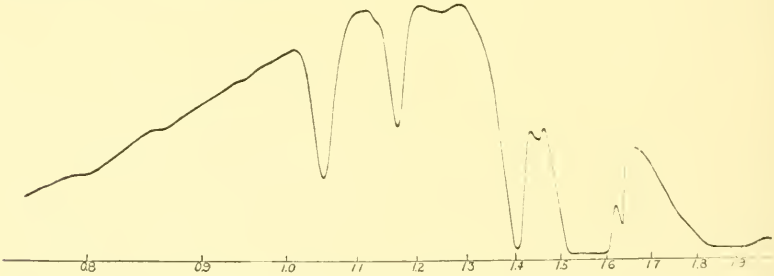

FIG. 2.—Energy transmission curve showing absorption spectrum of 5 cm. cell of liquid HCN at low dispersion. Slit width approx. 40 Å.

Figure 2 shows the absorption of a 5 cm. cell in the region from 7μ to 2μ. The steadiness of the thermocouple will be apparent from the smoothness of the record. This illustration shows the instrument set for a relatively narrow spread, covering the entire region, and gives a general idea of the relative intensities. Actual observations of wave

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[1] Rev. Sci. Instr., vol. 1, p. 181, 1930.

lengths, however, were made mostly on a much wider spread, including simply the region from 1μ to 2μ. A typical plate at this spread of the same cell length is shown in figure 3. Figure 4 shows an analysis of the bands in this region, the frequencies of the maxima being plotted against percentage absorption. Table 1 gives the summary of the data obtained. The values of the fundamentals in vapor are inserted for comparison since no liquid values have been obtained in that region. Intensity values, both as to percentage absorption and absorption coefficient are only approximate. Generally the estimated uncertainties in the frequency values indicated arise from the difficulty of setting upon broad absorption maxima like those shown in figure 3. Still less favorable are the conditions of the values for $4\nu_1$ and $3\nu_1+\nu_2$, which were obtained on a low spread plate such as that shown in figure 1. In other cases the larger uncertainties indicated arise from the proximity of strong absorption bands. It will be seen that the observed values of $\Delta\nu$ lie well within the probable values to be expected, taking into account the normal variation to be expected in the successive differences, together with the probable uncertainty of measurement. The agreement certainly excludes any uncertainty as to identification. Not only do the wave lengths lead definitely to

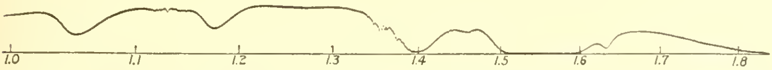

FIG. 3.—Energy transmission curve showing absorption spectrum of 5 cm. cell of liquid HCN at high dispersion. Slit width approx. 9Å.

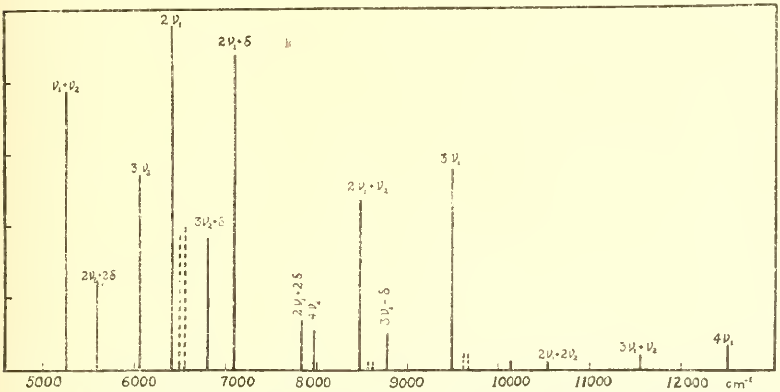

FIG. 4.—Diagrammatic representation of absorption maxima observed with assignments of designations. Broken lines show vapor absorption. Frequency is plotted against per cent absorption.

the identification indicated, but the approximate intensities are consistent with such an interpretation. Of the entire 15 bands observed, only one has not been identified. This is almost immeasurably weak, and occurs in a position slightly displaced from the frequency where we should expect $3\nu_1+\delta$. This excellent agreement throughout leaves little doubt as to the correctness of the choice of fundamentals proposed by Badger and Binder.

TABLE I.—*HCN Bands in Liquid*

Notation	Abs.	Abs. coeff.	λ	ν	Δν
	%	k	Å	cm.$^{-1}$	cm.$^{-1}$
$4\nu_1$	6.6	.014	8000	12500 ± 30	
					3000
$3\nu_1$	57.	.17	10527	9500 ± 10	
					3090
$2\nu_1$	96.0	.64	15600	6410 ± 10	
(ν_1) vapor				3290	
$2\nu_1+2\nu_2$	2.	.004	9500	10527 ± 20	
					2040
$2\nu_1+\nu_2$	47.	.13	11787	8487 ± 10	
					2077
$2\nu_1$				6410 ± 10	
$4\nu_2$	12.	.024	12540	7974 ± 10	
					1910
$3\nu_2$	(50)	..	16490	6064 ± 10	
$(2\nu_2)$					
(ν_2) vapor				2090	
$2\nu_1+2\delta$	14.	.029	12760	7837 ± 10	
					719
$2\nu_1+\delta$	88.	.42	14050	7118 ± 10	
					708
$2\nu_1$				6410 ± 10	
(δ) vapor				710	
$3\nu_1+\nu_2$	3.7	.008	8650	11561 ± 25	
					2061
$3\nu_1$				9500 ± 10	
					713
$3\nu_1-\delta$	10.	.017	11380	8787 ± 10	
$3\nu_2+\delta$	42.	.11	14690	6804 ± 10	
					740
$3\nu_2$				6064 ± 10	
$2\nu_2+2\delta$	(20)	..	17900	5587 ± 15	
$\nu_1+\nu_2$	78.	.30	19000	5263 ± 15	

INVESTIGATION OF VAPOR

The absorption spectrum has been obtained of saturated vapor at 22.5°C., with a 30 cm. length of cell. The three bands observed in the gas absorption, interpreted as $2\nu_1$, $3\nu_1$, and $2\nu_1+\nu_2$ all show clearly a doublet structure. In the stronger bands, $2\nu_1$ and $3\nu_1$ shown in figure 5, separations of maxima are obtained of 47 ± 2 cm.$^{-1}$ and 50 ± 2 cm.$^{-1}$, which yield moments of inertia $21\pm2\times10^{-40}$ g. cm.^{2}, and $18\pm2\times10^{-40}$ g. cm.^{2} respectively. This is consistent, within the order of the accuracy of the work, with the more accurate value obtained by Badger. The combination band is too weak to obtain separation values of significance. On the basis of this conclusive identification of fundamentals, the clearly doublet character of the gas absorption implying the absence of a *Q* branch, and the approximate values of moments of inertia, we had independently come to the same conclusions regarding the arrangement of atoms, the approximate separations, and the probable modes of vibration before the publication of the work of Badger and Binder.

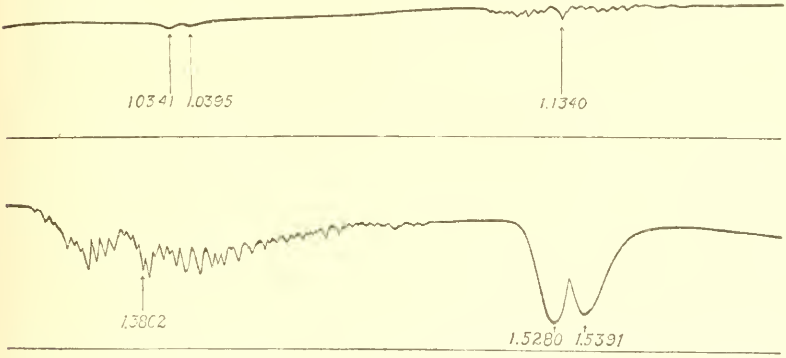

FIG. 5.—Energy curves showing absorption spectrum of 30 cm. Saturated HCN vapor. Slit width approx. 9Å.

The position of the $2\nu_1$ and $3\nu_1$ bands, however, is not consistent with the formula

$$\nu_n = 3333.7n - 43.7n^2$$

Assuming the formula

$$\nu = n\omega_0 - n^2\omega_0 x$$

our values indicate a variation in x. This is evident from table 2, where the values of $\Delta\nu_2$ or $2\omega_0 x$ have successive values 59, 107, and 133, indicating values of $\omega_0 x$ varying from 30 to 67, as against Badger's value of 43.7 based only upon ν_1 and $4\nu_1$. Third differences suggest that a constant value of $\omega_0 x$ may be approached equal to or slightly greater than 67. On the basis of this value we may compute a heat of dissociation corresponding to an absolute electron voltage of 5.5 volts. This is in much better agreement with the value computed from chemical data, 4.2 volts, than would be obtained from Badger's constant value of 43.7.

TABLE 2.—*HCN Bands in Vapor*

Notation	Abs. %	λ μ	ν cm.$^{-1}$	$\Delta\nu_d$ cm.$^{-1}$	I 10^{40}	ν(aver.) cm.$^{-1}$	$\Delta\nu$ cm.$^{-1}$	$\Delta\nu_2$ cm.$^{-1}$	ν_L cm.$^{-1}$	$\nu_V - \nu_L$ cm.$^{-1}$
$(4\nu_1)$						12636			12500 ± 30	136
							2991			
	6.6	1.0341	9670 ± 3							
$3\nu_1$				50 ± 2	18	9645		133	9500 ± 10	145
	6.5	1.0395	9620 ± 3							
							3124			
	80	1.5280	6544 ± 2							
$2\nu_1$				47 ± 2	21	6521		107	6410 ± 10	111
	75	1.5391	6497 ± 2							
							3231			
(ν_1)		3.04				3290		59		
							3290			
	2	1.1610	8613 ± 6							
$2\nu_1 + \nu_2$				44 ± 10		8591			8487 ± 10	104
	2	1.1670	8569 ± 6							
							2070			
$(2\nu_1)$						6521				
(ν_2)		4.7				2090				

The displacements to lower frequencies in passing from vapor to liquid show a marked increase for the higher harmonics, with the exception of the $4\nu_1$ value, for which it must be remembered that the liquid value is only approximate.

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MORPHOLOGY OF THE INSECT ABDOMEN

PART I. GENERAL STRUCTURE OF THE ABDOMEN AND ITS APPENDAGES

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CONTENTS

INTRODUCTION

The incision of the insect into head, thorax, and abdomen is in general more evident in the cervical region than at the thoracico-abdominal line; but anatomically the insect is more profoundly divided between the thorax and the abdomen than it is between the head and the thorax. The series of segmental appendages is continuous, and uniform except for minor adaptational modifications, from the head to the metathorax, inclusive; on the abdomen the appendages abruptly cease, or are greatly altered in form. The musculature of the abdomen, consequently, is sharply differentiated from that of the thorax. Even the respiratory mechanism attests that the thoracico-abdominal boundary marks some deep-seated change in the body organization, since the closing apparatus of the spiracles is almost invariably different in one way or another before and behind the intersegmental fold separating the thorax from the abdomen. The definitive head contains three segments that have been, comparatively speaking, but recently transferred from the body to the cephalic region; the waist line of the insect has long been definitely established, and only in a single order has an abdominal segment been given over to the thorax. The abdomen is distinctly the visceral region of the body, and its major active functions in adult insects are those of respiration, copulation, and oviposition.

Yet, notwithstanding the functional and structural differences that have come to separate the insect body into cephalothoracic and abdominal regions, we can not avoid the assumption that modern insects are derived from polypod ancestors, and that the abdominal segments at some time in the past history of the Hexapoda had the same essential structure as that of the primitive thoracic and gnathal segments. In studying the morphology of the abdomen and its appendicular organs, therefore, we must attempt to find in the modern structure a basic plan of organization the same as that we are led to believe exists in the cephalic and thoracic regions from a study of the segments, the appendages, and the musculature in the preabdominal parts of the body. Considering, then, the nature of the task, it is not surprising that students of insect morphology find in the abdomen problems far more difficult of solution than are those encountered in the head or thorax, and that there are many fundamental problems in the abdomen which are still unsolved.

To the systematist in entomology the study of the abdomen, or particularly of the genital appendages, is becoming of ever increasing importance, and specialists are coming to feel acutely the need of a fundamental understanding of the organs that have been found in so many cases to give the best characters by which species may be distinguished. Unfortunately, however, no investigator has yet discovered a means for determining with certainty the homologies of the organs most useful for diagnostic purposes. In truth, we may say that the morphology of the insect abdomen is a field in which no angel yet has trod, and is, therefore, one in which the fool unhindered may achieve his destiny. However, it is reputed that there is some merit in knowing oneself to be a fool, and, if it is the wisdom of the wise to enter only where the foolish have sprung the trap, the fool at least has a mission to perform. Hence, the writer offers the generalizations contained in this and a second paper to follow, not with the conviction that they will prove infallible, but in the hope that others will try to disprove them—and thereby establish their value.

The principal conclusions derived from the study of the abdomen and its appendages to be given later in detail may be itemized in advance as follows:

1. The insect abdomen consists primarily of 12 segments, the first 11 of which are true somites, while the last is the periproct, or telson.

2. The twelfth segment is practically obliterated in all the true Insecta, except for possible remnants in larval Odonata.

3. The eleventh somite becomes the functional anal segment with the suppression of the twelfth segment. Its tergum forms the epiproct. The venter of the eleventh segment is distinct in some Thysanura, but it is usually reduced or obliterated, except for two terminal lobes, which are the paraprocts. The appendages of the eleventh segment are the cerci.

4. The tenth segment is usually distinct in generalized insects, but it is often combined with the eleventh to form a composite terminal segment. The embryonic appendages of the tenth segment are suppressed in postembryonic stages of the more generalized insects; they form the postpedes of holometabolous larvae, and perhaps the appendicular processes of the proctiger, or tenth segment, of some adult Holometabola.

5. The eighth and ninth somites are the genital segments, which bear the gonopods. The median gonopore of the female is located typically behind the eighth sternum, that of the male behind the ninth. Deviations from these positions are secondary; but the opening of the paired oviducts of Ephemerida between the seventh and eighth abdominal sterna probably represents a primitive condition, exhibited also by the embryos of certain insects (see Heymons, 1892, and Wheeler, 1893).

6. The abdominal appendages of adult and larval insects are serially homologous with the legs and mouth parts. Each consists of a *basis*, and of one or two movable appendicular processes. The basis appears to comprise the coxal and subcoxal regions of a typical appendage, the two parts being either distinct or united. The coxal part often

bears an eversible or retractile sac having various functions, represented by the vesiculae of Thysanura, the gill-bearing lobes of certain neuropterous larvae, and the plantar lobes of caterpillars and sawfly larvae. The basis of an abdominal limb usually takes the form of a lobe or plate of the body wall, and in the pregenital segments the limb bases are generally united with the sterna in adult insects. The appendicular process of the basis more commonly present is the *stylus* of the lower insects, or its derivatives, including the clasper-like organs borne by the male gonopods of the higher insects. The other limb process is the *gonapophysis,* which occurs only on the gonopods. Both the styli and the gonapophyses may be movable by muscles arising within the supporting basal lobes or plates, or on segmental areas derived from the latter.

7. No positive evidence can be adduced from the known facts of anatomy or embryology to establish the homology of either the stylus or the gonapophysis. Many structural interrelations, however, suggest that the stylus is the telopodite of the appendage, and that the gonapophysis is an endite process of the basis.

8. The genital appendages, or *gonopods,* have the same essential structure as the appendages of the pregenital segments. Their distinguishing feature is the presence of the gonapophyses arising mesally from the bases. In the female, the gonapophyses of the two pairs of gonopods form the first and second pairs of *valvulae* of the ovipositor; in the male the gonapophyses of the ninth segment become the *parameres.* The styli of the gonopods are usually suppressed in the female of pterygote insects; those of the ninth segment of the male form the movable claspers, or *harpes,* of the copulatory apparatus in the Endopterygota.

9. The bases of the gonopods in adult female insects become plates supporting the first and second valvulae; those of the second genital segment may form a third pair of valvulae. In the male the bases of the single pair of gonopods often form distinct pleural plates of the ninth segmental wall between the tergum and the sternum, or they may fuse with either the tergum or the sternum, or with both; again they may unite with each other to form a plate either coalesced with the sternum or free and independently movable behind the latter.

10. The parameres of the male are associated with the median *penis* in the lower insects, generally uniting with the latter except in Thysanura; but the penis may be suppressed, and the parameres then unite with each other and inclose the terminal part of the ejaculatory duct to form the more complex copulatory organ known as the *aedeagus.* The parameres are to be identified throughout the

orders by the muscles inserted on them, which take their origins in the supporting basal plates.

11. The styli of the male gonopods become the movable claspers known as the *harpes* in the copulatory apparatus of holometabolous insects. They are to be identified by their muscles which arise in the supporting basal plates. The harpes may be divided each into a pair of movable claspers.

12. Numerous accessory appendicular lobes and processes may be developed on all parts of the male genital segment and on segments associated with it. These organs are secondary and are not necessarily homologous in the several orders; they are often flexible at their bases, but are to be distinguished from the true harpes and from the parameres, with which they are associated, by their lack of muscles.

13. The postpedes, present in holometabolous larvae of several orders, are the pygopods, or appendages of the tenth somite. The postpedes are probably transformed into the appendicular processes of adult males known as *socii*, found in adult Trichoptera and Lepidoptera, or into the cercus-like appendages of adult chalastogastrous Hymenoptera.

14. The cerci are the uropods, or the appendages of the eleventh somite. Typically each is situated in a membranous area laterad of the base of the epiproct, and above the paraproct. Muscles that move the cercus arise on the tenth tergum, or also on the epiproct, but these muscles are not necessarily primitive muscles of the cercal appendages. There is no intrinsic evidence that the cerci have any genetic relation with the paraprocts. It is doubtful if true cerci occur in any holometabolous insects, except possibly in females of Mecoptera.

It will be evident from statements given above, and more flagrantly apparent in discussion to follow, that the writer still gives much importance to the value of muscles as determinants of skeletal homologies—and this in the face of the edict against such practices recently put forth by H. J. Hansen (1930). However, there surely can be no question that in studying the insect skeleton we are dealing with the passive elements of mechanisms, in which the active parts are the muscles. The principal sclerotic areas of the body segments, and of the limb segments, are always directly or indirectly associated with muscle attachments or with mechanical strains resulting from muscle actions, and there is every reason for believing that sclerites have been correlated with muscles in their evolution, if not necessarily in their origin. It is, of course, true that, just as some sclerites are secondary productions, so undoubtedly are some muscles. We must admit that all kinds of deviations from a rule are possible; but a few exceptions do not discredit evidence supported by a long series of uniform interrelations between muscles and skeletal parts. However, a mere discussion of the matter is useless, and in a final analysis the identities of muscles must be established by a study of the muscle innervation. But, in the meantime, practical results may serve as a basis of judgment. The results of the studies to be given in the following pages will appear principally in Part II of this paper, which will attempt to analyze the organs of oviposition, and especially the male organs of copulation, according to the light thrown on the homologies of their parts by an examination of their musculature. The muscles furnish a means as yet but little used for identifying corresponding structures in the male genital apparatus of the various orders, and it will be found that they at least give something definite as a working basis in a comparative study of the genitalia.

For most of the identified material on which the present paper is based the writer is indebted to specialists in the United States National Museum, including the entomologists of the Bureau of Entomology, Department of Agriculture, and Dr. Waldo L. Schmitt and his associates, of the Museum's Division of Marine Invertebrates. Specimens of *Heterojapyx* and *Nesomachilis,* however, were obtained through the interest of Dr. R. J. Tillyard of Australia. Furthermore, much valuable criticism and information has been contributed by Dr. A. G. Böving, Mr. Carl Heinrich, Dr. H. E. Ewing, and other Museum entomologists of the Bureau of Entomology.

I. THE ABDOMINAL SCLEROTIZATION

For purposes of morphological description it is necessary to distinguish *regions* of the body wall from the *sclerites* that may partly or entirely occupy the regional areas. Considering the body as a whole, there are two principal surface regions, one including the back and sides above the limb bases, the other the under surface between the limb bases. The first is the *dorsum* (fig. 1 A, *D*) ; the second is the *venter* (*V*). Then, in a metameric animal, each somite is likewise divided into a *segmental dorsum* and a *segmental venter.* Separating the dorsum and venter of each segment are the latero-ventral limb bases (*LB, LB*). The regions of the limb bases may be termed the *pleural areas* of the segments. The free distal part of any limb, movable in a vertical plane on the basis, is the *telopodite* (*Tlpd*).

It is now well understood that the hardened areas, or sclerites, of the body wall of insects, as well as of other arthropods, are not " chitinized " or " strongly chitinized " regions, but that they are areas of the cuticula in which other substances than chitin predominate. It has been shown by Campbell (1929), for example, that the exocuticula of *Periplaneta* contains only about 22 per cent of chitin, while the soft endocuticula contains about 60 per cent; and according to Kunike (1926) the wing covers of a May beetle contain by weight 75 per cent of nonchitinous substances, and those of a grasshopper as much as 80 per cent. The writer, therefore, follows the suggestions of Ferris and Chamberlin (1928) in designating the sclerites as areas of *sclerotization* rather than of "chitinization."

Sclerotization of the body wall usually produces definite plates in the several segmental regions. According to the scheme of nomenclature adopted in this paper, a major segmental plate of the dorsum is a *tergum* (fig. 1 B, *T*), a corresponding plate of the venter is a *sternum* (*Stn*), and a single plate or group of plates in the pleural region is a *pleuron* (*Pl*). Subdivisions or component elements of these principal segmental plates then become *tergites, sternites,* and *pleurites,* respectively, since the suffix *ite* grammatically can mean only "a part of" some larger unit designated by the stem of the word to which it is appended.

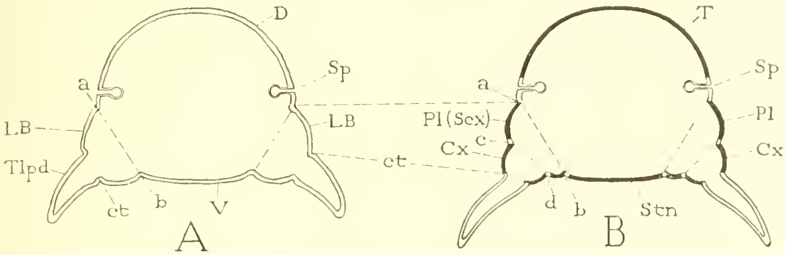

FIG. 1.—Diagrams illustrating the theoretical primitive structure of the appendages and their relation to the body wall.

A, cross section of a segment, showing the basis of each appendage (*LB*) movable antero-posteriorly on the body segment by an axis (*a-b*) in a vertical plane, and the telopodite (*Tlpd*) movable dorso-ventrally at the coxo-trochanteral joint (*ct*).

B, the basis of each appendage subdivided into a subcoxa (*Scx*) and coxa (*Cx*) by a secondary joint with a vertical axis (*c-d*); the upper part of the subcoxa forming the "pleuron" of the body segment.

The plan for distinguishing and naming the segmental regions, the major sclerites, and the subdivisions of major sclerites given above is not generally followed; but the writer has not found any nomenclatural scheme for these parts that is consistently applied, or that adequately meets the situation. Some writers define the terms "terga" and "sterna" as the segmental dorsal and ventral *regions,* and then designate the principal plates of these regions the "tergites" and "sternites." This usage is without other objections than that it leaves us no specific names for the subdivisions or component minor sclerites of major areas of sclerotization. Writers that adopt it seldom follow it consistently. On the other hand, many entomologists find it convenient for descriptive purposes to distinguish the segmental plates of the abdomen from those of the thorax as "tergites" and "sternites." The use of these terms in this manner, however, is not only arbitrary, but it is ungrammatical, since it is clear that the terms ending in *ite* may be applied to metameric units of any particular group of somites *only* if the names "tergum" and "sternum" are defined as the entire dorsum and entire venter of this limited group of somites—a usage which no one pretends to adopt. In general, nomenclatural troubles arise not so much from a scarcity of suitable terms as from a lack of consistent application of words in common use. The writer, therefore, employs the terminology recommended above as the one most adaptable to the needs of anatomical description. And yet, it will be found that absolute consistency is not possible; the insects are sure to present some anatomical conditions that can not be made to fit with any nomenclatural scheme that can be devised. Consistency is said to be a jewel, but an excess of jewelry may become a burden.

Little is known concerning the nature of the sclerotic substances in the cuticula of insects, or of the procedure by which a specific area of the body wall becomes continuously sclerotized. We may believe, however, that minor sclerites may have been produced phylogenetically by the secondary subdivision of major sclerites, though in the ontogeny of the individual they may proceed from separate centers of sclerotization. On the other hand, it is unquestionably true that primarily distinct areas of sclerotization may unite, and give no trace of their independent origin in the development of the embryo or pupa. In the abdomen of most adult insects, for example, the pleural sclerotizations derived from the limb bases are fused with the primitive sterna, and each definitive "sternal" plate in such cases is a triple structure, though it may lose all trace of its composite origin.

The spiracles are important landmarks in the study of the abdominal segments. They never exceed eight pairs in number, and while one or more of the posterior pairs may be absent, the presence of a pair of spiracles is often better proof of the site of a primitive segment than is evidence derived from the sclerites. The primary position of the spiracles is a matter on which opinion differs. There can be no doubt that the spiracles are subject to migration, and that in certain insects they have undergone an extreme displacement; but in the more generalized segments of most insects the spiracles lie in the sides of the segments above the regions of the limb bases, and therefore in the lateral parts of the dorsum (figs. 1, 2 A, *Sp*). If the tergal sclerotization of a segment does not invade the spiracular areas, the spiracles commonly lie in membranous lower parts of the dorsum between the tergum and the limb bases (fig. 2 A), or between the tergum and the definitive sternum, which has absorbed the limb bases (B). The tergal plates of the abdomen, however, often extend so far downward on the sides of the dorsum as to include the spiracles in their lateral parts (C). In some cases the spiracles occur in independent lateral, or paratergal, sclerites of the dorsum (D). Finally, the definitive ventral sclerotization is sometimes produced upward on the sides of the abdominal segments, and the spiracles may then be included in the lateral parts of the sternal plates (E); but in such cases it is to be suspected that the apparently sternal areas containing

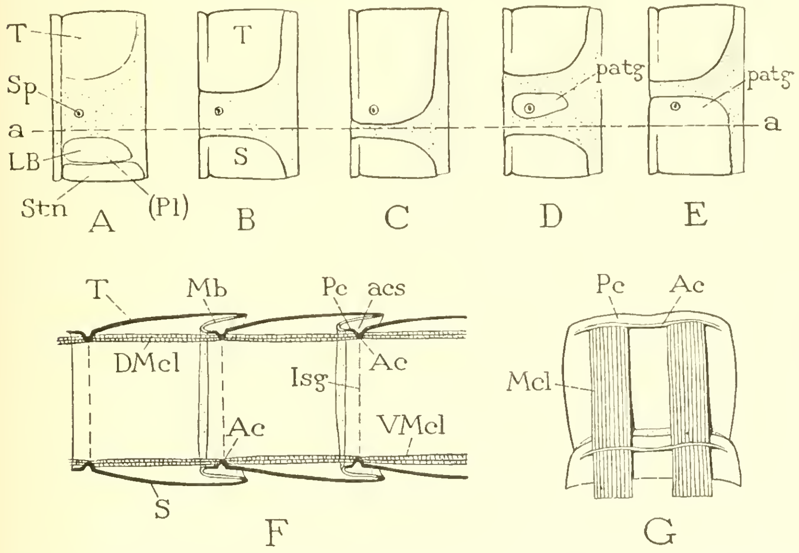

FIG. 2.—Diagrams showing the sclerotization and the retractor mechanism of the abdomen.

A-E, variations of sclerotization above and below the dorso-pleural line (*a-a*) separating the dorsum from the region of the limb bases (*LB*). F, the retractor mechanism as seen in vertical section, resulting from secondary segmentation produced by the usual type of sclerotization in adult insects. G, two consecutive segmental plates and their connecting muscles.

a-a, dorso-pleural fold; *Ac*, antecosta; *acs*, antecostal suture; *DMcl*, dorsal longitudinal muscles; *Isg*, primary intersegmental fold; *LB*, limb basis; *Mb*, secondary intersegmental membrane; *Mcl*, longitudinal muscle; *patg*, paratergite; *Pc*, precosta; *Pl*, pleural plate formed of the limb basis; *S*, definitive sternum including areas of limb bases; *Sp*, spiracle; *Stn*, primary sternal plate; *T*, tergum.

the spiracles are really paratergal sclerotizations that have secondarily united with the sterna.

In the larvae of holometabolous insects there is usually a more or less distinct groove extending along each side of the abdomen below the line of the spiracles (fig. 3 A, B, C, *a-a*), which is continued upon the thoracic region above the regions of the pleural, or subcoxal, sclerites, when the latter are present (B, C, Scx_3). This groove, therefore, evidently marks the division between the dorsal and pleural areas of the abdominal segments, and may be termed the *dorso-pleural groove*. Sclerites or lobes of the body wall lying immediately above this groove, then, belong to the dorsum, and may be called *paratergites* (fig. 3 B, *patg*), but not "pleurites" or "epipleurites." Latero-ventral plates or lobes lying below the tergo-pleural groove are properly termed *abdominal pleura* (B, *Scx*) if it is clear by their position or by the presence of appendicular organs upon them that they are the equivalents of the thoracic subcoxal pleura (Scx_3). It is convenient, however, to extend the term "pleurites" to any lateral sclerites situated ventrad of the dorso-pleural groove, or below the line of the spiracles, though such sclerites may be evidently secondary sclerotizations of this region (fig. 24 D, *1pl, 2pl,* etc.). But if there is

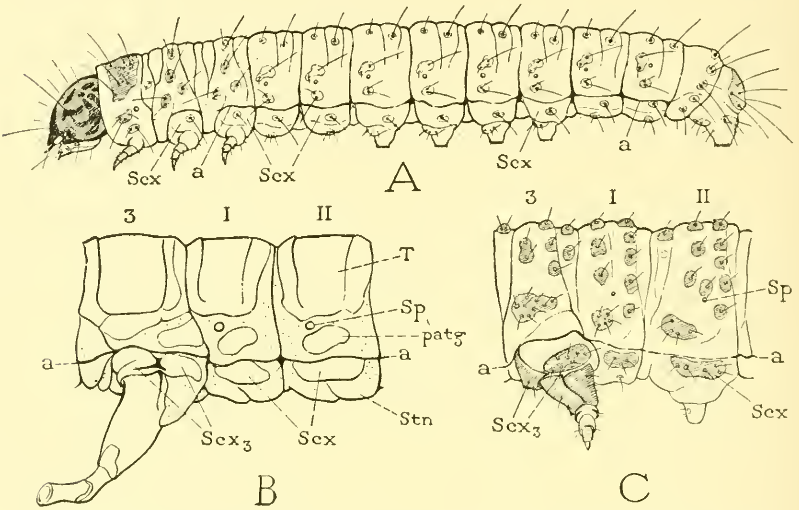

FIG. 3.—External structure of the abdomen in holometabolous larvae.

A, larva of *Carpocapsa pomonella*, showing the dorso-pleural fold (*a-a*) separating the dorsum from the subcoxal areas in both the thorax and the abdomen. B, larva of *Silpha obscura,* with series of paratergal sclerites (*patg*) above dorso-pleural fold, and series of pleural subcoxal sclerites (*Scx*) below fold. C, larva of *Pteronidea ribesii,* showing same structure as in B.

reason to believe that lateral sclerites are secondary subdivisions of earlier formed pleurosternal plates, they may be given the noncommittal name of *parasternites*. When true pleural plates or lobes of the abdomen are subdivided longitudinally, the upper and lower parts may appropriately be termed *epipleurites* and *hypopleurites*, respectively; but such a division seldom occurs in the abdominal pleura, and the term " epipleurite " is commonly misapplied by students of insect larvae to paratergal lobes, or sclerites of the dorsum.

The fact that the dorso-pleural groove forms a conspicuous line of infolding along the side of the abdomen in many insect larvae (fig. 3, *a-a*) is probably the reason for its frequently having been termed the " pleural suture." Hopkins (1909) thus named it in his study of the larva of *Dendroctonus,* and he designated the lateral lobes above the groove " epipleural " and those below it " hypopleural." The former he believed represented the epimeron of a thoracic pleuron, and the latter the episternum. No such homology as this, however, is possible, since the pleural suture of a thoracic segment is morphologically a vertical groove in the subcoxal sclerotization of the leg bases, taking only secondarily a horizontal position in the metathorax of adult beetles. The so-called " pleural suture " of the larval abdomen, moreover, as we have seen (fig. 3 A, B, C, *a-a*), extends into the thorax *above* the subcoxal sclerotizations (*Scx*), and thus throughout the body separates the dorsum from the true pleural region. Lateral lobes or sclerites of the abdomen lying above the dorso-pleural groove are, therefore, paratergal (fig. 3 B, *patg*), and not " epipleural." Only the so-called " hypopleural " areas lying ventrad of the dorso-pleural groove, that is, between it and the true sternal region, are properly pleural in the sense that they correspond with the subcoxal areas of the thorax (B, Scx_3) containing the sclerites of the thoracic pleura. The ventro-lateral lobes or plates of the larval abdomen may, then, be termed the *abdominal pleura* inasmuch as they appear to represent the subcoxae of the thorax. The abdominal pleura are never divided vertically in a way to suggest a true homology with the division of a thoracic pleuron into episternum and epimeron.

The relation of the muscles to the lateral lobes of the abdomen in the larvae of Coleoptera has been studied by Böving (1914) and by Craighead (1916). Böving, here following Hopkins (1909), calls the lateral groove of the abdomen the " pleural suture," but in all his subsequent work he terms it the " ventro-lateral suture." Craighead identifies the lateral areas of the abdomen with the corresponding areas of the thorax in cerambycid larvae, but since he regards the lateral groove of the abdomen as the "sternopleural suture," he takes the paratergal areas to be the abdominal pleura.

The abdominal terga.—The dorsal sclerotizations of the abdomen in general take the form of simple tergal plates characteristic of any region of the body in which a secondary segmentation has been established. Each tergum presents anteriorly a submarginal or often marginal internal ridge, the *antecosta* (fig. 2 F, G, *Ac*), on which the principal longitudinal muscles usually have their attachments. The *antecostal suture* (F, *acs*) is generally but faintly marked, and the precosta (F, G, *Pc*) varies from a scarcely perceptible marginal rim to a wide flange extending a considerable distance anterior to the muscle attachments (G, *Pc*). Apodemal processes are frequently extended from the anterior margins of the terga. From the antecosta of the first abdominal tergum there is commonly developed a pair of phragmatal lobes, and the precostal part of this tergum, together with the antecosta and the phragma, may be separated from the rest of the tergal plate to form a so-called postnotal or postscutellar plate of the metathorax. Otherwise the abdominal terga usually preserve their structural unity. The postcostal areas of the abdominal terga are seldom marked by sutural lines in adult or nymphal insects, and where such lines do occur they can not be supposed to have any homology with the sutures of a wing-bearing thoracic tergum, which adapt the latter to its function in the wing mechanism.

The dorsal regions of the abdominal segments of soft-bodied holometabolous larvae are usually divided transversely by impressed lines or by strongly pronounced topographical features. The dorsal areas thus formed are evidently mere adaptations to the contractile movements of the larvae and have no morphological significance. That the external body features of eruciform and vermiform larvae are secondary larval characters is evident from the structure of the head, which shows that such larvae are lateral derivatives from highly evolved adult forms representing the immediate ancestors of the order.

The abdominal sterna.—The definitive sternal plates of the abdomen are in general similar to the tergal plates, each being a continuously sclerotized area of the ventral integument of its segment, always including the primary intersegmental area anterior to the somite, corresponding with the intersternites, or spinisternites, of the thoracic region. The antecostae may be coincident with the anterior margins of the sternal plates, or set well back from the margins (fig. 2 F, *Ac*) with distinct precostal regions before them. In the Japygidae a short anterior division of each abdominal sternum is separated by a membranous fold from the rest of the plate, forming a distinct *sternal apotome* (fig. 24 D, *Apt*). Apodemal processes to give more effective action to protractor and dilator muscles are commonly developed from the anterior and lateral margins of the abdominal sterna.

Notwithstanding the apparent unity of structure in the abdominal sterna, it is probable, as already stated, that the ventral plates of the pregenital segments in most adult insects are triple structures, each including in its composition the area of the true sternal sclerotization of its segment, and the areas of the limb bases of the corresponding segmental appendages. A comparatively generalized condition is to be seen in larvae of Ephemerida, in which lateral lobes of the abdomen supporting the gills (fig. 34 A, B, *LB*), though forming a part of the ventral wall of each segment, are distinct from the areas of the primary sterna (*Stn*), and occupy the primitive position of limb bases on the sides of the segments between the tergal and sternal sclerotizations. A similar but less primitive condition is that occurring in some of the Thysanura, as in the Machilidae (fig. 4), where each of the definitive sterna in the pregenital region of the abdomen consists of a small, median, true sternal sclerite (*Stn*) and of two, large, lateral stylus-bearing plates (*LB, LB*) clearly representing the limb bases.

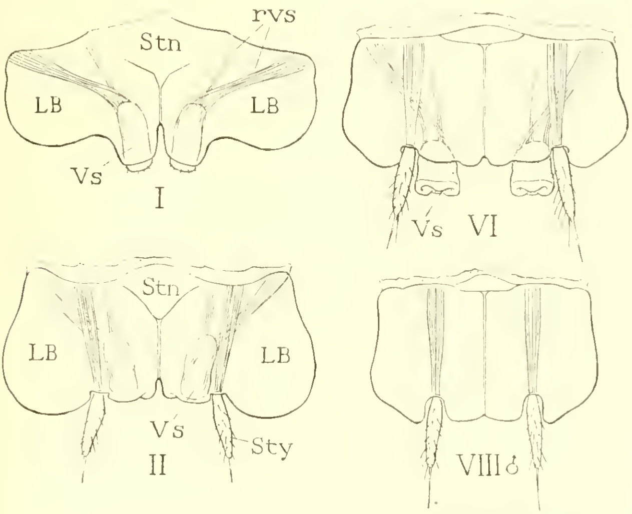

FIG. 4.—Ventral plates of abdomen of *Nesomachilis maoricus*.

I, II, VI, VIII, ventral plates of segments one, two, six, and eight in male. *LB*, limb basis, or basal plate of appendage; *rvs*, muscles of retractile vesicle; *Stn*, primitive sternal sclerite; *Sty*, stylus; *Vs*, eversible and retractile vesicle.

The frequent occurrence of styli on abdominal segments of insects in which the sterna are undivided plates leaves little doubt that the definitive abdominal sterna of insects in general are composite plates including the limb bases as integral parts of their areas. Evidence of the inclusion of the limb bases in the adult abdominal sterna might be derived also from other sources, as in the Lepidoptera, where the abdominal appendages of the larva at the time of pupation are flattened out in the form of discs, and merge into the ventral areas from which later the adult sterna are produced.

A definitive sternal plate that includes the primitive sternum and the bases of the adjacent limbs is sometimes called a "coxosternum," but, as will be shown later, there is a question as to whether the abdominal limb bases represent the coxae or the subcoxae, or include both of these usual basal elements of the appendages. A composite sternal plate, therefore, is more appropriately distinguished from a primitive sternal plate by the term *zygosternum* proposed by Prell (1913). For the same reason the name "coxite," often given to the limb base element of the zygosternum, is objectionable as being more specific in its meaning than is warranted by the known facts of the origin of the part in question. Besides this, the suffix *ite* implies that a structure so-named is "a part of" a coxa, and this implication is clearly not intended.

II. THE ABDOMINAL SEGMENTS

Entomologists sometimes nominally distinguish the segments of the insect abdomen from those of the thorax as "urites," a term perhaps recommended by its brevity, but one which, by inference, reduces the entire abdomen to the status of a "tail." Consistent with this usage, the abdominal appendages would all be "uropods," but the custom of carcinologists in applying the latter term only to the terminal pair of appendages has better anatomical sanction. (Lankester, 1909; Sedgwick, 1909.)

From embryological evidence there appears to be little doubt that the primitive number of abdominal segments in typical insects is at least 12 (fig. 5 A). Twelve segments are actually present in adult Protura (B), each having distinct tergal and sternal plates, but the tenth and eleventh are said to be added by "epigenesis," that is, they are developed during postembryonic growth. In many of the Apterygota and in the lower Pterygota, 11 segments are present without question, while in some forms there are possible rudiments of a twelfth segment. The twelfth or primitive terminal segment is the periproct (fig. 5 A, *Prpt*), which carries the anus, but does not have appendages. It is the terminal piece of the body anterior to which the true somites are formed, segmentation of arthropods being intrasomatic and not a process of budding. Some investigators claim that a pair of coelomic sacs is formed in the periproct. The presence of not more than six segments in the abdomen of Collembola is usually taken to be the result of reductive specialization, or " degeneration," in these insects, considering that the existence of even six segments is obscure in some forms by a loss of intersegmental lines. Tillyard (1930), however, sees in the Collembola a primitive " protomorphic " condition in which only nine postcephalic somites have ever been developed. He points out that segmentation in the collembolan embryo produces six abdominal segments and no more, and that we have, therefore, no evidence of a greater number of somites ever having been present in this group of arthropods, which he would not ally closely with the other insects. A reduction in the number of abdominal segments is the rule in both immature and adult insects generally. As just stated, evident remnants of the periproct are rare except in the Protura. While 11 segments are distinct in many of the more generalized insects, in the higher orders, especially in the Holometabola, not more than 10 segments are usually present, and sometimes only nine are evident. In the more specialized insects there is a tendency toward elimination of the first abdominal segment, but generally reduction takes place at the posterior end of the body. Since the periproct is commonly lacking, or reduced to a circumanal membrane, the eleventh somite, which carries the last pair of segmental appendages, becomes the definitive anal segment. The tenth

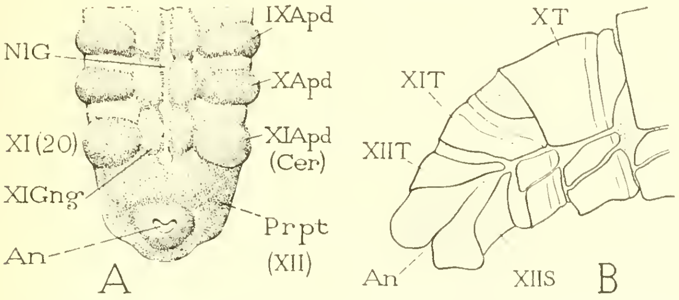

FIG. 5.—Examples of the presence of twelve segments in the hexapod abdomen.

A, posterior end of abdomen of young embryo of *Gryllotalpa* (from Heymons, 1895), with large periproct (*Prpt*), or twelfth segment, behind the last true somite (*XI*) bearing the cerci (*Cer*). B, end of abdomen of adult proturon, *Acerentulus confinis* (from Berlese, 1910), showing twelve distinct segments.

segment is sometimes more or less united with the eleventh in orthopteroid insects; but in the Holometabola the eleventh segment is generally suppressed, and the body ends with the tenth segment, though possibly in certain holometabolous larvae the terminal segment contains a remnant of the eleventh somite, while in coleopterous larvae the abdomen ends in a distinct anal lobe, which appears to represent the eleventh segment.

The association of the organs of copulation and oviposition with the eighth and ninth segments of the abdomen is usually accompanied by adaptive structural modifications in these segments that conspicuously differentiate the latter as the *genital segments,* and separate the rest of the abdomen into a pregenital region and a postgenital region. Since the pregenital region contains most of the internal abdominal organs, its segments may be termed the *visceral segments.* The segments beyond the ninth, which are usually more or less reduced and united with each other, constitute the *postgenital segments.* It is not possible, of course, in all cases to divide the abdomen consistently into visceral and genital regions, since modifications adaptive to the major functions of the eighth and ninth segments often affect one or several of the preceding segments, but yet, for general descriptive purposes, the term " genital segments " will have a specific meaning.

THE VISCERAL SEGMENTS

To describe here in full the visceral region of the abdomen would be to repeat many well known facts without adding anything of importance. The seven segments of this region are usually of simple structure and differ but little from one another. In adult pterygote insects they lack appendicular organs, and the definitive sterna probably always include the areas of the primitive limb bases. The first segment is more subject to modifications than are any of the others. In winged insects the antecosta of its tergal plate bears the third pair of phragmatal lobes, and the precosta is usually much enlarged, forming the so-called postnotal, or postscutellar, plate of the metathorax (fig. 16, PN_3), which, together with the base of the phragma, is frequently removed from the tergal region of the first abdominal segment and more closely associated with that of the metathorax. The rest of the first segment is often reduced, or fused with the second, and the sternal sclerotization is sometimes obliterated. The first pair of spiracles, however, are nearly always retained, and the spiracles will generally furnish a key to the basal segmentation of the abdomen where the segmental limits are obscured. In the aculeate Hymenoptera the entire first abdominal segment is so intimately united with the metathorax that it forms anatomically a part of the thoracic region of the body. Modification of the posterior visceral segments will be noted in connection with a study of the genitalia. In females of higher Diptera the functional visceral region is reduced to five segments by the conversion of the posterior segments into a tubular organ of oviposition.

THE GENITAL SEGMENTS

The lateral ducts of the reproductive organs in the majority of the Hexapoda open into a common, median outlet tube. Exceptions to this rule occur in the males of Protura, in both males and females of Ephemerida, and in males of some Dermaptera, the two lateral ducts in these cases opening separately to the exterior. The position of the genital apertures varies within the Hexapoda through an extreme of six segments. In the Collembola the gonopores of both sexes are situated on the fifth abdominal segment, while in the Protura they occur between the eleventh and twelfth segments. In the Ephemerida the paired oviducts open between the seventh and eighth abdominal segments, and the vasa deferentia open on the penes between the ninth and the tenth segments. In all other Pterygota, except Dermaptera, and in Thysanura and Dicellura, the single female aperture lies between the eighth and ninth segments, and the male aperture between the ninth and tenth segments. Apparent exceptions to this rule occur where some of the terminal segments are fused, where one or more of the pregenital segments have been obliterated, or where, as in female Lepidoptera, the gonopore has evidently undergone a secondary change in position.

The genital apertures are described by some writers as being situated on the segments, while others state that they occur between segments. The gonopores, in truth, are probably located on the posterior parts of the ventral surfaces of primary segmental areas, but since these parts of the primitive somites become the intersegmental membranes of the definitive segments, the gonopores of adult insects are anatomically intersegmental. They lie behind the primary sterna of the segments on which they are situated, and only rarely is a secondary sclerotization formed behind them (male Odonata). The male gonopore is usually carried outward on an evagination of the body wall forming a simple *penis*, or it is situated on a more complex copulatory organ composed of the penis and the parameres, or of the parameres alone, known as the *aedeagus*.

Owing to the uniformity in the relation of the genital apertures to the eighth and ninth abdominal segments, these segments in the majority of insects become specifically the genital segments. Their appendages form the principal organs of egg-laying and copulation, and may therefore be designated *gonopods.* In some of the simpler insects the gonopods are lacking and the genital segments have no distinctive external features; but usually the segments show some conspicuous structural adaptation to the functions of copulation or oviposition.

The eighth segment.—Modifications of the eighth segment (fig. 6, *VIII*) occur principally in the female, since it is on the ventral part of this segment that the first gonapophyses (*1Gon*), or genital processes of the eighth gonopods, are developed, and become the ventral blades, or first valvulae, of the ovipositor in all species provided with an ovipositor. The female genital opening is normally situated between the bases of the first gonapophyses in the membrane behind the primitive eighth sternal plate, but the latter is frequently prolonged beneath the base of the ovipositor, forming the *subgenital plate* of the female. The bases of the gonopods of the eighth segment are never united with the eighth sternum in female insects having an ovipositor. In the Thysanura they are large, stylus-bearing plates or lobes which retain the normal position of limb bases, but in pterygote insects they

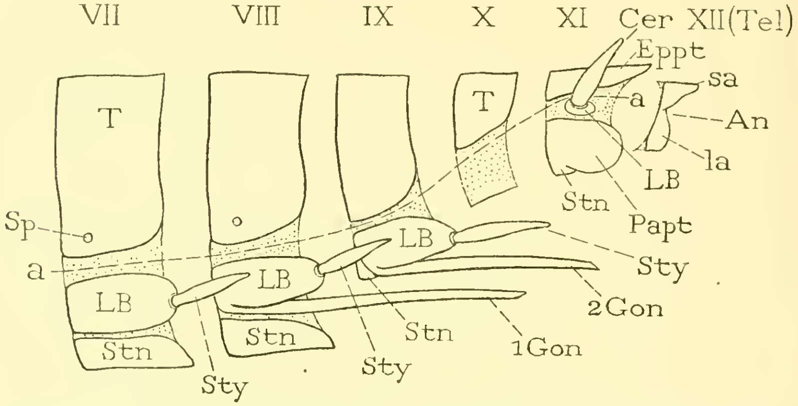

FIG. 6.—Diagram illustrating the concept of the structure of the abdomen adopted in this paper.

a-a, dorso-pleural line separating tergal region from pleuro-sternal region; *Cer,* cercus; *Eppt,* epiproct; *1Gon, 2Gon,* first and second gonapophyses; *la,* lamina subanalis; *LB,* limb basis; *Papt,* paraproct (lobe of eleventh sternum); *sa,* lamina supra-analis; *Sp,* spiracle; *Stn,* primary sternum; *Sty,* stylus; *T,* tergum; *Tel,* telson (twelfth segment, greatly reduced or obliterated in insects).

appear to form small suspensional sclerites of the first valvulae, known as the valvifers, which always lack styli. Gonapophyses of the eighth segment are known to be present in male insects only in some species of *Machilis*, but the eighth segment of the male is frequently more or less modified when associated with the ninth in the copulatory mechanism.

The ninth segment.—The second genital segment (fig. 6, *IX*) usually has less of the typical form than does the first. It is the somite of the second gonapophyses (*2Gon*), or genital processes of the ninth gonopods, which form the second valvulae of the ovipositor in the female, and the usual parameres in the male. The sternum of the ninth segment is generally reduced or rudimentary in the female, but the bases of the gonopods are commonly retained, either in the form of lobes, or as blade-like pieces of the ovipositor, the third valvulae. In the male the ninth segment retains a generalized structure in the Thysanura (fig. 33, B, C), but in the pterygote insects it is subject to many modifications and takes on a great variety of forms. The bases of the gonopods in male Pterygota either remain as distinct lobes of the segment, or they unite with each other, or with the sternum, or with both the sternum and the tergum. The styli, if retained, usually take the form of movable clasping organs. Various immovable lobes also may be developed from the ninth segment of the male, and sometimes from the eighth, which serve as accessory organs in copulation.

The intromittent organ of the male arises in the Thysanura behind the region of the ninth sternum and between the bases of the gonopods (fig. 33 B, C, *Pen*); but in insects having the gonopod bases united with the sternum, it arises posterior to, or usually above, the limb base area of the composite sternum. The membranous area from which the organ arises is, furthermore, generally more or less inflected between the ninth and tenth segments, forming a *genital chamber* above the ninth sternum, and the ninth sternum is often extended posteriorly as the male subgenital plate, or *hypandrium*. The intromittent organ has the form of a simple, tubular penis in the Thysanura, but in most pterygote insects it is a more complex structure, called the aedeagus, formed of the penis and parameres, or of the parameres alone. The external genitalia will be fully described in Part II of the present paper.

THE POSTGENITAL SEGMENTS

Beyond the second genital segment there are never more than three segments represented in the hexapod abdomen (fig. 6, *X*, *XI*, *XII*), and it is only in the Protura that the last of these segments is well developed (fig. 5 B, *XII*). In some of the lower insects apparent traces of the terminal segment are to be found, but in most of the true Insecta there are only two postgenital segments present. A still further reduction, however, has taken place in many insects, with the result that but one segment is to be recognized beyond the ninth. Where two postgenital segments are present there is little doubt that they are the tenth and the eleventh; and where the number of postgenital segments is reduced to one, it is usually to be assumed that the single end-segment is the tenth somite, and that the eleventh has disappeared, though it is probable that the tenth and the eleventh somites are in some cases combined in the definitive terminal segment.

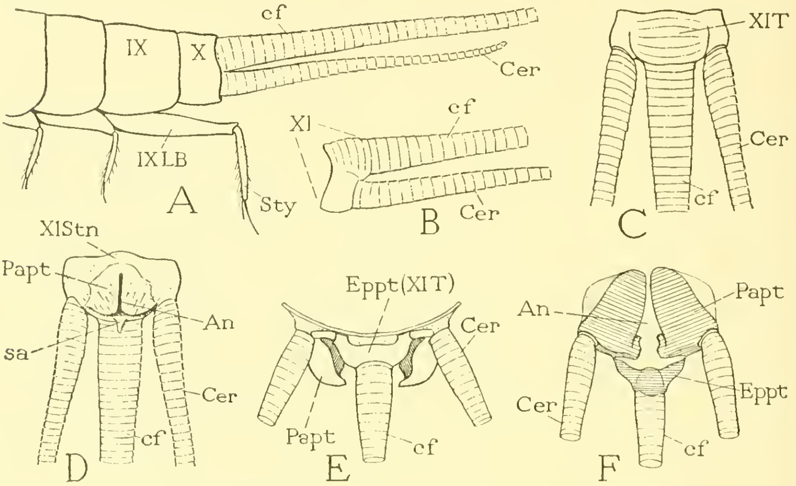

FIG. 7.—Terminal abdominal structures of *Thysanura*.

A, end of abdomen of male *Nesomachilis maoricus*. B, caudal filament and cercus of same removed, showing their origin from small eleventh segment normally retracted into the tenth. C, dorsal view of same. D, ventral view of eleventh segment, with bases of caudal filament and cerci. E, dorsal view of eleventh segment and terminal appendages of *Thermobia*. F, ventral view of same.

An, anus; *Cer*, cercus; *cf*, caudal filament; *Eppt*, epiproct; *LB*, limb basis; *Papt*, paraproct; *sa*, possible rudiment of lamina supra-analis; *Stn*, primary sternum; *Sty*, stylus.

The tenth segment.—The tenth somite of the abdomen is clearly retained as the numerical tenth segment in insects in which there are two distinct postgenital segments. It is a complete annulus in the Thysanura (fig. 7 A, *X*), quite distinct from the eleventh segment (B, *XI*), which is mostly concealed within it. In the Odonata the tenth segment is a continuously sclerotized ring (fig. 12 B, C, *X*), beyond which are the parts of the eleventh segment, and apparent remnants of the twelfth (*A*). Likewise, in larvae of Plecoptera the tenth segment is cylindrical in form (fig. 8 A, *X*), and the parts of the eleventh segment (*Eppt, Papt*) are quite distinct from it. The structure in an adult plecopteron is essentially the same as that of the larva, but the tenth segment is smaller. In the Ephemerida, both larval and adult forms, the tenth somite is a well-developed segment, which, because of the reduction of the eleventh somite, forms the terminal segment of the body and appears to carry the long cerci. Its tergal region is produced posteriorly in a median lobe, and thus resembles the supra-anal plate of other insects, but the small true epiproct of the eleventh segment lies beneath the lobe of the tenth tergum and carries the median caudal filament. The venter of the ephemerid tenth segment appears to contain the anal opening, but it is evident that the anus is drawn forward and that the paraprocts are united with the bases of the cerci.

Among orthopteroid insects the tenth segment is variable; its ventral region is usually membranous, and in some families its tergal plate is fused with the eleventh tergum, or epiproct. In the Phasmidae, however, the tenth segment is large and normally developed (fig. 8 E, G, *X*). In *Diapheromera* it has distinct tergal and sternal plates, the tergum overlapping the edges of the sternum in the female (F), though the two plates are ankylosed in the male to form a strong support for the clasper-like cerci (E). The paraprocts are united ventrally with the tenth sternum (F, *Papt*) and appear to be lobes of the latter. The ventral region of the tenth segment is membranous in most other Orthoptera (fig. 8 D), though the dorsum usually contains a distinct plate (*XT*). In Acrididae the tenth tergum is a narrow transverse sclerite fused laterally with the ninth tergum, but it is separated from the epiproct by a complete suture. In Blattidae (fig. 40 A), Tettigoniidae, and Gryllidae (fig. 8 B), however, the tergum of the tenth segment (*X*), is generally fused with the epiproct (*Eppt*), and since the paraprocts become continuous with the membranous ventral wall of the segment, the tenth somite in these families loses the status of an independent body segment.

It must be noted here that the principal muscles of the cerci arise on the tergum of the tenth segment. The size of the tenth segment, therefore, generally varies according to the size of the cercal muscles, the segment being large in insects having long, mobile cerci (fig. 8 A, *XS*), and strongly developed in insects in which the cerci have a grasping function, as in *Japyx* (fig. 40 C), and in *Diapheromera* (fig. 8 E, *X*). When the cercal musculature is weak the tenth segment is usually reduced, and its tergal plate becomes small, or unites with the epiproct. In certain cases, however, the tenth segment is developed quite independently of any relation to the cerci, as in some of the Homoptera, in which the cerci are rudimentary or absent. In the cicada (fig. 8 C) the tenth tergum is a strong plate produced downward on the sides into a pair of hooked lobes (*l*) embracing the distal end of the aedeagus.

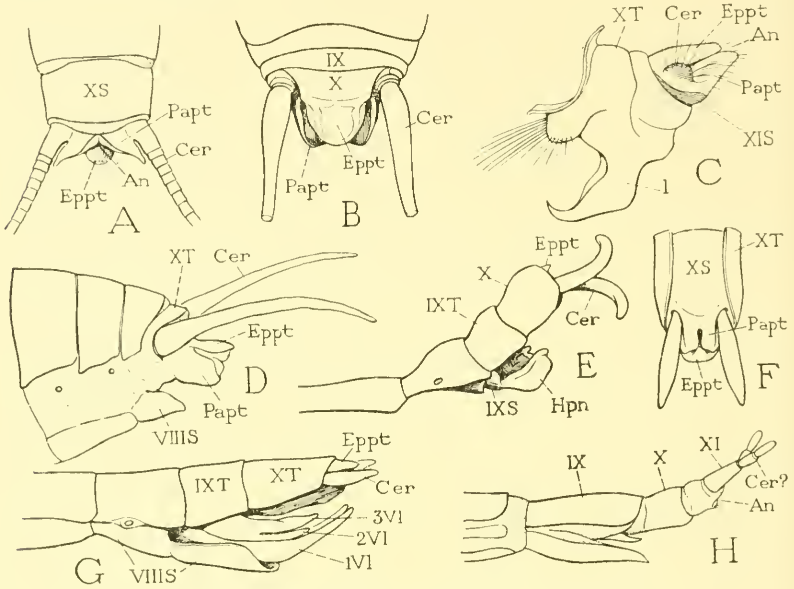

FIG. 8.—Terminal abdominal structures of various insects.

A, larva of plecopteron, ventral view, showing cerci, paraprocts, and epiproct as parts of eleventh segment. B, *Gryllus assimilis*, dorsal view, showing union of epiproct with tenth tergum. C, *Magicicada septendecim*, with eleventh segment distinct from tenth. D, *Scapteriscus didactylus*, female. E, *Diapheromera femorata*, male. F, female of same, showing paraprocts fused with tenth sternum. G, lateral view of genital and postgenital segments of female *Diapheromera femorata*, showing ovipositor, and subgenital plate produced from eighth sternum. H, end of abdomen of female *Panorpa consuetudinis*.

True appendages are absent from the tenth segment in postembryonic stages of all Apterygota and hemimetabolous Pterygota. Rudiments of appendages, however, are well known to be present on the tenth segment of many insect embryos (figs. 5 A, 9 A, *XApd*). The idea that these appendages are developed in the female into the third pair of valvulae of the ovipositor is now generally regarded as erroneous, since it is clear that both the second and the third pairs of valvulae are parts of the gonopods of the ninth segment. Berlese (1906) records an anomaly found in an adult female of *Locusta* *viridissima,* consisting of two pairs of appendicular processes on the tenth abdominal segment closely resembling the two pairs of valvulae on the ninth segment, the outer pair corresponding with the valvulae formed of the basal plates, the inner pair with those formed of the gonapophyses. It is scarcely to be supposed, however, that an abnormality of this kind is a " reversion " to an ancestral normality. The embryonic limb rudiments of the tenth abdominal segment in all the more generalized insects are normally suppressed before hatching. In the Holometabola, on the other hand, appendicular structures frequently occur on the tenth segment in postembryonic stages, and there is little doubt that such organs on the larva, typically represented by the postpedes of caterpillars, are true limb structures; in adults they include the socii of Lepidoptera and Trichoptera, and the cercus-like processes of Tenthredinidae, which appear to be derived from the larval postpedes. The appendages of the tenth, or pygidial, segment of the abdomen may be generally designated the *pygopods.*

The eleventh segment (*uro-segment*).—The eleventh abdominal segment represents the last true somite of the body, and is present in the embryos of many insects as a well-developed ring bearing the rudiments of the terminal pair of appendages (fig. 5 A, *Cer*). The segment is present in adult Protura as a fully formed annulus with tergal and sternal plates (B, *XI*), and in some of the lower Insecta having 11 distinct segments in the abdomen the eleventh segment is retained likewise as a complete annulus. This condition is well shown in *Nesomachilis* (fig. 7 B) where the eleventh segment, though mostly concealed within the tenth (A), consists of continuous tergal and sternal regions (C, D), and bears laterally the long, filamentous cerci (*Cer*). The tergal region is produced into the median caudal filament (*cf*), and the sternal bridge supports a pair of broad subanal lobes, the paraprocts (D, *Papt*), separated by a median cleft. In *Thermobia* the eleventh segment has a distinct tergal plate, or *epiproct* (E, F, *Eppt*), but the sternal bridge is lost, and the sternal region of the segment is represented only by the paraprocts (F, *Papt*), upon which are borne the cerci (*Cer*). The median ventral region of the eleventh segment is generally obliterated in pterygote insects that have a well-developed tenth segment, but in some of the Homoptera, as in the cicada (fig. 8 C), the venter of the eleventh segment is not only present but it contains a distinct sclerotic sternal remnant (*XIS*).

The adult abdomen of most of the lower Pterygota ends with a supra-anal plate (fig. 6, *Eppt*) which is in every way suggestive that it corresponds with the epiproct, or tergum of the eleventh segment, in the Thysanura. Some entomologists, however, basing their opinion on

Heymons' (1895) assertion that the eleventh segment of the embryo in *Gryllotalpa* and other Orthoptera is lost during development, regard the supra-anal plate of pterygote insects as belonging to the twelfth segment. On the other hand, Wheeler's (1893) observations on the development of *Xiphidium* are fully convincing that the cercus-bearing eleventh segment persists in the Orthoptera, and, though it becomes reduced, forms the terminal parts of the adult abdomen associated with the cerci. Wheeler's idea that the rudimentary appendages of the tenth segment become the inner valvulae of the ovipositor in the female does not conform with the evident facts of comparative anatomy, but this detail of interpretation does not affect his exposition of the segmentation.

When we compare the usual circumanal structures of pterygote insects with the parts of the eleventh segment in the Odonata (fig. 12 A, *Eppt, Cer, Papt*), in which Heymons himself has shown that the twelfth segment (*Prpt*) is present though rudimentary, we can scarcely question the identity of the parts in all cases. In other words, the epiproct, the cerci, and the paraprocts, which in larval Odonata clearly belong to the eleventh segment, must be eleventh segment structures in all Pterygota, as they are in Thysanura. Heymons' (1904) claim that the appendages of the eleventh segment in the Odonata are not true cerci, and that the latter are represented in the apparent paraprocts finds no support in comparative anatomy, and has been generally rejected on the ground that it would set the Odonata apart from all other insects.

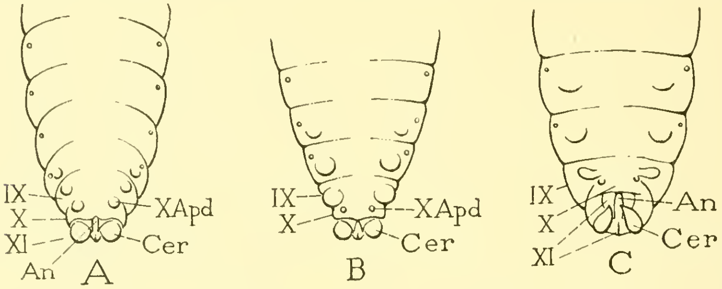

FIG. 9.—Posterior segments and appendage rudiments of embryos of *Xiphidium*. (Outlines from drawings by Wheeler, 1893, showing segmentation and appendages, but with other details omitted.)

A, male embryo. B, female embryo, each with cercal appendages (*Cer*) on eleventh segment. C, female embryo in later stage, showing retention of eleventh segment structures (*XI*).

The writer would, therefore, agree with Crampton (1918) that the epiproct is in all insects the tergum of the eleventh segment (fig. 6, *Eppt*), but would dissent from Crampton's opinion that the cerci and paraprocts pertain to the tenth segment, since in such forms as *Nesomachilis* (fig. 7 B) they clearly belong to the eleventh segment, and embryologists agree that the cerci are appendages of the eleventh segment (fig. 5 A). That the paraprocts at least belong to the same segment as the epiproct is evident from their usual anatomical relations with the latter. Ford (1923), in her review of the musculature of orthopteroid insects, says, " from the musculature we find that the supra-anal plate and paraprocts form a symmetrical group," and further she observes that " the transverse muscles between the supra-anal plate and paraprocts show that all three belong to the same segment." The segment represented by the epiproct and paraprocts Ford believes is the twelfth, but she bases her opinion largely on Heymons' statement that the eleventh segment is suppressed in the adult.

Furthermore, the anatomical relations between the paraprocts and the cerci do not support Crampton's (1920, 1921) contention that the paraprocts are the bases of the cercal appendages. The cerci may be united with the paraprocts (figs. 7 F, 8 A), but generally they arise independently in membranous areas behind the tenth tergum between the epiproct and paraprocts. The cerci never have muscles arising in the paraprocts, and the ventral musculature of the paraprocts indicates that these plates are merely lobes of the eleventh sternum (fig. 6, *Papt*), as they are actually in *Nesomachilis* (fig. 7 D). With the usual suppression of the eleventh sternal area, however, the paraprocts may appear to arise from the posterior margin of the tenth sternum, and they are sometimes continuous with the latter (fig. 8 F, *Papt*).

The cerci, as shown by their development, are the *entire* appendages of the eleventh segment. Their primitive bases may be represented by a small, ring-like segment at the root of each organ (Heymons, 1896, Walker, 1922), and, as noted above, they are sometimes united with the sternal paraprocts, but the muscles of the cerci always have a tergal origin. As already observed, most of the cercal muscles arise on the tergum of the tenth segment. These anterior muscles of the cerci, however, appear to be derived from the intersegmental, longitudinal muscle fibers primitively extending between the tenth and eleventh terga, which have secondarily become motors of the cerci. In some Orthoptera, each cercus has a single muscle arising on the epiproct.

The terminal structure of the generalized insect abdomen has a certain resemblance to that of a malacostracan crustacean (fig. 10 A). The twentieth body segment of the crustacean represents the eleventh segment of the insect abdomen, and its appendages, the uropods (*20Apd*), evidently correspond with the cerci. The telson (*Tel*) being suppressed in insects, the tergum of the eleventh abdominal segment (twentieth somite) becomes the supra-anal plate, or epiproct. The cerci, therefore, may be regarded as the *uropods* of insects.

The twelfth segment.—Among adult Hexapoda a twelfth segment of the abdomen is developed as a complete annulus with tergal and sternal plates only in Protura (fig. 5 B, *XII*). In the arthropods generally the terminal segment is the periproct, or end piece of the body containing the anus, anterior to which the true appendage-bearing somites are formed. In the malacostracan Crustacea the periproct forms the telson (fig. 10 A, *Tel*), typically a broad terminal lobe of the abdomen, having the anus situated in the basal part of its ventral surface (B, *An*) between two lateral valve-like flaps (*la*). A distinct, anus-bearing, terminal lobe of the body is said to be present in the embryos of some insects (fig. 5 A, *Prpt*), but in adult insects there is never more than a vestige of the periproct, or rudiment of a segment beyond the cercus-bearing eleventh somite (fig. 6, *XII*).

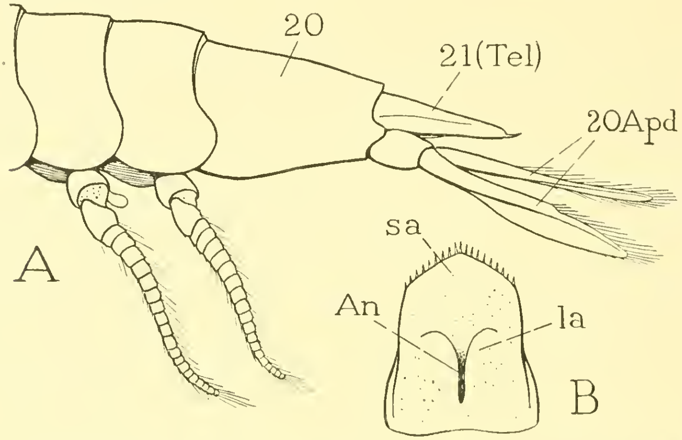

FIG. 10.—Terminal abdominal structures of a crustacean, *Anaspides tasmaniae*. A, posterior part of abdomen, showing the uropods (*20Apd*) as terminal appendages of penultimate segment. B, ventral view of telson, showing lamina supra-analis (*sa*) and laminae sub-anales (*la*) surrounding anus (*An*).

The best example of the retention of a twelfth segment in insects is furnished by the larvae of some Odonata, in which the anus is contained in a small circular fold (fig. 12 A, *Prpt*) ordinarily concealed between the bases of the epiproct (*Eppt*) and the paraprocts (*Papt*). In the walls of this circumanal fold, as Heymons (1904) has shown,

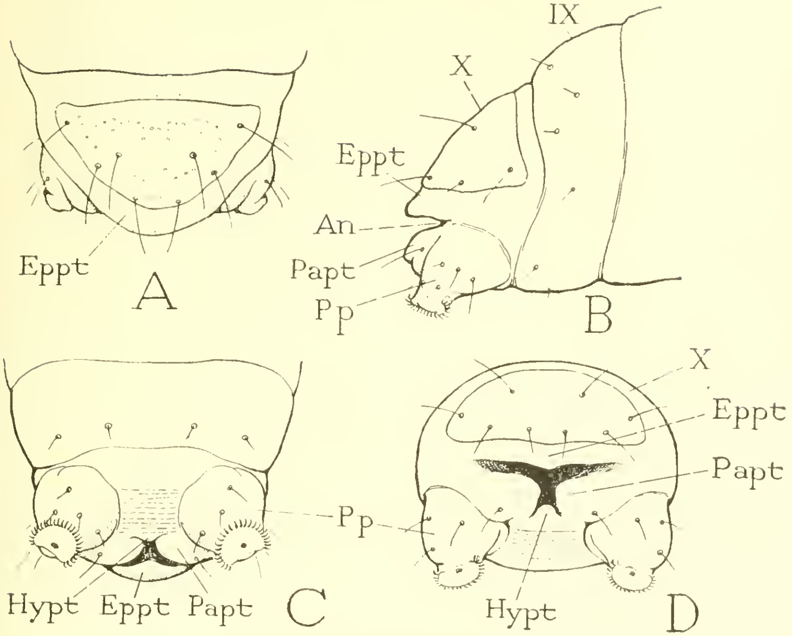

Fig. 11.—Posterior segments of a noctuid caterpillar.

A, dorsal view. B, lateral. C, ventral. D, posterior.
An, anus; *Eppt,* epiproct; *Hypt,* hypoproct; *Papt,* paraproct; *Pp,* postpedes (pygopods).

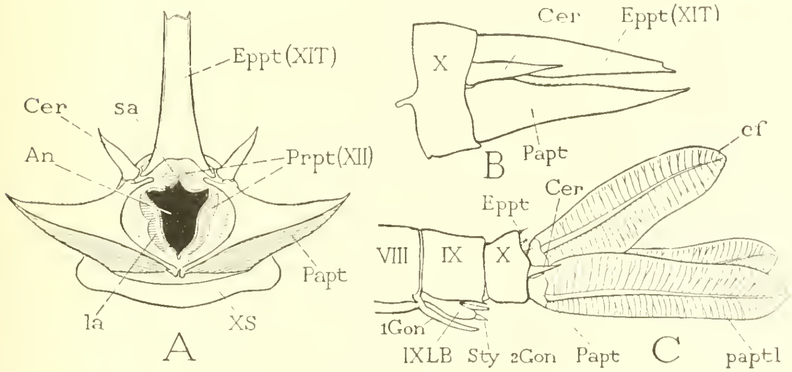

Fig. 12.—Terminal abdominal structures of odonate larvae.

A, aeschnid larva, posterior view of end of abdomen, with epiproct and paraprocts spread out, exposing the periproct (*Prpt*) containing lamina supra-analis (*sa*) and laminae sub-anales (*la*) surrounding the anus (*An*). B, lateral view of same with parts in normal position. C, end of abdomen of larva of *Archilestes grandis,* showing gill plates formed of caudal filament (*cf*) of epiproct (*Eppt*), and of lobes (*paptl*) of paraprocts (*Papt*).

there is a small dorsal sclerite, or *lamina supra-analis* (*sa*), and two lateroventral sclerites, or *laminae infra-anales* (*la*). These sclerites are lost in adult Odonata, but a small supra-anal lobe, possibly a remnant of the lamina supra-analis, projects from beneath the epiproct. A similar lobe occurs in *Nesomachilis* (fig. 7 D, *sa*), as well as in some other Thysanura, and in larvae of Ephemerida. The supra-anal lobe of these insects might be regarded, therefore, as a dorsal remnant of the telson (fig. 6, *Tel*). In most insects, however, no trace of a twelfth segment is to be found, and the periproct must be supposed to have been reduced to the membranous area at the end of the eleventh segment in which the anus is situated.

III. THE ABDOMINAL MUSCULATURE

We do not have as yet a sufficient knowledge of the comparative myology of Arthropoda to furnish a basis for any theory as to the nature of the primitive body musculature in this group of animals, in which mobility of the body is a characteristic feature. Widely different patterns of muscle arrangement are encountered in the several arthropod classes, and even within a single class, while, among the insects, extraordinary differences occur often between larval and adult stages of the same species.

In the Insecta the abdominal musculature consists typically of dorsal and ventral longitudinal fibers, dorsal and ventral transverse fibers, and lateral dorsoventral fibers; but in none of these muscle groups do all the fibers often retain their characteristic positions.

The development of the body muscles has been described by Cholodkowsky (1891), Heymons (1895), and Nelson (1915). The dorsal and lateral muscles are formed from the lateral somatic plates of the mesoderm; the ventral muscles arise from the median ventral parts of the mesoderm where the somatic and splanchnic layers are united. The muscle rudiments, or anlagen, according to Heymons, in insects having open coelomic sacs (Blattidae, *Gryllus*, Acrididae), are formed from sac-like evaginations of the mesodermal walls of the segmental cavities, which are at first tubular, but sooner or later become solid strands of cells. In the higher insects, however, in which the coelomic sacs are small or but little developed, the muscles either are formed by the proliferation of cells from the mesoderm segments, or they arise directly from mesenchyme tissue at points corresponding with the position of the coelomic sacs of lower insects.

Since the muscles are derived from the walls of the embryonic coelomic sacs, or from the metameric divisions of the mesoderm, we may assume that the primitive somatic fibers were all *intra-segmental* in arrangement, as they are in the Annelida. With the acquisition of secondary segmentation in arthropods, however, consequent upon the development of sclerotic plates in the body wall, the principal longitudinal fibers became functionally *intersegmental* (fig. 2 F). The body of the animal can thus be shortened by a telescoping of its segments brought about by contraction of the longitudinal muscles, and it can be compressed by contraction of the lateral dorsoventral muscles. In most cases the opposite movements result either from the elasticity of the body wall, or from pressure generated by contraction in one part of the body transmitted to another through the medium of the body liquid and the visceral organs; but in many insects a dilator apparatus is developed in which certain muscles in both the longitudinal and dorsoventral systems become antagonistic to the retractors and compressors.

The abdominal musculature of adult insects is simpler than the thoracic musculature because of the absence of leg muscles. There is no evidence that the definitive lateral muscles of the abdomen have been derived from the body muscles of the limbs. Muscles of the movable parts of the abdominal appendages, as will be shown in the next section, arise generally within areas of the body wall that may be attributed to the limb bases (figs. 32 B, C, 34 B, 36 D), except the muscles of eversible or retractile sacs which in some cases have evidently extended to the dorsum. The general segmental plan of the abdominal musculature is usually repeated with only minor variations in each of the visceral segments; in the genital and postgenital segments it is more or less obscured by special modifications.

A rather simple scheme of abdominal muscle arrangement prevails throughout all adult pterygote insects; but in the Apterygota and in larval forms of holometabolous insects the musculature may be highly complex. Some students regard the complex types of musculature as representative of a primitive condition from which the simpler types have been derived by elimination. There are reasons, however, for taking the opposite view, as will later be shown.

Something is known of the abdominal musculature in most of the principal orders of insects; but the Odonata, Orthoptera, Coleoptera, Hymenoptera, and the larvae of Lepidoptera and Diptera have received special attention. Trichoptera and Neuroptera, on the other hand, have been particularly neglected, and little has been done on the abdominal musculature of Hemiptera, and of adult Lepidoptera and Diptera. The following literature contains the principal descriptions of the abdominal muscles of the various orders of insects known to the writer.

PROTURA: Berlese (1910). COLLEMBOLA: Lubbock (1873). THYSANURA: Grassi (1887), giving the characteristics of the abdominal musculature of *Campodea, Japyx, Machilis,* and *Lepisma.* ODONATA: Wallengren (1914), Whedon (1919), Ford (1923), Steiner (1929), with descriptions of muscles of first three segments in adult by Backhoff (1910) and Schmidt (1915), figures showing larval musculature by Calvert (1911, 1915), and a tabulation of the muscles by Tillyard (1917). EPHEMERIDA: Dürken (1907). ORTHOPTERA: *Gryllus,* Voss (1905), DuPorte (1920); *Dixippus,* first three abdominal segments, Jeziorski (1918); general comparative study of abdominal muscles of orthopteroid insects, Ford (1923). HEMIPTERA: *Aphis fabae,* Weber (1928). ANOPLEURA: *Haematopinus suis,* Florence (1921). COLEOPTERA: *Melolontha,* Straus-Dürckheim (1828); *Hydrophilus,* first three abdominal segments, Berlese (1909); *Dytiscus,* Bauer (1910), Speyer (1922), Korschelt (1924); larval musculature of other species, Berlese (1909), Böving (1914), Craighead (1916), Paterson (1930). LEPIDOPTERA: larval musculature, Lyonet (1762), Lubbock (1859), Berlese (1909), Forbes (1914, 1916). HYMENOPTERA: larval muscles of a chalcid, Tiegs (1922), of the honeybee, Nelson (1924); adult musculature of pregenital segments of *Vespa,* Berlese (1909), of *Apis,* Carlet (1890), Betts (1923), Snodgrass (1925); full account of abdominal musculature of *Apis,* Morison (1927). DIPTERA: larval musculature partly or briefly described or figured in Syrphidae, Künckel d'Herculais (1875), in *Chironomus,* Miall and Hammond (1900), in *Anopheles,* Imms (1908), in *Musca,* Hewitt (1910, 1914), in *Rhagoletis,* Snodgrass (1924); full account of larval muscles of *Psychoda,* Dirkes (1928), of Culicidae, Samtleben (1929).

Less appears to have been done on the body musculature of other Arthropoda than on that of insects. Descriptions of the abdominal muscles of Crustacea will be found in the paper on the musculature of *Astacus fluviatilis* by Schmidt (1915), in that on *Pandalus danae* by Berkeley (1928), and in that on *Copilia dana* by Riester (1931). A paper by Becker (1926) describes the dorsal body musculature of Chilopoda.

GENERAL PLAN OF THE ABDOMINAL MUSCULATURE

A review of the literature cited above gives a fairly comprehensive survey of the abdominal musculature of insects in most of the principal orders. There are notable blanks, however, since such important orders as Neuroptera and Trichoptera are omitted entirely, and adult Lepidoptera and Diptera have been given scant attention. On the other hand it is gratifying to find that we have, as a basis for a comparative study of insect myology, very full accounts of the body musculature of the Odonata, Ephemerida, and Orthoptera. In the Apterygota, we are indebted to Berlese for an excellent study of the muscles in Protura, to Lubbock for a description of the collembolan musculature, and to Grassi for brief descriptions of the characteristic differences in the musculature of representative genera of Dicellura and Thysanura, to which is added in this paper an account of the abdominal muscles of *Heterojapyx;* but a more complete study of the musculature of Machilidae and Lepismatidae, and perhaps of *Campodea*, is still to be desired. When we look to the papers treating of holometabolous larvae, we find again satisfactory and in some cases complete accounts of the body musculature in Coleoptera, Lepidoptera, Hymenoptera, and Diptera, but note with regret a lack of information on Neuroptera and Trichoptera.

To present here even a summary of the details known concerning the abdominal muscles of insects would occupy an unwarranted amount of space. A careful review of the facts to be obtained from the works above listed, however, shows that we may with confidence make certain broad generalizations concerning the fundamental plan of the abdominal musculature of adult pterygote insects. The basic plan is found to be simple; but, as so often occurs in insect morphology, more difficulties are encountered in finding suitable terms to express the facts than in discovering the facts themselves.

Voss (1905) classified the abdominal muscles as *longitudinal muscles, transverse muscles*, and *lateral muscles* (Flankenmuskeln). This classification is logical inasmuch as it probably conforms with the primitive arrangement of the fibers. The muscles of the so-called longitudinal groups, however, do not always preserve a lengthwise arrangement; they are often strongly oblique, and some of them frequently take a transverse position. The lateral muscles are designated "dorsoventral" muscles by many writers, but, though their attachments are usually dorsal and ventral, some of their fibers commonly run in an oblique direction. The lateral muscles have also been termed "transverse" muscles, but, as Samtleben (1929) points out, only the crosswise dorsal and ventral muscles are literally transverse in position. Again, the body muscles are sometimes classed as *dorsal, ventral*, and *lateral* muscles, the dorsals and ventrals comprising longitudinal, oblique, and transverse fibers, and the laterals including dorsoventral and oblique fibers. This classification is evidently the most nearly consistent one that can be devised, and it has the added merit of being in conformity with the embryonic development of the muscles. Unfortunately, however, in naming the secondary muscle groups or individual muscles according to it, the plan brings out such terms as " median longitudinal dorsal muscles," " external median longitudinal dorsal muscles," or " second internal median longitudinal dorsal muscle." Still more unwieldy do such terms become when put into Latin form.

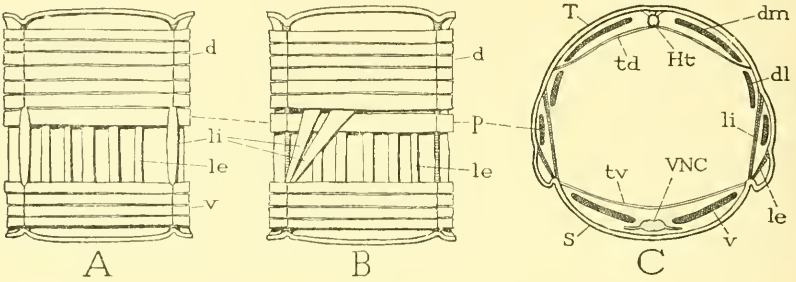

Fig. 13.—Diagrams of the more simple types of segmental musculature.

A, simple condition of musculature in right half of a segment, with dorsal (*d*) and ventral (*v*) fibers attached intersegmentally, external laterals (*le*) intrasegmentally, and internal laterals (*li*) on intersegmental folds.

B, upper ends of internal lateral muscles (*li*) migrated posteriorly, separating a paratergal muscle band (*p*) from the rest of the dorsal muscles (*d*).

C, cross section of segment, showing relations of principal groups of muscles. *dl*, lateral dorsal muscles; *dm*, median dorsals; *le*, external laterals; *li*, internal laterals; *p*, paratergal muscle; *td*, dorsal transverse muscles; *tv*, ventral transverse muscles; *v*, ventrals.

It is evident that strict anatomical and nomenclatural consistency in dealing with the body musculature leads to impractical results. The writer, therefore, has adopted a classification and nomenclature that recognizes the anatomical arrangement of the muscles, but which, in order to shorten the names, errs somewhat on the side of specificity in terminology. Five principal groups of muscles are distinguished and designated as follows: I. DORSAL MUSCLES (fig. 13 A, *d*), the fibers of which are typically longitudinal and primarily intersegmental in their attachments. II. VENTRAL MUSCLES (*v*), resembling the dorsals in that their fibers are typically longitudinal and attached primarily on the intersegmental lines. III. LATERAL MUSCLES (*l*), typically dorso-ventral, their fibers both intersegmental and intrasegmental. IV. TRANSVERSE MUSCLES (C, *t*), lying internal to the longitudinals, including *dorsal transverse muscles* (*td*), and *ventral transverse muscles* (*tv*). V. SPIRACULAR MUSCLES (*s*), generally not more than two connected with each spiracle, one an *occlusor* (*os*), the other a *dilator* (*dls*).

All the body muscles are bilateral in their origin, and all of them except the transverse muscles remain so in the definitive state. The fibers of the ventral transverse muscles, which primarily are intersegmental, Heymons (1895) says are at first attached mesally on a fold of the body wall between the nerve cords. Later the fold is suppressed and the fibers from opposite sides become continuous across the sternal region. The fibers of the longitudinal dorsal and ventral muscles are always separated into symmetrical lateral groups along the midline of the dorsum and venter, but the lateral sets of dorsal transverse muscles come together on the ventral wall of the heart.

Each primary group of muscles may undergo an endless diversification resulting both from a multiplication of fibers in the group, and from a rearrangement of the fibers brought about by changes in the points of attachment. With respect to the dorsal and ventral muscles, the most general departure from the simple plan, in which the fibers all lie in a single plane, consists of a differentiation of the fibers in each group into *internal muscles* and *external muscles*. Thus it is found in nearly all insects that the dorsal and ventral muscles comprise each two layers of fibers, namely, *internal dorsals* (*di*) and *external dorsals* (*de*), and *internal ventrals* (*vi*) and *external ventrals* (*ve*). A second form of diversification affecting the dorsal and ventral muscles is a more or less distinct grouping of the fibers into median and lateral muscles. In most insects, therefore, we may distinguish four sets of dorsal fibers, and correspondingly four sets of ventral fibers. The several resulting muscles may then be distinguished as *median* and *lateral internal dorsals* (fig. 14 A, B, *dim*, *dil*), *median* and *lateral external dorsals* (*dem*, *del*), *median* and *lateral internal ventrals* (*vim*, *vil*), and *median* and *lateral external ventrals* (*vem*, *vel*).

The lateral muscles are more subject to irregularities than are the dorsal and ventral muscles, but they likewise are often divided into *internal laterals* (fig. 13 B, C, *li*) and external laterals (*le*).

Associated with the dorsoventral lateral muscles there is sometimes present a longitudinal muscle or group of longitudinal fibers lying external to the upper ends of the internal laterals (fig. 13, *p*). This muscle is called the "epipleural" muscle by Ford (1923), but since it occurs on the region of the dorsum, being situated above the line of the spiracles, and therefore not on the true pleural region, the writer would term it the *paratergal muscle* (*p*). Since this muscle belongs to the dorsum it should be classed as a dorsal muscle.

The fibers of the transverse muscles are never differentiated into distinct layers, but they may be variously grouped in both the dorsal system (fig. 13 C, *td*) and the ventral (*tv*).

The spiracular muscles comprise usually not more than two muscles associated with each spiracle. One is an occlusor of the spiracle, the other a dilator. The occlusor is seldom lacking; the dilator is less constant.

To express more concisely the principal groups of abdominal muscles and their subdivisions, we may tabulate the muscles in the following manner:

I. MUSCULI DORSALES (*d*).
  1. M. dorsales interni (*di*).
    a. M. dorsales interni mediales (*dim*).
    b. M. dorsales interni laterales (*dil*).
  2. M. dorsales externi (*de*).
    a. M. dorsales externi mediales (*dem*).
    b. M. dorsales externi laterales (*del*).
  3. M. paratergales (*p*).
II. MUSCULI VENTRALES (*v*).
  1. M. ventrales interni (*vi*).
    a. M. ventrales interni mediales (*vim*).
    b. M. ventrales interni laterales (*vil*).
  2. M. ventrales externi (*ve*).
    a. M. ventrales externi mediales (*vem*).
    b. M. ventrales externi laterales (*vel*).
III. MUSCULI LATERALES (*l*).
  1. M. laterales interni (*li*).
  2. M. laterales externi (*le*).
IV. MUSCULI TRANSVERSALES (*t*).
  1. M. transversales dorsales (*td*).
  2. M. transversales ventrales (*tv*).
V. MUSCULI SPIRACULORUM (*s*).
  1. M. occlusores spiraculorum (*os*).
  2. M. dilatores spiraculorum (*dls*).

Each secondary group of muscles is often again subdivided into several bundles of fibers. These ultimate individual muscles may be given numerical designations, beginning medially in the case of the longitudinal muscles and anteriorly with the lateral muscles. Thus the individual muscles of the median internal dorsals may be specifically indicated *1dim*, *2dim*, *3dim*, etc., the external laterals *1le*, *2le*, *3le*, etc., and the muscles of the other groups in like manner (fig. 15 A). If it is desired to show that a muscle belongs to a particular segment, this may be expressed by adding to its symbol a Roman numeral designating the number of the segment, thus *1dimII*, *3vimIV*, *2leVI*, etc. In describing the complete musculature of a species, however, the writer has found it more practical to number the muscles with Arabic numerals, rather than to attempt to follow any system of lettering that pretends to identify homologous muscles in consecutive segments.

The dorsal muscles.—The muscles of the dorsum are primarily composed of longitudinal fibers of segmental length attached on the intersegmental folds; in many larvae the principal dorsal fibers retain this primitive condition. Wherever the dorsum, however, contains fully-developed sclerotic terga, a secondary segmentation is established, and the folds on which the dorsal muscles are attached become the antecostae of the definitive tergal plates (fig. 14 C, *Ac*). The longitudinal, primitively intrasegmental muscles thus become functionally intersegmental, and serve to contract the abdomen in a lengthwise direction by retracting each tergum into the posterior end of the segment preceding, as far as the intersegmental membrane will allow. The anterior end of a longitudinal abdominal muscle, therefore, may be termed the *origin*, and the posterior end its *insertion*.

The differentiation of the dorsal fibers into internal and external muscles is the rule in both adult and larval stages of pterygote insects. The internal dorsals commonly retain their longitudinal positions, their segmental lengths, and their attachments on the antecostae; but there are many departures from this generalized condition. Frequently the fibers take an oblique position, and sometimes they become shorter than segmental length by a migration of their origins to the postcostal area of the tergum, or of their insertions to the precostal area. The external dorsals seldom retain a segmental length; typically they are short muscles lying in the posterior parts of the segments (fig. 14 C, *dc*), and often they become strongly oblique, sometimes actually transverse, giving a movement of torsion between the two segments they connect. Finally, the external dorsals may become completely reversed in position (D, *dc*), their origins being so far back on each tergum that they lie posterior to the points of insertion on the anterior edge of the precostal rim of the following tergum. In such cases, the external dorsals become antagonistic to the internal dorsals (*di*), and function as abdominal *protractors,* since their contraction lengthens the abdomen by decreasing the overlap of the segments.

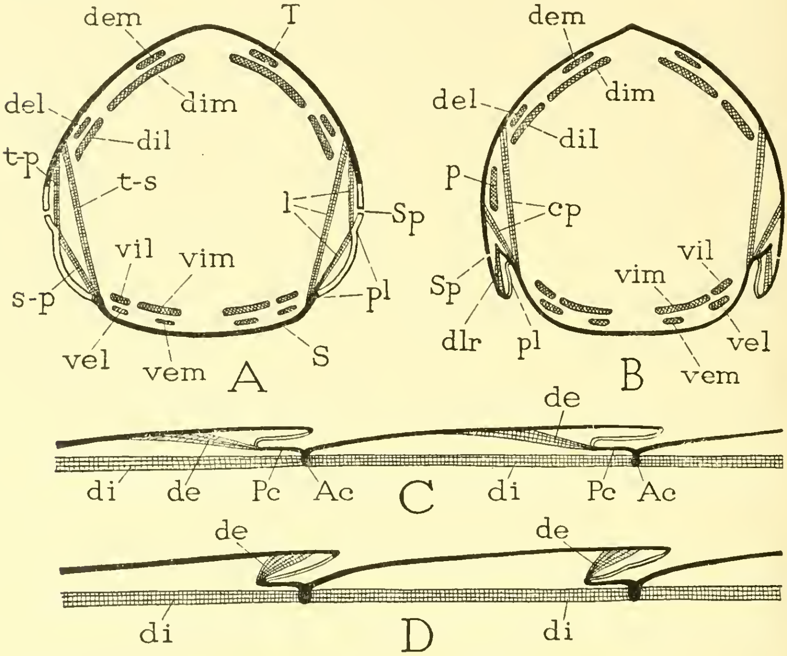

FIG. 14.—Diagrams illustrating more evolved types of musculature, and segmental mechanisms.

A, dorsal muscles differentiated into internal and external median dorsals (*dim, dem*), and internal and external lateral dorsals (*dil, del*); lateral muscles (*l*) differentiated into tergo-sternal (*t-s*), tergo-pleural (*t-p*), and sterno-pleural (*s-p*) groups; ventral muscles differentiated into internal and external median ventrals (*vim, vem*), and into internal and external lateral ventrals (*vil, vel*).

B, illustrating the compressor and dilator mechanism of an abdominal segment, in which some of the lateral muscles function as compressors (*cp*), and others, attached ventrally on edge of tergum, become dilators (*dlr*).

C, usual arrangement of dorsal muscles as seen in longitudinal section, with internal dorsals (*di*) attached intersegmentally on antecostae (*Ac*), and external dorsals (*de*) arising on posterior parts of terga, both sets acting as retractors of the terga.

D, modification by which external dorsals (*de*), attached in posterior folds of terga, become antagonistic to internal dorsals (*di*) and act as protractors of the terga.

The division of the dorsal muscles into median and lateral groups of fibers affects both the inner and the outer layers (fig. 14 A, B, *dim, dil,* and *dem, del*), but it is not always apparent, and the lateral dorsals are sometimes absent. The line of division of the inner dorsals into median and lateral muscles is sometimes marked by the points of origin of the dorsal transverse muscles on the tergal wall (figs. 13 C, 15 B, *td*).

The paratergal muscle of the dorsum (figs. 13 B, C, 14 B, *p*) is not commonly present in adult insects, or, at least, its fibers are not generally separated from those of the other lateral dorsal muscles. It is well developed in the Acrididae (fig. 15 B, *169*), where it is represented in each of the pregenital segments but the first (fig. 16) by a band of intertergal fibers lying above the line of the spiracles external to the upper ends of the internal lateral muscles (fig. 15 B, *175*, *176*). According to Ford (1923) it is also present in the Plecoptera ("epipleural muscle"). The paratergal muscle occurs more commonly in larval insects. In the abdomen of the larva of *Dytiscus* it is represented by a lateral band of fibers (fig. 18, *p*) cut off from the other dorsal muscles (*dil, dill*) by the upper ends of the internal lateral muscles (*lill*). An apparently corresponding muscle, consisting of a pair of parallel fibers extending lengthwise on each side of the body above the line of the spiracles, is characteristic of the caterpillars (figs. 20, 21, *p*). In the larva of *Tipula* there is a broad band of paratergal fibers on each side of the body attached on the middle of the laterodorsal areas of successive segments (fig. 22, *p*).

The ventral muscles.—The ventral abdominal muscles undergo an evolution parallel in most respects with that of the dorsal muscles. Their fibers are nearly always differentiated into internal and external layers, and those of both groups are commonly separated into median and lateral groups. The fibers of the internal layer are typically intersegmental wherever complete sternal plates are developed, and serve as *retractors* of the ventral arcs of the segments. The external ventrals are usually short and take their origins on the posterior parts of the sterna. Frequently they become sternal *protractors* by a reversal of their position, owing to the carrying forward of their points of insertion on apodemal arms of the anterior margins of the sterna until their morphologically posterior ends lie anterior to their points of origin on the preceding sterna. The length of the sternal apodemes commonly gives to the ventral protractor mechanism of the abdomen a greater effectiveness than has that of the dorsum.

The lateral muscles.—It is difficult to make satisfactory generalizations concerning the lateral muscles of the abdomen, because these muscles are subject to more variations in position and attachments than are either the dorsals or the ventrals. Most commonly the lateral muscles are tergo-sternal in their attachments (fig. 13 C, *li*, *le*), and typically they are vertical in position; but they may comprise tergopleural and sterno-pleural fibers (fig. 14 A, *t-p, s-p*), as well as tergo-sternal fibers (*t-s*), and generally some of them are oblique. A division of the lateral muscles into *internal laterals* and *external laterals* (fig. 13 B, C, *li, le*) is not always apparent, often because of the absence of the internal group, but it is of common occurrence.

The internal lateral muscles, when present, are longer than the external laterals because their upper attachments are at a higher level on the dorsum than are those of the external muscles (figs. 13 C, *li,* 15 B, *175, 176*). The position of the internal laterals along the sides of a segment is variable. The muscles are usually situated in the middle or anterior parts of the segments (fig. 16), but in some cases they are limited to the extreme anterior regions, and in certain holometabolous larvae they lie on the intersegmental folds. The internal lateral muscles, however, do not in all cases constitute a homogeneous group of muscles; one or more sets of anterior fibers, such as those forming the first internal lateral muscle of *Dissosteira* (fig. 15 B, *175*), lie internal to the lateral tracheal trunk, while the more posterior fibers, as the second internal lateral of *Dissosteira* (*176*), may lie external to the tracheal trunk. In some insects, on the other hand, the entire series of internal lateral fibers are internal to the lateral tracheal trunk (fig. 22).

An example of the limitation of the internal lateral muscles to the intersegmental regions is well shown in the larva of *Rhagoletis pomonella* (fig. 23), a trypetid fly, in which the muscles consist of slender bands of fibers (*li*) lying laterally on the intersegmental folds in both the abdomen and the thorax. Similar intersegmental muscles, comprising each three groups of fibers, are described by Samtleben (1929) in the larvae of Culicidae as "musculi dorsoventrales mediales," the upper attachments of which are between the ends of the dorsal longitudinal muscles, and the lower attachments between the ends of the ventral muscles. In the larva of *Tipula* (fig. 22) the internal lateral muscles consist of a series of approximately vertical fibers (*li*) occupying the anterior half of the lateral wall of each segment, but the anterior fibers in each segmental group are attached on, or close to, the intersegmental fold. All of these fibers lie internal to the ventrolateral tracheal trunk (*LTra*) and a broad band of longitudinal paratergal fibers (*p*). In the caterpillars a group of several internal lateral fibers (figs. 20, 21, *li*) arise from the lateral extremity of each ventral intersegmental fold and diverge posteriorly to the dorsum, going internal to the lateral tracheal trunk (*Tra*) and the paratergal muscles (*p*).

Similar groups of internal lateral muscles occur in both the abdomen and the thorax of the larva of *Dytiscus*. According to Speyer (1922), a two-branched internal lateral muscle, "musculus dorsoventralis abdominis *a*," occurs in the anterior part of each of the first five segments of the abdomen in the larva of *Dytiscus marginalis* (fig. 18, *liII*). The lower ends of these muscles are inserted on the intersegmental folds, but their upper ends are attached in the anterior parts of the segments following on the tergal plates between median and lateral groups of fibers of the dorsal longitudinal muscles (*di*, *p*). In the thorax, the upper ends of the corresponding muscles (*li*) are more nearly intersegmental; their lower attachments are on the intersegmental "furcillae" and on the sternal apophyses. These muscles of the larval thorax possibly correspond with muscles of the adult described by Bauer (1910), "*musculi levatores prothoracis* and *mesothoracis*," extending from the sternal apophysis of the prothorax and mesothorax to the first and second phragmata, respectively. Similar muscles are sometimes present in the thorax of other adult insects; one such occurs in Acrididae attached ventrally on the prosternal apophysis and dorsally on the intersegmental fold in front of the mesepisternum (see Snodgrass, 1929, figs. 32, 34, 59).

The fragmentary review of the position of the internal lateral muscles given above suggests that the anterior fibers at least of each segmental group represent lateral dorsoventral muscles that are primarily intersegmental (fig. 13 A, *li*). The fibers have a tendency in the abdomen to migrate posteriorly, especially on the dorsum (B), though they may extend backward along the lateral edges of the sternum also (fig. 22). Their upper ends thus cut off a lateral group of fibers (fig. 13 B, *p*) from the longitudinal dorsals, which become the paratergal muscles. These primarily intersegmental internal lateral muscles run mesad to the lateral tracheal trunks in some insects (Acrididae, lepidopterous larvae, tipulid larvae), and their homologues presumably should do so in all insects, but this point has not been determined. Other internal lateral muscles of the abdomen, lying external to the lateral tracheae, are probably intrasegmental in their origin.

The external lateral muscles are typically dorsoventral and intrasegmental (fig. 13 A, B, *le*). Some of them, however, are frequently oblique (fig. 15 B, *178*, *179*), and the latter may include an intersegmental muscle (fig. 15 A, *jl*). The dorsoventral fibers are sometimes attached on the pleural membrane or on "pleural" sclerites, forming thus tergo-pleural and sterno-pleural muscles (fig. 14 A, *t-p*, *s-p*).

While most of the lateral muscles are *compressors* of the abdomen (fig. 14 B, *cp*), since they serve to approximate the sternum to the tergum in each segment, some of them, at least in insects that make active respiratory movements, serve as *dilators* (*dlr*). The lateral dilators become mechanically antagonistic to the compressors by reason of the fact that their points of origin are on the lower edges of the terga ventral to their insertions on the overlapped edges of the sterna. As in the case of the sternal protractor muscles of the abdomen, the effectiveness of the dilators is commonly increased by the dorsal extension of their points of insertion on apodemes of the sterna.

There is no evidence to suggest that any of the lateral abdominal muscles of adult pterygote insects are derived from the primitive body muscles of the lost appendages. In larval forms that retain appendage rudiments on the abdomen, the lateral muscles lie mesad of the limb bases (figs. 34 A, 36 C, *l*), attached above on the tergum and below on the sternum. The persisting muscles of the abdominal appendages pertain to the distal movable parts of the organs, and these muscles take their origins within the limb bases (figs. 34 A, 36 D). Exceptions to this occur in the case of the muscles of retractile vesicles of holometabolous larvae (fig. 36 C, D, *rvs*), which take their origin on the dorsum, but these muscles are not retained in the adult. The branchial muscles of ephemerid larvae (fig. 15 A, *bmcls*) are said to persist in the adult stage, but they do not appear to correspond with any of the lateral muscles in other pterygote insects.

The transverse muscles.—The transverse muscles of the abdomen are best known as the muscles of the dorsal and ventral diaphragms (fig. 13 C, *td, tv*). It seems probable that primitively these muscles were intersegmental in position, their fibers being attached on the intersegmental folds, one set being dorsal, the other ventral.

The fibers of the dorsal transverse muscles arise typically in groups on the anterior edges of the lateral parts of the abdominal terga, and spread mesally to their insertions along the ventral wall of the heart. Only in a few insects are they evenly distributed along the entire length of the tergum, or collected into anterior and posterior groups. The usual anterior origin of the fibers, therefore, suggests that the dorsal transverse muscles are primarily intersegmental. In the caterpillars (fig. 21 A, *td*) they practically have this position, except that the diverging inner ends of the fibers spread into the anterior and posterior parts of the adjoining segments. Usually the muscles of the dorsal diaphragm extend from the second to the eighth or ninth abdominal segment, but in the Blattidae they are said to occur not only in the first abdominal segment, but also in the mesothorax and the metathorax (Brocher, 1922). In the larvae of anisopterous Odonata, according to Whedon (1919), a muscular dorsal diaphragm is present only in the fourth or the fifth segment of the abdomen.

The ventral transverse muscles in some of the Orthoptera (Tettigoniidae and most of the Gryllidae) take the form of widely separated compact bundles of fibers crossing the anterior parts of the segmental sterna. In others, as in the Acrididae, the origins of the fibers are distributed along the sides of the sterna, and the muscles form a typical ventral diaphragm occupying most of the length of the abdomen. Ford (1923) thinks that the compact type, that is, the one in which the fibers form individual transverse muscles segmentally arranged, is the primitive type, and that it has been derived from a diffuse or web-like type. The writer, however, believes that the relations may be the reverse, especially considering Heymons' (1895) statement that the transverse muscles of Orthoptera are formed in the embryo along the intersegmental folds. In the larvae of anisopterous Odonata, according to Whedon (1919), there is in the abdomen only a single, large, spindle-shaped, somewhat flattened ventral transverse muscle lying in the extreme anterior part of the sixth segment, attached laterally on the intersegmental fold.

In the higher insects in which ventral transverse muscles are present in the adult, as in Hymenoptera, the muscles form a continuous sheet of tissue over the ventral sinus. Ventral transverse muscles are usually absent in holometabolous larvae. In the honeybee larva, Nelson (1924) says, there is present in the newly hatched larva a well-developed ventral diaphragm consisting of a continuous sheet of transverse fibers, but in older larvae it becomes a vestigial structure formed of more or less isolated fibers entirely too few in numbers to constitute more than a loose and insignificant meshwork.

The spiracular muscles.—The musculature of the abdominal spiracles includes one or two muscles associated with each spiracle. The muscle most generally present is an occlusor. This is a short muscle usually attached at both ends on the base of the spiracular atrium, where its contraction compresses the inner end of the atrium and so closes the entrance to the trachea. In the Acrididae the occlusor muscle arises dorsally on the tergal wall close behind the spiracle. A dilator, or opening muscle of the spiracle, antagonistic to the occlusor, occurs at least in most of the Orthoptera, Lepidoptera, and Hymenoptera, but it is absent in Odonata, some Orthoptera, and Coleoptera. The dilator commonly takes its origin on the tergum or on the lateral margin of the sternum of the segment in which the spiracle is situated.

The musculature of the thoracic spiracles is usually different from that of the abdominal spiracles, as is the structure of the spiracles themselves. The spiracles of Apterygota and Ephemerida are said to have no musculature.

THE ABDOMINAL MUSCULATURE OF ADULT PTERYGOTA

The musculature of the visceral segments of the abdomen in pterygote insects adheres closely to the generalized plan of structure, though there are usually slight aberrations in the first segment or first and second segments. The musculature of the genital and postgenital segments is often highly specialized or reduced, but it is undoubtedly derived from the same muscle pattern as that prevailing in the less modified segments. The usual departures from the generalized musculature in the visceral region of the abdomen consist principally of a reduction in the number of muscles, a shortening in the length of some of them, and a shifting of the points of attachment, bringing about simple changes in the position of certain muscles. A brief examination of the orders in which the abdominal musculature is best known will serve to show the extent and nature of the modifications that take place in the visceral segments. The more extensive modifications in the specialized genital and postgenital segments need not concern us here.

Ephemerida.—The most generalized abdominal musculature of the adult pterygote type occurs in the Ephemerida, and the muscle pattern is here essentially the same in both adult and larval stages. We may, therefore, follow Dürken's account of the larval musculature of *Ephemerella ignita*, which can easily be verified in any ephemerid species. Most of the abdominal muscles (fig. 15 A), except those inserted on the gill bases (*bmcls*), lie in a single plane against the body wall, and are comprised in dorsal (*d*), lateral (*l*), and ventral (*v*) groups. The first two dorsals (*1d, 2d*), counting outward from the median line, and the second and third ventrals (*2v, 3v*) in most of the segments are typical intersegmental, longitudinal muscles attached on the anterior margins of successive segmental plates. The third dorsal (*3d*), however, is atypical in that most of its fibers take their origin on the middle of the tergum and cross the following segment to be inserted on the anterior margin of the second tergum following. This muscle Dürken calls a "compound intersegmental" muscle. The fourth dorsal (*4d*) and the first and fourth ventrals (*1v, 4v*) are short muscles arising on the posterior parts of the segmental plates before those of their insertions. These muscles thus appear to correspond with the external dorsal and ventral muscles usually more definitely differentiated from the internal muscles in the majority of the Pterygota.

The true lateral body muscles of *Ephemerella* include only the intrasegmental, vertical, tergo-sternal muscles (fig. 15 A, *1l, 2l, 3l*), and the intersegmental, oblique tergo-sternal muscle (*4l*). The groups of branchial muscles (*bmcls*), inserted in the larva on the bases of the gills, are described and figured by Dürken as arising on the lateral parts of the sterna. The areas on which these muscles arise, however, are clearly distinct from the true sterna (fig. 34 A, B, *Stn*), and very evidently represent the bases of the abdominal limbs (*LB*), of which the gills (*Brn*) are the distal movable parts. The branchial muscles, therefore, are not body muscles, but are intrinsic muscles of the appendages, and take their origins within the limb bases. The true lateral body muscles (fig. 34 A, *l*) are tergosternal in their attachments and lie mesad of the lobes (*LB, LB*) supporting the gills. The gill muscles of the ephemerid larva, Dürken says, are retained without change in the adult. They do not appear

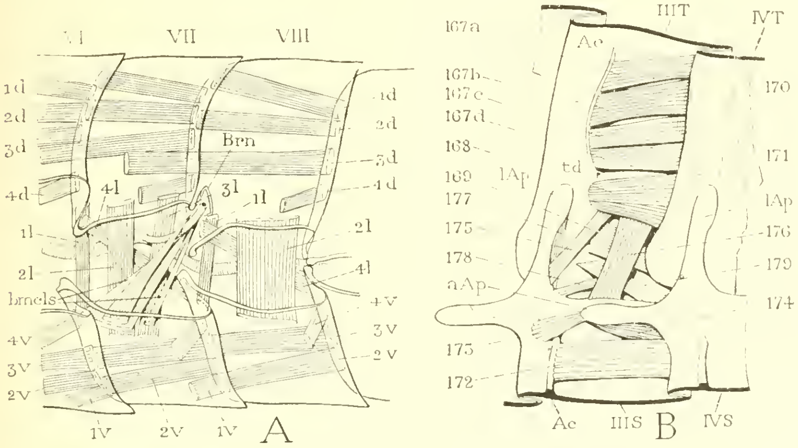

FIG. 15.—Examples of abdominal musculature.

A, musculature of left half of seventh and eighth segments (seen externally) of abdomen of larva of *Ephemerella ignita* (from Dürken, 1907); *bmcls*, branchial muscles, shown here as originating on lateral part of sternum, which is probably the ventral area of limb basis (see fig. 34 B).

B, muscles of right half of third abdominal segment (seen internally) of an acridid, *Dissosteira carolina*. *167*, internal median dorsals; *168*, internal lateral dorsal; *169*, paratergal muscle; *170*, external median dorsal; *171*, external lateral dorsal; *172*, median ventral; *173*, internal lateral ventral; *174*, external lateral ventral; *175*, *176*, internal laterals; *177*, *178*, *179*, external laterals; *td*, insertion point of dorsal transverse (cardiac) muscles.

to have representatives in the pregenital segments of any other adult pterygote insect.

Odonata.—The muscles of the first three abdominal segments of adult Odonata are described by Backhoff (1910) and by Schmidt (1915) in connection with a study of the male genital organs, and some of the abdominal muscles of odonate larvae are figured by Calvert (1911, 1915). A more complete description of the larval musculature as a part of the respiratory mechanism is given by Wallengren (1914), and of that of the adult by Steiner (1929), while a full account of both the adult and larval muscles in Zygoptera and Anisoptera will be found in the paper by Whedon (1919) on the morphology of the odonate abdomen, a few errors in which are corrected by Steiner (1929).

In the abdominal musculature of the Odonata there is nothing to suggest a type of structure more primitive than that of other Pterygota; the fundamental plan of the muscle arrangement is that of pterygote insects in general, and has little to distinguish it from the muscle pattern of orthopteroid insects. The generalized plan of musculature is best retained in the larvae of Zygoptera. The muscles here comprise internal and external longitudinal dorsals, internal and external longitudinal ventrals, and dorsoventral and oblique lateral muscles. The internal dorsal and ventral fibers are of segmental length; but the externals in each set are short, taking their origins on the posterior parts of the segments. In the Anisoptera the larval muscles are more strongly developed than in the Zygoptera, evidently as an accommodation to the respiratory and locomotor functions of the rectum, and the broad internal dorsal and ventral bands of fibers take on oblique direction. The adult musculature is much reduced in the abdomen, and most of the muscles are very short, but the arrangement of the muscles shows no radical departure from the fundamental pterygote pattern better preserved in the larva.

Orthoptera.—The comparative myology of the abdomen is better known in the Orthoptera than in any other of the larger orders of insects owing to the comprehensive review by Ford (1923) of the abdominal musculature of orthopteroid insects. Then, too, Voss (1905) in his thorough study of the thorax of *Gryllus* includes an account of the muscles of the anterior abdominal segments, and Du Porte (1920) describes the entire musculature of the abdomen in the same genus.

The abdominal musculature of the Orthoptera and related orders shows in all groups a differentiation of the dorsal and ventral muscles into internal and external layers of fibers, and in most cases a well marked separation between median and lateral fibers in each of these groups. In a general statement on the abdominal musculature of orthopteroid insects, Ford (1923) says: "In the common ancestors of the orthopteroid insects the tergal musculature probably consisted of two broad layers, an internal longitudinal and an external oblique, with the inner layer approximately equaling the length of the tergum, and the outer layer much shorter. Of the present-day orders the Blattaria approach closely this hypothetical type." Of the ventral musculature Ford says: "The hypothetical type of sternal musculature is similar to the tergal, having the two-layered arrangement of longitudinal ental and oblique ectal muscles. The Blattaria again resemble the hypothetical type."

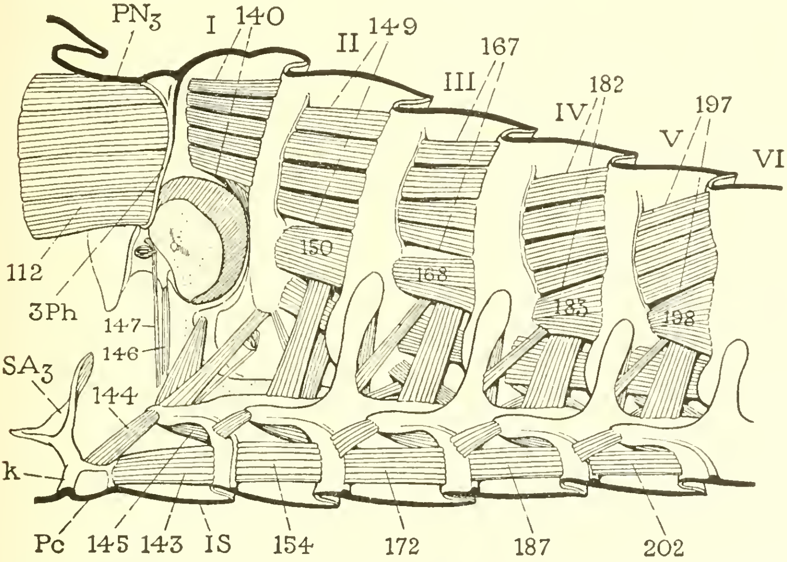

FIG. 16.—Musculature of the right half of the first five segments of the abdomen of *Dissosteira carolina*, together with dorsal muscles (*112*) of metathorax. (Compare with fig. 15 B.)

140-197, median internal dorsals; *150-198*, lateral internal dorsals; *143-202*, median ventrals; *144*, first lateral internal ventral; *145*, first lateral external ventral.

Since the external muscles of the dorsum and venter are not always oblique, being often parallel with the internal muscles, and since, furthermore, the dorsal and ventral muscles are not always differentiated into external and internal layers (fig. 15 A), it would seem to the writer more probable that all the dorsal and ventral fibers were primarily longitudinal and of segmental length, and that they had this arrangement in pre-orthopteroid insects. The internal dorsals and ventrals are likewise often oblique. Obliquity, therefore, would appear to be secondary also in the external muscles, in which it may be so accentuated that the muscles lie in a transverse direction, or are even reversed in position.

The lateral muscles of the Orthoptera are variable in their positions and in their attachments. They include typical vertical and oblique intrasegmental tergo-sternal muscles, oblique intersegmental tergo-sternal muscles, and in some cases muscles that may be termed "tergo-pleural" and "sterno-pleural," since they are inserted on the lateral membranes or on sclerites below the line of the spiracles. The so-called pleural areas on which these last named muscles are attached, however, probably really belong either to the dorsum or to the venter of the segment, and, if so, none of the lateral muscles is properly a "pleural" muscle.

In the Acrididae the internal dorsal muscles are distinctly separated into median and lateral groups of fibers (figs. 15 B, 16, *167, 168*) by the points of attachment of the dorsal transverse fibers on the tergum (fig. 15 B, *td*). The external dorsals assume very oblique or transverse positions (*170, 171*). The ventral muscles are well differentiated into median and lateral groups of internal fibers (*172, 173*) and into lateral external muscles (*174*). The external ventrals (*174*) are sternal protractors by a complete reversal in the relation between their points of attachment. The lateral muscles in the third and succeeding segments (figs. 15 B, 16) comprise two internal dorsoventral laterals (fig. 15 B, *175, 176*), and three external laterals (*177, 178, 179*), of which the first (*177*) is an abdominal dilator by reason of its sternal attachment being on the upper end of a large lateral sternal apodeme (*lAp*). The upper ends of the internal laterals (*175, 176*) are attached on the tergum between the lateral internal dorsals (*168*) and a broad paratergal dorsal muscle (*169*). This last muscle is the "epipleural" muscle of Ford (1923), who says a similar muscle also is present in the Plecoptera.

Coleoptera.—The abdominal musculature of adult Coleoptera is known principally from the description of *Melolontha vulgaris* by Straus-Dürckheim (1828), and of *Dytiscus marginalis* by Bauer (1910) and Korschelt (1924).

The adult musculature of the abdomen of Dytiscus is relatively simple. As described by Bauer (1910) it consists of dorsal longitudinal muscles, ventral longitudinal muscles, and lateral muscles, to which list should be added the transverse muscles of the dorsal diaphragm.

Bauer terms the lateral muscles "musculi transversales abdominis," but, as pointed out by Samtleben (1929), the lateral muscles are dorsoventral and should not be termed "transverse." The largest muscles of the Dytiscus abdomen are the dorsal muscles. These consist of broad bands of fibers forming a wide sheet of muscles against the tergal region in each of the first six segments. The ventral muscles are present only in segments III, IV, and V. They include large median ventrals and small lateral ventrals. The median ventrals form three pairs of muscle sheets occupying the median sternal region of the segments, the fibers of the opposite groups in each pair converging posteriorly. The lateral ventrals ("musculi ventrales externi" of Bauer) are very small, each arising on the posterior lateral angle of the sternum of its segment, and being inserted on the anterior margin of the sternum following. The lateral muscles ("musculi transversales" of Bauer) comprise a pair of small, oblique tergo-sternal muscles crossing each other in the form of an X in each side of segments II to V inclusive, and a single oblique muscle in segment VI.

Hymenoptera.—The honeybee furnishes the principal information that we have on the abdominal musculature of Hymenoptera. The muscles of a typical abdominal segment of the honeybee have been described by Carlet (1890), Betts (1923), and Snodgrass (1925); the complete abdominal musculature is given by Morison (1927). The muscles characteristic of the part of the abdomen involved in respiration are well shown in the third and fourth segments (fig. 17). The dorsal muscles consist of three sets of fibers in each half of the segment, two of which are internal and one external. The internals form a broad median band of fibers (*dim*) slanting from in front posteriorly and medially, and a slenderer lateral muscle (*dil*) extending from in front posteriorly and laterally. The external dorsal is a short muscle (*del*) arising laterally on the posterior margin of the tergum and extending forward to its insertion on the tip of a lateral tergal apodeme of the following segment. The two sets of dorsals are thus antagonistic, the internal fibers being tergal retractors, and the external fibers tergal protractors. The ventral musculature comprises internal and external muscles, which are likewise antagonistic. The internal fibers form an oblique median internal ventral (*vim*) on each side of the sternum, the two converging mesally in the form of a V, and a slenderer lateral muscle (*vil*) oblique in the opposite direction. The external ventrals consist of a single small, fan-shaped lateral muscle on each side (*vel*), arising laterally on the posterior part of the sternum and inserted anteriorly on the lateral anterior apodeme of the following sternum. The lateral muscles comprise three tergosternal muscles in each side of the segment. .The first (*1l*) is a dilator of the abdomen, since it arises ventrally on the lateral part of the tergum and is inserted dorsally on the tip of the lateral apodeme of the sternum; the second and third laterals (*2l, 3l*) are oblique tergosternal compressors of the abdomen.

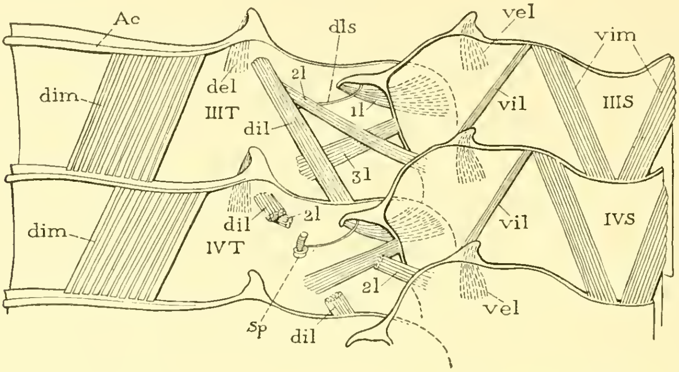

FIG. 17.—Musculature of two consecutive abdominal segments of adult *Apis mellifica,* showing the muscles on the left side.

Ac, antecosta; *del,* lateral external dorsal muscle; *dil,* lateral internal dorsal; *dim,* median internal dorsal; *1l, 2l, 3l,* first, second, and third laterals; *dls,* dilator muscle of spiracle; *Sp,* spiracle; *vel,* lateral external ventral muscle; *vil,* lateral internal ventral; *vim,* median internal ventrals.

The first lateral muscles (*1l*) are dilators of the abdomen, the second and third laterals (*2l, 3l*) are compressors; the internal dorsal and ventral muscles (*dim, dil, vim, vil*) are retractors of the segments, the external dorsals and ventrals (*del, vel*) are protractors.

THE ABDOMINAL MUSCULATURE OF ENDOPTERYGOTE LARVAE

The body musculature of endopterygote, or holometabolous, larvae, in its higher forms of development, attains an extreme degree of complexity; in its simpler forms it differs but little from the body musculature typical of all adult Pterygota. It appears, therefore, that the complex types of larval musculature represent specialized conditions adapting the larvae to their individual ways of living, and are not to be interpreted as meaning that insects are derived from ancestral worm-like forms having an intricate body musculature. The changes in the musculature that occur during the pupal metamorphosis are to be regarded as alterations necessitated by the restoration of the normal adult musculature, which involve varying degrees of destruction or reconstruction in the special, temporary larval musculature.

Coleoptera.—The larval musculature of Trichoptera and Neuroptera has not been fully studied, nor do we have any comparative work on the larval muscles of the Coleoptera. The complete account of the muscles of the *Dytiscus larva* given by Speyer (1922) and by Korschelt (1924), however, furnishes a basis for an understanding of the relation between the larval musculature and the musculature of adult insects. The structural changes which take place in the transformation from the larval to the imaginal musculature have been described by Breed (1903) in a trogositid, *Thymalus marginicollis.*

The abdominal musculature of the larva of *Dytiscus marginalis,* as described by Speyer, consists of four primary groups of fiber bundles, namely, dorsal muscles, ventral muscles, and, on each side, a set of lateral (dorsoventral) muscles. In the region of the first seven abdominal segments, the dorsal muscles comprise an internal set of intersegmental longitudinal fibers of segmental length (fig. 18, *diI, diII*), and outer sets of short fibers extending from the posterior parts of the terga to the following intersegmental folds. The ventral muscles consist likewise of internal (*viI, viII*) and external sets of intersegmental fibers. In each side of the first five abdominal segments Speyer distinguishes six lateral (dorsoventral) muscles. Five of these are external laterals, three of which are tergo-sternal and two tergo-pleural in their attachments. The other lateral muscle is an internal lateral and consists of two bundles of fibers (*liII*), which arise ventrally by a common base on the intersegmental fold. Dorsally the two branches are inserted on the anterior lateral part of the tergum between median and lateral sets of the dorsal longitudinal fibers (*di* and *p*). In the thorax the muscles (*li*) corresponding with

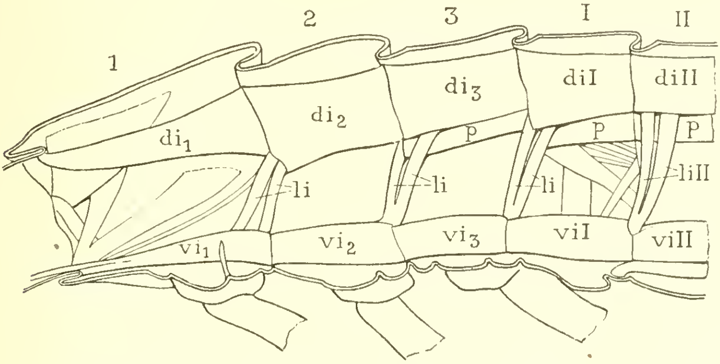

FIG. 18.—Body muscles in right half of thorax and first two abdominal segments of *Dytiscus marginalis* larva. (Outline from figure by Speyer, 1922, relettered in accord with muscle nomenclature adopted in this paper.)

di, internal dorsal muscles; *li,* internal lateral muscles, upper ends of which cut off paratergal muscles (*p*) from the other dorsals; *vi,* internal ventrals.

the internal laterals of the abdomen occur between the prothorax and mesothorax, between the mesothorax and metathorax, and between the metathorax and first abdominal segment. They are attached above more nearly on the anterior margins of the terga, and are inserted ventrally on the intersegmental " furcillae " and on the sternal apophyses. The posterior migration of the upper ends of the internal laterals in the metathorax and abdomen cuts off a lateral group of fibers (*p*) from the longitudinal dorsals that evidently corresponds with the paratergal muscle of *Dissosteira* (fig. 15 B, *169*).

It is clear that the abdominal musculature of the *Dytiscus* larva differs in no essential respect from that characteristic of adult insects generally. It presents a more primitive condition in that the internal lateral muscles retain ventrally their intersegmental attachments, whereas in most adult insects, when present, their ventral ends have migrated posteriorly along the edges of the sterna (fig. 15 B, *175, 176,* fig. 16).

The figure given by Berlese (1909) of the muscles in the first three abdominal segments of the larva of *Pentodon*, and the studies of Böving (1914) and of Craighead (1916) on the abdominal musculature of coleopterous larvae, including species of Cleridae, Trogositidae, Elateridae, and Scarabaeidae, suggest that the chief deviation from the *Dytiscus* larval muscle pattern consists only of a greater diversification in the position of the muscles, and of an increase in the number of muscles or individual fibers in each group. In any case it is clear that the larval musculature in the Coleoptera presents at most but a small increase in complexity beyond the minimum characteristic of adult pterygote insects. Proceeding from this condition found in the Coleoptera, therefore, we may expect to find that the more complex musculature of other holometabolous larvae represents only a more highly specialized condition.

Hymenoptera.—In the larvae of Hymenoptera the body musculature also retains a relative simplicity. The pattern of the abdominal muscles of the honeybee larva (fig. 19), as described by Nelson (1924), departs but little from the basic plan of the general adult pterygote musculature, though it is somewhat more complex than the abdominal musculature of the adult honeybee (fig. 17), and is not at all like the latter in detail. The dorsal muscles of a typical abdominal segment of the larva (fig. 19) consist of broad bands of internal longitudinal fibers (*di*) of segmental length, and of shorter, oblique external fibers (*de*). Some of the external fibers, by a transposition of their posterior attachments on the intersegmental fold, have come to overlap internally the internal dorsals. The ventral muscles include internal oblique (*vi*) and external oblique muscles (*ve*), all of segmental length. The lateral muscles comprise dorsoventral and oblique external laterals (*le*), and a strong, oblique, internal sterno-tergal muscle (*li*) attached on the consecutive intersegmental folds. It may be questioned whether this last muscle represents the internal laterals of the *Dytiscus* larva (fig. 18, *li*), but the only difference between the two is that the upper end of the muscle in the bee larva is attached on the intersegmental fold following that of its ventral attachment, a change that might have come about by a posterior migration of its dorsal end.

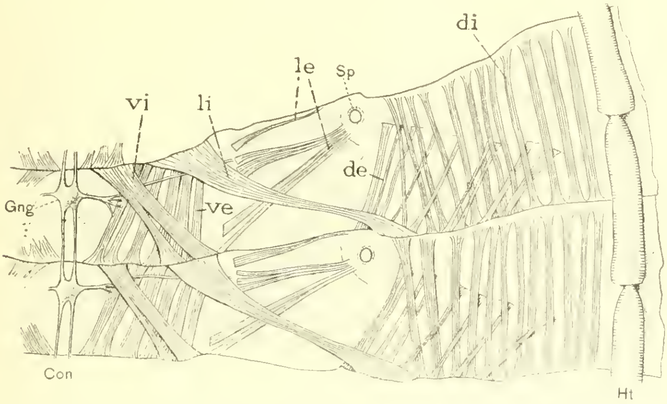

Fig. 19.—Musculature of right half of two consecutive abdominal segments of honeybee larva. (Figure from Nelson, 1924, but relettered in accord with muscle nomenclature adopted in this paper.)

Con, ganglionic connectives; *de*, external dorsal muscles, some of them secondarily internal at posterior ends; *di*, internal dorsals; *Gng*, segmental ganglion; *Ht*, heart; *le*, external lateral muscles; *li*, internal lateral muscle; *Sp*, spiracle; *ve*, external ventral muscles; *vi*, internal ventrals.

Lepidoptera.—The larvae of Lepidoptera have long been noted for the great number of muscles that lie against the body wall, and for the extreme complexity in the arrangement of the fibers. Fully 150 muscles, mostly individual fibers, may be counted in a typical abdominal segment of any caterpillar (figs. 20, 21). The principal muscles of the innermost layer (figs. 20, 21 A) are definite bands of parallel longitudinal fibers having segmental lengths and attached on the intersegmental folds. In the ventral region there are also strong external muscles of segmental length having an oblique position. Most of the external fibers, however, are of various lengths and are disposed in all directions against the body wall (fig. 21 B). On each side of the body, between the principal dorsal and ventral groups of muscles there is a pair of slender, longitudinal paratergal muscles (figs. 20, 21 A, B, *p*) lying just above the line of the spiracles and the lateral tracheal trunks (*Tra*). Anteriorly in each segment the paratergal muscles are crossed internally by a group of internal lateral fibers (*li*) arising ventrally on the intersegmental fold, and diverging dorsally and posteriorly to their attachments on the dorsum. These internal lateral muscles of the caterpillar lie internal to the lateral tracheal trunks. The dorsal transverse muscles of the caterpillar (figs. 20, 21 A, *td*) arise in groups immediately dorsad of the paratergal muscles from the posterior margins of the intersegmental folds.

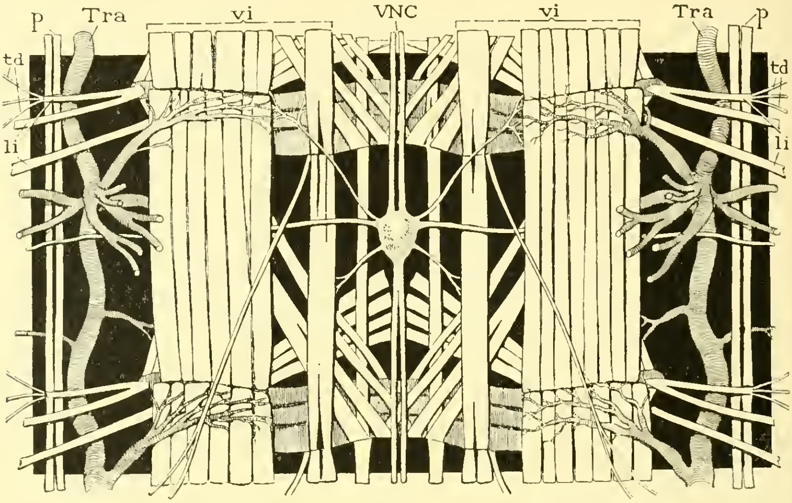

Fig. 20.—Ventral musculature of fourth abdominal segment of a caterpillar, *Estigmene acraea*.

li, internal lateral muscles; *p*, paratergal muscle; *td*, origins of dorsal transverse (cardiac) muscles; *Tra*, lateral tracheal trunk; *vi*, internal ventral muscles; *VNC*, ventral nerve cord.

The complexity of the body musculature of the caterpillar appears to demonstrate that the muscle system of insects has no limits imposed on its possibility of diversification both by multiplication and by rearrangement of its fibers, since there is no reason to believe that the intricate pattern of the caterpillar muscles represents in any way the primitive plan of insect musculature. In the other organization of the lepidopterous larva there is little to suggest a primitive condition. The head and mouth parts present the typical fundamental structure of these organs that has been developed in adult Pterygota, and on this basic structure have been built up the many special features of the caterpillar head and mouth parts adapted to the needs of the larva. The alimentary canal of the caterpillar is highly specialized in its musculature. The simplicity of the nervous and tracheal systems is not necessarily an indication of a primitive state; it is merely the retention of a generalized structure in these organs accompanying a high specialization in others. The presence of appendages on the pre-

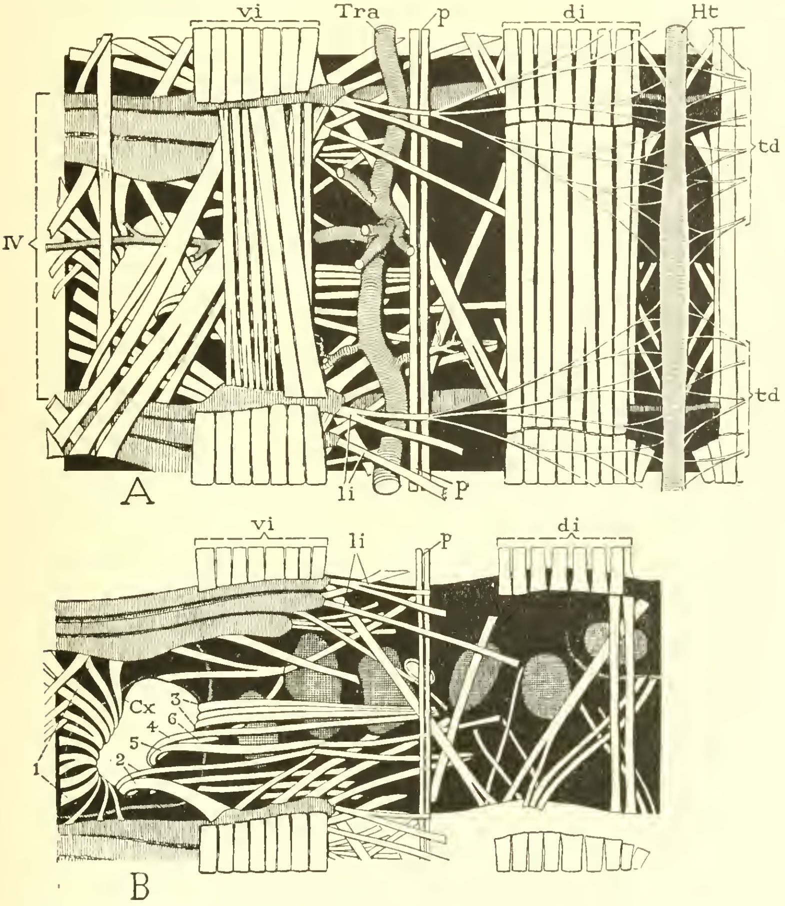

FIG. 21.—Abdominal muscles of a caterpillar, *Estigmene acraea*, seen by removal of inner muscles shown in figure 20.

A, muscles of right half of fourth segment (*IV*) after removal of internal ventrals (*vi*). B, outermost muscles in right half of third segment, showing particularly the leg muscles; cross-hatched areas represent bases of hair-bearing tubercles.

Cx, basal rim of leg; *di*, internal dorsal muscles; *Ht*, heart; *li*, internal lateral muscles; *p*, paratergal muscles; *td*, dorsal transverse (cardiac) muscles; *Tra*, lateral tracheal trunk; *vi*, internal ventral muscles.

genital segments of the abdomen likewise signifies nothing more than the retention of organs useful in the larval stage. In short, the wormlike form of the caterpillar and of other holometabolous larvae has no phylogenetic significance. It is a secondary adaptation, derived from the normal adult pterygote structure, accompanied by numerous specializations peculiar to the larva, and later discarded. The complex musculature of the caterpillar is only one of the features in the larval organization that have been specially evolved from the generalized adult structures of the immediate ancestors of the Lepidoptera to enable the caterpillar to perform more efficiently the duties that have devolved upon it from the apportionment of the life processes between the immature and adult stages of the individual.

Diptera.—The musculature of the larvae of Diptera shows a unique type of specialization in its highest development, but at the other extreme it has a pattern corresponding entirely with that of the generalized plan of abdominal musculature in adult Pterygota.

The simpler forms of dipterous larval musculature, known in the Tipulidae, Psychodidae, Chironomidae, Culicidae, and Tabanidae, consist of dorsal and ventral bands of longitudinal fibers, and of lateral dorsoventral muscles. A primitive type of musculature occurs in the Psychodidae, where, as described by Dirkes (1928) for *Psychoda alternata,* the dorsal and ventral muscles are mostly longitudinal and attached on the intersegmental folds, though a few in each set are shorter than segmental length. In the first abdominal segment there are five dorsoventral laterals and two oblique laterals on each side. The first of the dorsoventral muscles is attached on the intersegmental fold between metathorax and abdomen, the others follow along the side of the segment. A similar condition exists in the Culicidae, as described by Samtleben (1929), except that here some of the inner muscles of the dorsal and ventral series in each segment cross obliquely over the outer muscles, and the inner lateral muscles are confined to the anterior parts of the segments, where they are attached on the intersegmental folds between the ends of the dorsal and ventral muscles. In the larva of *Tipula* (fig. 22) the musculature is complicated by a great increase in the number of fibers in all the principal groups, and by a diversification in their points of attachment, but there are few fibers taking an oblique course. In both the dorsal and ventral groups certain sets of fibers are attached regularly on the intrasegmental transverse folds of the body wall, and some of the median ventral fibers form somewhat oblique interlacing bundles. The internal lateral muscles (*li*) comprise a series of dorsoventral fibers lying in the anterior half of each segment *internal* to the lateral tracheal trunk (*LTra*). Outside of these muscles, and external to the tracheal trunk, is a wide band of longitudinal paratergal fibers (*p*) of

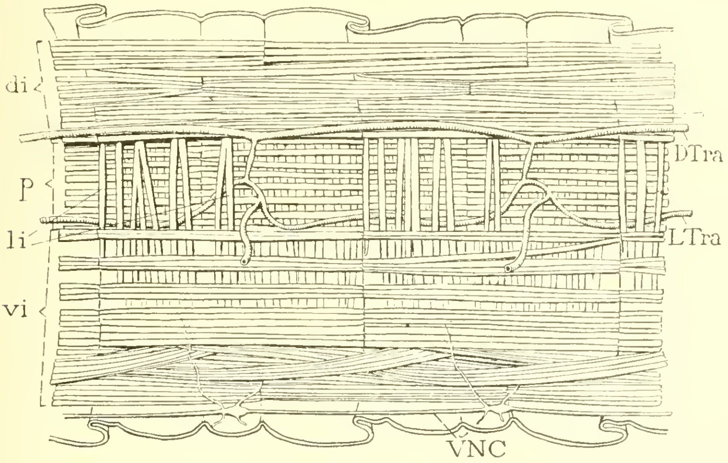

FIG. 22.—Musculature of right half of two consecutive abdominal segments of *Tipula abdominalis* larva.

di, internal dorsal muscles; *li*, internal lateral muscles distributed in anterior half of segment internal to lateral tracheal trunk (*LTra*); *p*, band of paratergal fibers; *vi*, internal ventral muscles.

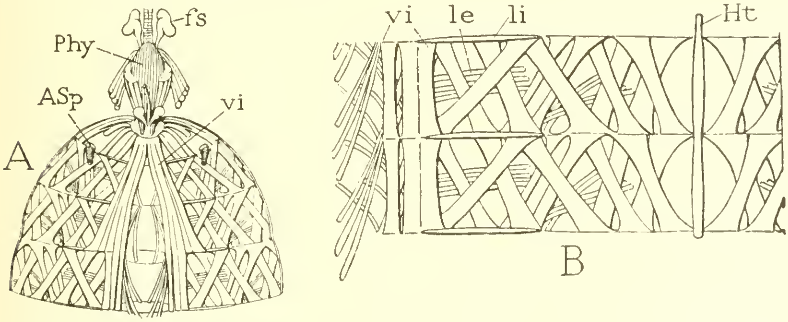

FIG. 23.—Musculature of the body wall of the larva of a cyclorrhaphous dipteron, *Rhagoletis pomonella*.

A, musculature of the thoracic and first abdominal segments, seen from above, with pharynx and connected parts turned forward. B, musculature of right half of two consecutive abdominal segments.

ASp, anterior spiracle; *fs*, frontal sacs; *Ht*, heart; *le*, external lateral muscles; *li*, internal lateral muscles; *Phy*, pharynx, turned forward; *vi*, longitudinal bands of internal ventral muscles.

segmental length, but attached on the median intrasegmental folds of the dorsum. The numerous external laterals lie against the body wall external to the paratergal fibers.

In the larvae of the higher Diptera the dorsal and ventral musculature appears to be merged into a double series of oblique muscles regularly crossing one another to form a network pattern repeated throughout the thorax and the abdomen (fig. 23). The only muscles that preserve a longitudinal direction are two bands of ventral fibers continued from the prothorax to the end of the abdomen (*vi*). There can be little doubt that this type of musculature represents a highly specialized condition, correlated with the great specialization which the maggot shows in nearly all other parts of its body organization. The lateral muscles, on the other hand, appear to retain a primitive condition. The internal laterals consist of slender fibers lying on the intersegmental folds (*li*) along the sides of the body. The external laterals (*le*) comprise a small group of fibers in the side of each segment against the body wall external to the network of oblique muscles.

THE ABDOMINAL MUSCULATURE OF APTERYGOTA

The body musculature of apterygote hexapods is not well known in all the major apterygote groups; it has been carefully studied in representatives of Protura, Collembola, and Dicellura, but only casually examined in Thysanura. Particularly desirable, therefore, would be a complete account of the body muscles of Machilidae and Lepismatidae.

Protura.—The abdominal musculature of the Protura is fully described by Berlese (1910) in his monograph on the " Myrientomata." In this group of hexapods, Berlese says, " the musculature is extraordinarily complex by reason of the great multiplicity of fibers extending in all directions, very much as in the larvae of metabolic insects." The muscle pattern of the proturan abdomen as shown by Berlese, however, is not complex by comparison with that of a caterpillar or of a muscoid maggot, and the proturan body muscles clearly fall into the three usual categories of insect muscles, namely, dorsal muscles, ventral muscles, and lateral muscles, to which are to be added the body muscles of the appendages.

The dorsal abdominal muscles of Protura are divided into external dorsals and internal dorsals. The internal dorsals (muscles of the second stratum of Berlese) consist of broad bands of fibers in the Acerentomidae attached on the successive tergal antecostae. In the Eosentomidae they are differentiated into median and lateral groups of fibers. The external dorsals (muscles of the third stratum of Berlese) include two large oblique muscles on each side of each segment; one (the intersegmental tergal muscle of Berlese) arising medially on the anterior part of the tergum and inserted laterally on the antecosta of the following tergum, the other (the intersegmental tergopleural muscle of Berlese) arising anteriorly on the tergal antecosta and inserted posteriorly on the "pleuron" of the following segment. The so-called "pleuron," however, is probably to be regarded as a paratergal sclerite.

The ventral muscles of the abdomen include likewise external ventrals and internal ventrals. The internal ventrals consist of paired bands of longitudinal fibers extending throughout the length of the abdomen. Each muscle band is divided into a median group of fibers attached on the sternal antecosta of each segment, and into longer lateral muscles in the first five segments attached on alternate sterna. The external ventrals occur only in the first three abdominal segments of Acerentomidae. Those of the first segment extend from the center of the sternum laterally to the bases of the appendages of this segment, and serve as adductors of the appendages. In the second and third segments corresponding pairs of muscles arising on the anterior median part of each sternum diverge posteriorly to the antecosta of the following sternum.

The lateral musculature of the abdomen in Protura has a very simple pattern. The lateral muscles comprise intrasegmental vertical tergo-sternal muscles, and intersegmental oblique tergo-sternal muscles. The intrasegmental laterals include in each of the first three abdominal segments of Eosentomidae, and in the first segment only of Acerentomidae, a pair of tergal muscles inserted ventrally on the base of the appendage, and in the following segments of Acerentomidae a single lateral tergo-sternal muscle. The intersegmental laterals consist of two slender muscles arising laterally at each end of the tergal antecosta in each segment, one of which goes to the anterior margin of the sternum of the preceding segment, the other to a corresponding point on the sternum of the following segment. From the first abdominal tergum a muscle extends downward to the posterior edge of the metathoracic sternum, and another goes forward to the posterior edge of the mesothoracic sternum.

An analysis of the proturan musculature, as described by Berlese, thus shows that the Protura suggest nothing different as to the pattern of the primitive body musculature of the Hexapoda from the idea to be derived from a study of the muscles of adult Pterygota. Since the lateral musculature in the Protura does not match with that of any pterygote insect, it does not appear to be the prototype of the lateral musculature characteristic of the Pterygota, and therefore, probably represents a special development. The Protura have no transverse muscles. Berlese describes a dorsal septum above the alimentary canal, but, he says, it is composed entirely of a connective tissue membrane and contains no muscle fibers. A closed dorsal vessel is likewise absent.

Collembola.—The account of the body musculature of the Collembola given by Lubbock (1873) is so complete and so convincing in its detail that no doubt can be entertained of its accuracy, though apparently no subsequent investigator has verified it, or given any attention to the musculature, other than that of the appendages, in this interesting group of insects. Lubbock describes the muscles of *Tomocerus* as an example of the musculature of a " linear " species, and those of *Smynthurus* to illustrate the musculature of a " globular " species. It is clear that the muscle pattern in the abdomen of the former is more generalized than in that of the latter, but that in both forms the musculature is modified in adaptation to the specialized functions of the abdominal appendages.

The abdominal musculature of *Tomocerus* is highly developed, consisting of strong bands of longitudinal dorsal and ventral muscles differentiated into internal and external groups of fibers, and of vertical and oblique dorsoventral lateral muscles. In the first segment two strong muscles arising on the tergum are inserted on the eversible vesicle of the collophore. In the third segment groups of lateral muscles are attached ventrally on the sternal region in the neighborhood of the tenaculum, but they do not appear necessarily to be primarily muscles of the pair of appendages presumably combined in this organ. The muscles of the furcula, or spring supported on the fifth segment, take their origins in the fourth and third segments, but they appear to be parts of the system of longitudinal body muscles rather than specific muscles of the leaping appendage. In *Smynthurus* the abdominal musculature is highly modified. The longitudinal muscles appear to be reduced and are mostly absent in typical form. On the other hand, there is a great development of vertical and oblique dorsoventral muscles associated with the base of the furcula, taking their origins in the posterior and middle parts of the abdomen.

In no respect can the collembolan musculature be said to be primitive; but it is evident that it may be derived from the same generalized plan of muscle arrangement that underlies the abdominal musculature of adult pterygote insects.

Dicellura.—It is most interesting to find in Grassi's description of the muscles of *Campodea* that the pattern of the abdominal musculature of this primitive apterygote insect conforms closely with the fundamental plan of the abdominal musculature of pterygote insects. According to Grassi, the musculature of an abdominal segment of *Campodea* comprises longitudinal dorsal and ventral muscles, oblique dorsal and ventral muscles, and dorsoventral lateral muscles. The longitudinal muscles are clearly the internal dorsals, and internal ventrals. The oblique dorsal muscles are the external dorsals. The external ventrals are represented by a pair of muscles convergent from the posterior margin of the segment to the mid-sternal region below the ganglion. These muscles Grassi terms *musculi subganglionares*. In addition to these there are also small oblique and transverse lateral ventral muscles. The true lateral muscles include several small tergosternal fibers on the sides of each segment. Finally there are the muscles of the styli and eversible vesicles.

By comparison with *Campodea,* or with almost any other insect, the body musculature in the Japygidae is extremely intricate, being highly complicated by the presence of numerous muscles that appear to have no relation to muscles in a simple type of musculature. The following account of the abdominal musculature of a member of this group is based on a study of specimens of the Australian *Heterojapyx gallardi,* for which the writer is indebted to Dr. R. J. Tillyard. Females of this huge japygid reach a length of 40 millimeters, and a dissection of the muscles in well preserved specimens is not a particularly difficult task.

The entire body musculature of *Heterojapyx* anterior to the ninth abdominal segment is highly complex, there being in each of the first eight segments of the abdomen at least 40 pairs of muscles, the arrangement of which makes a most intricate pattern against the body wall (fig. 24). In the mesothorax and metathorax the musculature is quite as complex, and in many details quite different from that of the abdomen, and is more diversified by the presence of the leg muscles. In the ninth abdominal segment the musculature is simplified. In the tenth it consists of a single pair of fiber bundles, but these constitute two great lateral muscles, almost completely occupying the segment, which act as adductors of the cercal forceps.

The 40 muscles in either half of a typical abdominal segment of *Heterojapyx,* shown in figure 24 representing segment VI, are comprised in the following groups:

I. DORSAL MUSCLES.—A median band *of inner longitudinal intersegmental dorsals* (A, *1a, 1b, 1c*) ; two *medio-lateral oblique intersegmental dorsals* (A, B, *2, 3*) ; two *latero-median oblique intersegmental dorsals* (B, *4, 5*) ; and an *outer longitudinal intersegmental dorsal* (B, *6*).

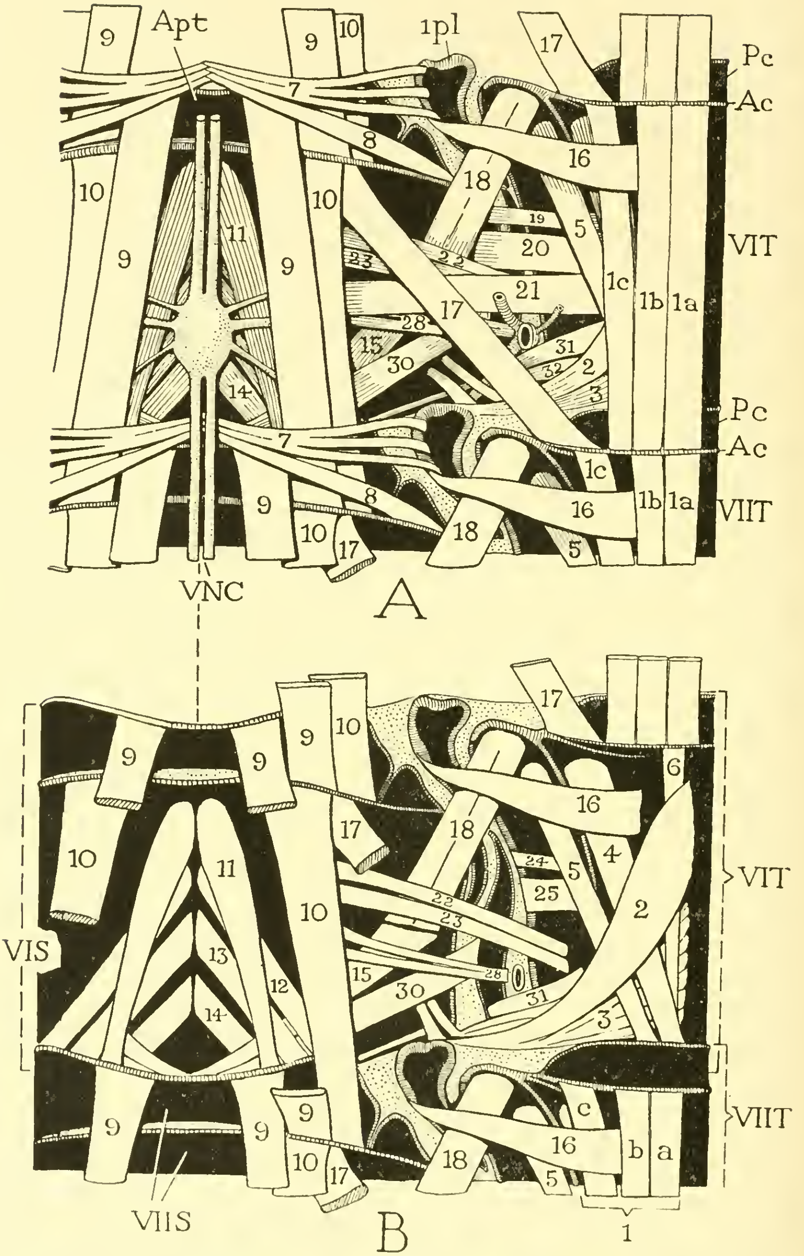

Fig. 24 A, B.—Musculature of sixth abdominal segment of *Heterojapyx gallardi*.

A, muscles of ventral region and right half of sixth segment, and anterior part of seventh segment. B, same view with muscles *7, 8, 9, 17, 19, 20, 21* partly or entirely removed.

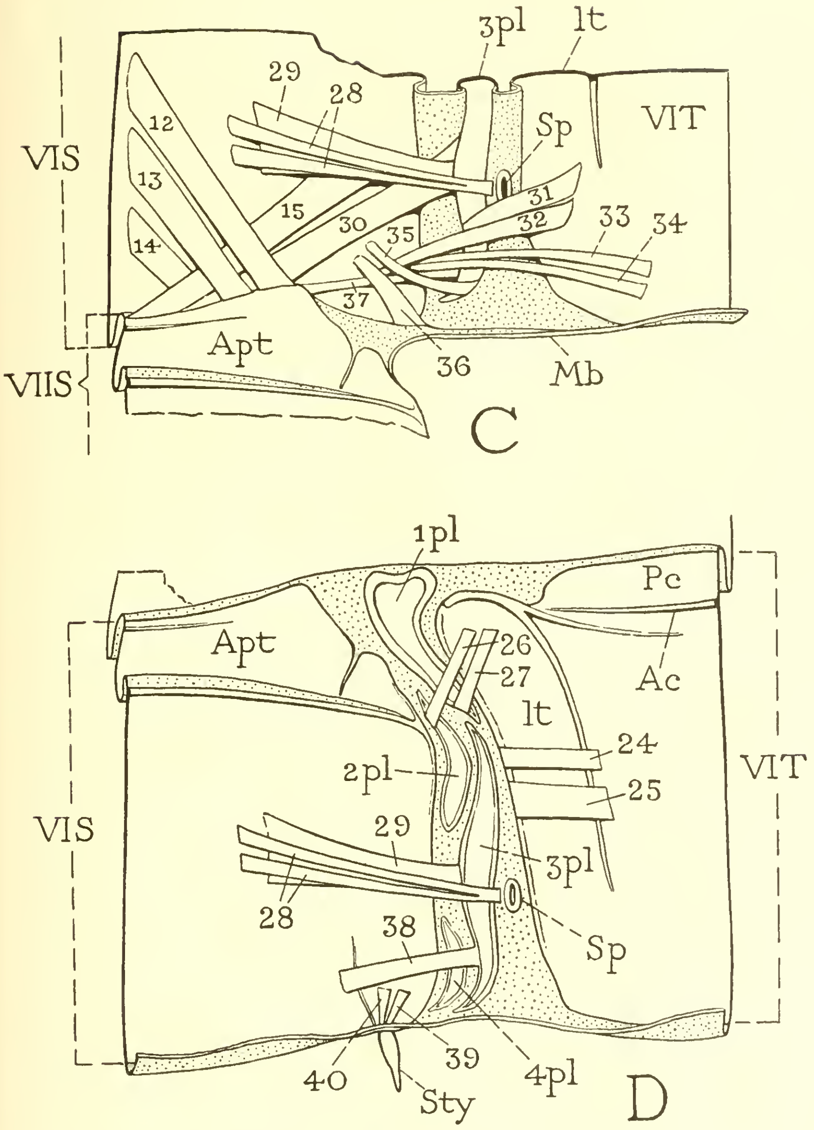

FIG. 24 C, D.—Outermost muscles of right half of sixth abdominal segment of *Heterojapyx gallardi*.

C, posterior part of right half of sixth segment and anterior part of seventh sternum. D, right half of sixth segment, showing segmental sclerites.

Ac, antecosta; *Apt*, sternal apotome; *lt*, laterotergal lobe; *Mb*, intersegmental membrane; *Pc*, precosta; *1pl*, *2pl*, *3pl*, *4pl*, pleural sclerites; *Sp*, spiracle; *Sty*, stylus; *VIS*, *VIIS*, sixth and seventh abdominal sterna; *VIT*, *VIIT*, sixth and seventh abdominal terga; *1-40*, muscles of sixth segment (see text, pages 59, 62).

II. Ventral muscles.—A group of *internal transverse intersegmental sterno-pleural* fibers (A, *7*) ; an *oblique intersegmental sterno-sternal muscle* (A, *8*) ; two *inner longitudinal intersegmental ventrals* (A, *9, 10*) ; five *outer oblique intersegmental ventrals*, four of which are median (B, *11, 12, 13, 14*), and one lateral (*15*).

III. Lateral muscles.—An *anterior intrasegmental tergo-pleural muscle* (A, B, *16*) ; an *oblique intersegmental sterno-tergal muscle* (A, *17*) ; an *oblique intrasegmental tergo-sternal muscle* (A, B, *18*) ; a series of five *intrasegmental transverse tergo-sternal muscles* (A, *19, 20, 21, 22, 23*) ; two short *lateral intra-tergal muscles* (D, *24, 25*) ; two small *anterior intrasegmental tergo-pleural muscles* (D, *26, 27*) ; two *median intrasegmental pleuro-sternal muscles* (C, D, *28, 29*) ; an *oblique intersegmental pleuro-sternal muscle* (A, B, C, *30*) ; a group of small external posterior lateral intrasegmental muscles (C, *31, 32, 33, 34, 35;* D, *38*) ; and two small posterior intersegmental muscles, one sterno-pleural (C, *36*), the other pleuro-sternal (*37*).

IV. Muscles of the stylus.—Two small muscles (D, *39, 40*) arising in the posterior lateral lobe of the sternum, inserted on the base of the stylus (*Sty*).

This complex and strongly developed musculature of *Heterojapyx*, which presumably is characteristic at least of the Japygidae, contains nothing to suggest that it represents the primitive plan of the body musculature of insects. It indicates, on the other hand, a highly specialized condition giving to these very small creatures a strength out of proportion to their size, which might enable them to burrow into hard soil or to insinuate their bodies into minute irregular spaces. In the multiplicity of individual muscles and in the diversity of their attachments, the body musculature of *Heterojapyx* resembles that of a caterpillar, but there is not the remotest likeness in detail, showing that the complexity of the muscle pattern in each case is but the result of a high degree of specialization adaptive to demands for dexterity of body movements. Both the caterpillar and *Heterojapyx* demonstrate the limitless potentiality of the insect muscular system, and make it all the more surprising that there are so few departures from the fundamental plan of muscle arrangement.

IV. THE ABDOMINAL APPENDAGES

There is no more vexing subject in the whole field of insect morphology than that of the homologies of the appendicular organs of the abdomen. Embryology shows at most that these organs are derivatives of the segmental appendages; it gives no positive evidence as to what part of a primitive limb may be preserved in the definitive rudiment, since the latter, whatever it may be, develops directly from the embryonic rudiment, instead of following what we should suppose would be the course of the phylogenetic evolution of the organ. Comparative anatomy is more likely to foster illusions than to lead to definite results, for while certain categories of facts may seem to align themselves satisfactorily in some limited scheme of suggested homology, the plan invariably breaks down when wider generalizations are attempted. The writer, therefore, can offer nothing new on the fundamental morphology of the abdominal appendages of insects that is likely to be generally accepted. Even so, however, it will be sufficiently worth while to bring together the principal facts at present known concerning the anatomy of the various appendicular structures.

Though the appendages of the insect abdomen are rudimentary in the sense that they do not in any case represent a fully-developed limb, they are in all cases specialized by a structural adaptation to some particular use. The abdominal appendages of most interest to entomologists are those of the genital segments, and if we can discover a means of identifying these organs in the various insect orders, this discovery alone will be of much practical value, and it then becomes a less consequential matter if we can not fully decide the exact morphological nature of the organs themselves.

It is not possible, however, to study with profit any modified or specialized appendicular organ without having some concept of the nature of the primitive limb structure from which it has been derived. Since there are current several different ideas concerning the fundamental structure of a primitive arthropod limb, it is therefore necessary for a writer to make clear at the outset of a discussion the particular theory from which he proceeds. The following sketch will give briefly the view on this subject here taken, and a more extensive discussion at the conclusion of this section will examine the possibilities of interpreting the structures of the abdominal appendages of insects according to the terms of the theory adopted, which is essentially that of Börner (1921), though with differences in special applications.

A comparative study of arthropod appendages soon shows that the number of segments in the limbs, the relative size of the segments, and even the segmental musculature are so variable in different arthropod groups that none of these features can be used as a guide for establishing the homologies of the segments or parts of the limb in any specific case. There are two joints of the limb, however, that recur in the same form in such a large number of appendages in the various arthropod groups as to suggest that they represent two primary points of flexure in the primitive ambulatory appendages, and that they may, therefore, be accepted as "constants" in the limb structure. These joints in a thoracic leg of an insect are the *coxo-trochanteral joint,* and the *femoro-tibial joint* (the *Hüftgelenk* and the *Kniegelenk* of Börner, 1921). The first (fig. 25 A, *f-g*) divides the appendages into a basal region, or *limb basis* (*LB*), and a distal shaft, or *telopodite* (*Tlpd*), which is movable on the basis in a vertical plane by a horizontal, dicondylic hinge (*f-g*). The limb basis, in the sense here understood, includes the potential coxa and subcoxa, which in some arthropods are differentiated as distinct parts of the basis (B, *Cx, Scx*), the coxa then becoming the functional or movable base of the appendage, while the subcoxa becomes a part of the lateral and ventral walls of the supporting body segment. The second fundamental joint of the limb forms the "knee" (A, *ft*), and divides the telopodite into a proximal trochantero-femoral piece, and a distal tibio-tarso-praetarsal piece, the two movable on each other in a vertical plane by an articulation which is either monocondylic, or dicondylic.

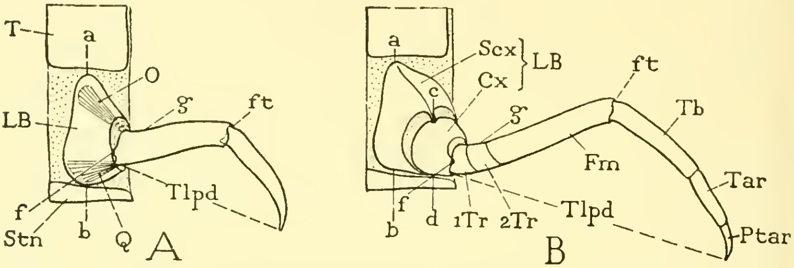

FIG. 25.—Diagrams showing the relation of the base of a leg to the body, and the theoretical progress of segmentation in the limb.

A, theoretically primitive appendage divided into a basis (*LB*) and a telopodite (*Tlpd*); the first movable antero-posteriorly on the body by a vertical axis (*a-b*) between tergum and sternum, the second movable on the basis in a vertical plane by a dicondylic, horizontal hinge (*f-g*) with levator and depressor muscles (*O, Q*) arising in the basis.

B, the fully segmented appendage: the basis divided into coxa (*Cx*) and subcoxa (*Scx*), the latter becoming the pleuron; the telopodite divided into the usual segments of an arthropod leg beyond the coxa.

If we conceive, thus, that the primitive arthropod limb is divided primarily into a basis and a telopodite, we should expect the baso-telopodite joint to be the point of flexure most generally preserved, and, as above noted, a joint does occur in the proximal part of practically all fully-developed arthropod appendages that is evidently, from its structure and musculature, to be identified as the joint between the primitive basis and the telopodite. This joint is the coxotrochanteral joint of an insect's leg. It is then reasonable to assume that the same joint is retained in reduced appendages, and that, finally, in an unsegmented limb rudiment it is the telopodite that has been lost, and that the part which remains is the basis.

The appendages of arthropods are prone to develop appendicular processes on the limb segments. Such processes may be either *endites* or *exites,* or both forms may occur on the same segment. Endites are developed particularly on the basis, serving as masticatory lobes on the gnathal appendages. In the Crustacea, exites of the basis are often gill-bearing organs, and an exite of the proximal segment of the telopodite commonly forms an outer branch of the appendage known as the exopodite. The study of rudimentary appendages becomes complicated by the fact that it is often difficult or impossible to determine whether a persisting part represents the main shaft of the limb, or an appendicular process of the latter.

BODY APPENDAGES OF CHILOPODA

The centipedes furnish a good example of arthropods that have retained a long series of body appendages preserving the form and function of ambulatory limbs. Each appendage of the pregenital region of the body is implanted in a membranous pleural area of its supporting body segment between distinct tergal and sternal plates (figs. 26, 27 A). The movable basal piece of a typical chilopod leg is a small segment generally termed the coxa, or coxopodite (*Cx*). The

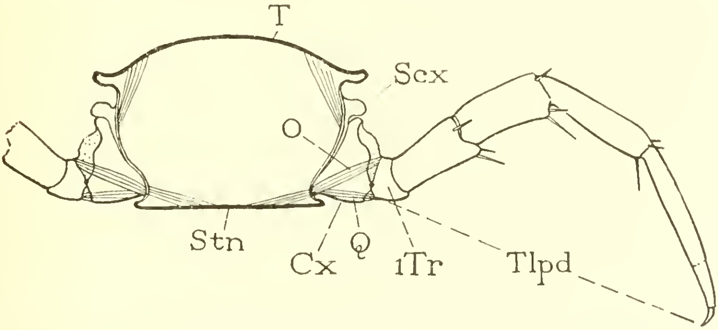

FIG. 26.—Somewhat diagrammatic cross section of a body segment of *Lithobius,* showing the relation of the subcoxa (*Scx*) and coxa (*Cx*) to the body and to the telopodite (*Tlpd*).

coxa supports the six-segmented telopodite (fig. 26, *Tlpd*), the proximal segment of which, or first trochanter (*1Tr*), is articulated to the coxa by a typical coxo-trochanteral hinge (fig. 25 B, *f-g*). Surrounding or partly surrounding the base of the coxa, in most of the pregenital segments but the last, is an area of the body wall containing one or several small sclerites (fig. 27 A, *Scx*). These sclerites appear to belong to the subcoxal region of the primitive limb basis, since upon this region are inserted the tergal muscles of the appendage, and within it arise muscles of the coxa. The coxa turns antero-posteriorly upon the subcoxa by an approximately dorso-ventral axis (fig. 25 B, *c-d*).

The large terminal pair of legs of a chilopod borne by the last pregenital segment (fig. 27 A, *Tlpd*) are supported each upon a single large plate in the lateral segmental wall (*LB*). The basal joint of each of these legs clearly corresponds with the coxo-trochanteral joints of the preceding appendages, and a comparison of the leg-bearing plate of this segment (*LB*) with the coxal and subcoxal sclerites of the segments immediately anterior to it leaves little doubt that the single "pleural" plate of the last segment represents both the coxa and the subcoxa of the preceding segments (*Cx, Scx*). In other words, the large pleural plates supporting the legs of the last pregenital segment are the limb bases (*LB*) undivided into coxal and subcoxal parts as in the other segments. The condition here, of course, may be the result of a secondary union of the subcoxal sclerotizations with the coxa, but it gives a convincing demonstration of the potential unity of the coxal and subcoxal regions of the limb basis, and at least suggests a primitive condition in which the limb basis occupied the lateral walls of the body segment between the tergal and sternal plates (A, C, *lT, lStn*). The levator and depressor muscles of the telopodite of the last pair of legs arise on the plate of the limb base and on the sternum (D, *O, Q*), and have their insertions on the first trochanter (*1Tr*).

The basal structure of the last pair of legs in the chilopoda is paralleled exactly in that of the legs of more generalized Arachnida as in the Phalangidae (fig. 46 A), in which the free part of each leg is supported on a large basal plate (*LB*) implanted in the lateral wall of the body. Börner (1904) regards the single basal plate of the terminal pair of chilopod legs as the united coxa and subcoxa; but in the Arachnida, he concludes (1921) that subcoxae are absent and that the plates supporting the telopodites are the coxae alone. It is not clear why structures so evidently similar should be differently interpreted.

In the Diplopoda the free basal segment of the leg, judging from its structure and the nature of its articulation with the next segment, would appear to be the coxa, and since the sternal plates of the Diplopoda surround the bases of the legs, we may conclude with Börner (1921) that the definitive sterna include the subcoxae. Silvestri (1903), however, regards the free basal segment of the diplopod leg as the subcoxa, and the next segment as the coxa, though the latter segment has all the structural features and usual relations of a first trochanter.

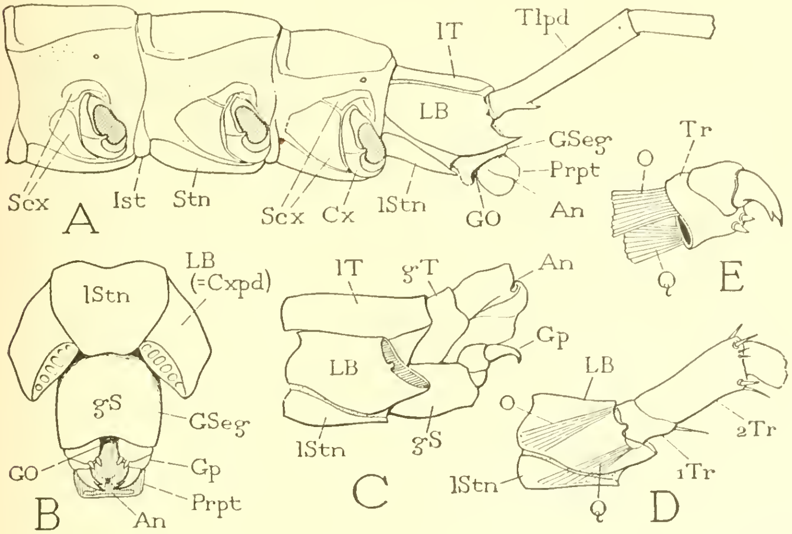

FIG. 27.—Appendages and terminal body structures of Chilopoda.

A, posterior part of body of *Scolopocryptops sexspinosa*, telopodites removed except from last segment, showing union of subcoxal sclerites with coxa in large pleural plate (*LB*) on last pregenital segment. B, ventral view of genital and pregenital segments of *Lithobius*. C, lateral view of same. D, base of pregenital appendage of *Lithobius*. E, telopodite of right gonopod of *Lithobius*, mesal surface.

An, anus; *Cx*, coxa; *Cxpd*, coxopodite; *GO*, gonopore; *Gp*, gonopod; *gS*, sternum of genital segment; *GSeg*, genital segment; *Ist*, intersternal sclerite; *LB*, limb basis; *lStn*, sternum of pregenital segment; *lT*, tergum of pregenital segment; *O*, levator of telopodite; *Prpt*, periproct; *Q*, depressor of telopodite; *Scx*, subcoxa; *Stn*, segmental sternal plate; *Tlpd*, telopodite; *1Tr*, first trochanter; *2Tr*, second trochanter (praefemur).

Following the last leg-bearing segment in the Chilopoda comes the definitive genital segment (fig. 27 A, *GSeg*), beyond which is the periproct (*Prpt*), or anal segment. According to Heymons (1901) the genital region of the body contains two small somites in the embryo, parts of both of which are sometimes retained in the adult stage. The apparently single genital segment of the adult may be a mere membranous ring (A, *GSeg*), or it may be a well-developed segment with dorsal and ventral plates (C, *gT, gS*). In *Lithobius* the ventral plate of the genital segment bears laterally on its posterior margin a pair of small, three-segmented appendages, the *gonopods* (B, C, *Gp,* E), the basal muscles of which (E, *O, Q*) arise on the sternal plate of the segment. The definitive sternum of the genital segment, therefore, is clearly a composite plate which includes the true bases of the genital appendages united with the primitive segmental sternum. The free genital appendages, then, are not the entire gonopods, but are the telopodites of the latter, and their muscles (E, *O, Q*) are the levators and depressors of the first trochanter (*Tr*).

In the males of many insects of the higher orders the structure of the second genital segment and its clasperlike appendages (the harpes) closely resembles the condition in *Lithobius.* Though the claspers are but one-segmented, they are movable by muscles arising in the gonopod bases, and the latter are generally more or less united with the sternum. In the insects, however, it is not so clear that the claspers are the true telopodites of the gonopods, since there is evidence to suggest that they may be other appendicular processes of the bases of the genital appendages.

ABDOMINAL APPENDAGES OF CRUSTACEA

All the body segments of the Crustacea anterior to the telson are usually provided with well-developed appendages. In the lower crustacean groups, the appendages of the entire body series, as in *Apus* (fig. 28 A), are fundamentally uniramous in form, though the various segments may be provided with endite and exite lobes. Each limb consists of a basis (*LB*), called the coxopodite, and of a telopodite (*Tlpd*). The frequent biramous form of crustacean appendages (C) is evidently the result of the hyper-development of an exite of the basal segment of the telopodite (the first trochanter, or basipodite, *Bspd*). The shaft of the telopodite beyond the basipodite then becomes the endopodite (*Endpd*). The exite lobes are movable by muscles arising in the limb segments that support them.

The abdominal appendages of the Malacostraca are typically biramous limbs (fig. 28 C) in which the endopodite (*Endpd*) is usually reduced to the size of the exopodite (*Expd*). The basis, or coxopodite (*Cxpd*), and the basipodite (*Bspd*) may be distinct segments, but in some forms (B) they are united in a single protopodite (*Prtpd*). In certain cases the abdominal appendages become practically uniramous by a suppression of the endopodite (B, *Endpd*), or by its conversion into a genital process. In such cases the functional or locomotory shaft of the appendage is the exopodite (*Expd*). A crustacean limb of this type of structure furnishes an analogy with the abdominal limbs of Thysanura on the assumption that the stylus of the latter (fig. 31 A, *Sty*) is the exopodite, and that the endopodite has been entirely suppressed, or preserved only in the gonapophyses of the genital appendages (B, *Gon*).

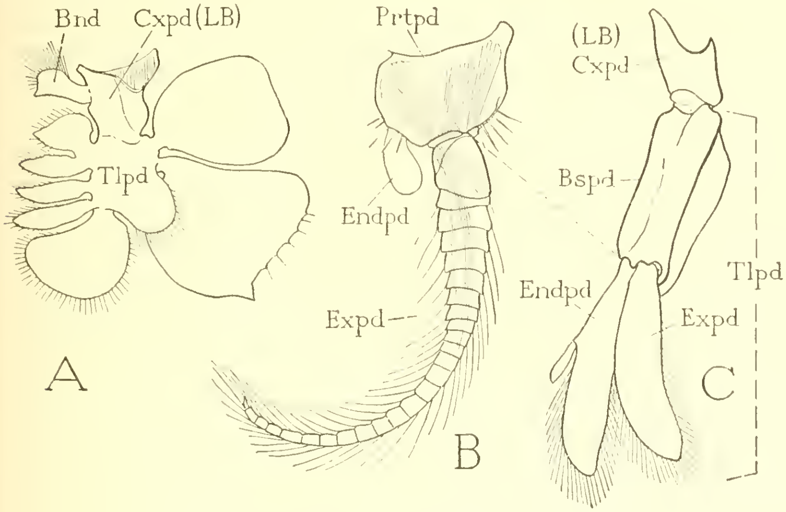

FIG. 28.—Abdominal appendages of Crustacea.

A, *Apus longicaudata*, appendage from posterior part of body, left, anterior surface. B, *Anaspides tasmaniae*, third abdominal appendage of left side, anterior surface. C, *Spirontocaris groenlandicus*, abdominal appendage of left side, anterior view.

Bnd, basendite; *Bspd*, basipodite; *Cxpd*, coxopodite, or limb basis; *Endpd*, endopodite; *Expd*, exopodite; *LB*, limb basis, or coxopodite; *Prtpd*, protopodite (united basis and basipodite); *Tlpd*, telopodite.

The genital claspers of the higher insects, which are clearly homologues of the abdominal styli of the Thysanura, may thus be likened either to the gonopods of the Chilopoda (fig. 27 C, *Gp*), if we assume that they are the main shafts of the telopodites, or to the abdominal appendages of such crustaceans as *Anaspides* (fig. 28 B), if we assume that they are exites of the appendages. As will later be shown, however, it is difficult to obtain positive evidence as to the nature of the insect abdominal styli; whether they are likened to the main shaft of the telopodite or to an exopodite branch depends largely on the student's bias toward a myriapodan or a crustacean ancestry for the insects.

THE ABDOMINAL APPENDAGES OF PROTURA

A pair of short, cylindrical appendages is present on each of the first three abdominal segments of all adult Protura. These appendages arise from the membranous parts of these segments between the posterior angles of the tergal and sternal plates. They are best developed in Eosentomidae, where the three pairs are alike in size and structure, and each organ (fig. 29 B) consists of two segments and a small terminal vesicle (*v*) which is eversible and retractile. In Acerentomidae (A) the appendages of the first pair are like those of the Eosentomidae, but the second and third pairs are simple, tuberculiform protuberances, unsegmented and lacking the terminal vesicle. Each appendage of the larger type in the two families, as described by Berlese (1910), is movable by two tergal muscles (B, *I, J*) inserted on the basal segment, one anteriorly, the other posteriorly. The second segment is provided likewise with two muscles, one arising anteriorly, the other posteriorly in the proximal segment, the two crossing each other axially to be inserted on opposite sides of the base of the distal segment. The terminal vesicle is retracted by a single large muscle (*rv*), which takes its origin mesally on the base of the first segment of the appendage, and is inserted on a central depression of the ventral face of the vesicle. The extrusion of the vesicle is evidently brought about by blood pressure from within the body.

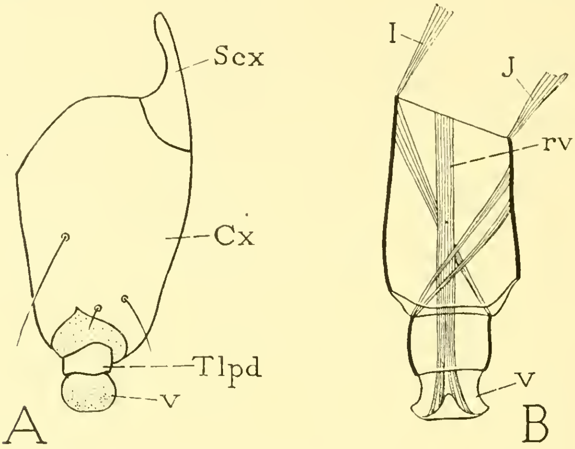

FIG. 29.—Abdominal appendages of Protura.

A, *Eosentomon germanicum*, abdominal leg (from Prell, 1913). B, *Acerentomon doderoi*, first abdominal leg (from Berlese, 1910).

Cx, coxa; *I*, promotor muscle of limb base; *J*, remotor muscle; *rv*, retractor of vesicle; *Scx*, subcoxa; *Tlpd*, rudiment of telopodite; *v*, terminal vesicle.

There appears to be no reason to doubt that these abdominal appendages of the Protura are remnants of true post-thoracic limbs. They have, as Berlese points out, a certain resemblance to the abdominal legs of lepidopterous larvae; but a closer comparison shows differences in the segmentation and musculature which makes it seem probable that there is no close genetic relation between the two sets of organs. Prell (1913), in his study of *Eosentomon germanicum,* finds at the base of each abdominal leg two small sclerotizations which he regards as remnants of the subcoxa (fig. 29 A, *Scx*). The large basal segment he believes is the coxa (*Cx*) and the smaller distal segment the rudimentary telopodite (*Tlpd*). The homology of the terminal vesicle (*v*) is doubtful. The organ does not appear to represent the eversible sacs of Thysanura, since the latter are borne by the limb bases (fig. 4, *Vs*); it might be, however, as Prell suggests, the praetarsus, since it has a certain resemblance to the vesicular praetarsus of Thysanoptera. The most likely homologue of the proturan leg vesicles is to be found in the eversible sac on the collophore of Collembola (fig. 30 B, *v*), which probably represents the united vesicles of a pair of fused appendages.

GENERAL STRUCTURE OF THE ABDOMINAL APPENDAGES OF INSECTS

Most of the appendicular organs found on the abdominal region of insects fall into two quite distinct categories distinguished by the insertion points of their muscles. In those of one group the muscles are inserted *on the base* of the organ; in those of the other the muscles *traverse* the organ and are inserted *within its distal extremity.* Appendicular structures of the first class are typically stylus-like in form, though they take on various other shapes. They include such organs as the abdominal styli of the Thysanura and the more generalized Pterygota, the furcula of Collembola, the gills of ephemerid larvae, the terminal claws of trichopterous larvae, the lateral abdominal appendages of larvae of Sialidae, the gonapophyses, the movable claspers of male pterygote insects, and the cerci. Organs of the second class are sac-like or tubular in form, and are usually retractile and eversible. They include the collophore of Collembola, the eversible vesicles of Thysanura, the gill-bearing tubercles of some sialid larvae, and the plantar lobes of the abdominal legs of larvae of Lepidoptera and chalastogastrous Hymenoptera.

If we could accept the two categories of abdominal appendicular structures, distinguished by the muscle insertions, as morphological groups of organs, the study of the abdominal appendages of insects would be much simplified. But, unfortunately, there are other features than the muscle insertions to be considered, such as the origins of the muscles and the position of the organs on the body, that make it doubtful if either constitutes a homogeneous group. Furthermore, organs of each type frequently occur together supported on a common basal structure, and the latter must then be reckoned as an essential part of the primitive appendage, of which the free, movable parts are but accessory structures of one kind or another. Any attempt to make theoretical generalizations on the primitive form or on the homologies of the abdominal appendages of insects will be premature until we have more closely examined the structure of the principal types of such organs as occur in both larval and adult stages of the various insect orders.

The abdominal appendages of insects fall into three groups corresponding with the subdivision of the abdomen into pregenital, genital, and postgenital regions. The appendages of the pregenital segments may be designated the *pregenital appendages;* those of the genital segment are the *gonopods;* those of the first and second postgenital segments are conveniently termed the *pygopods* and *uropods,* respectively. The pygopods are the anal legs, or postpedes, of holometabolous larvae, and probably the socii and so-called " cerci " of holometabolous adults. The uropods are the true cerci.

THE ABDOMINAL APPENDAGES OF COLLEMBOLA

The well known appendicular organs on the abdomen of Collembola include organs of each type of structure as defined above according to the muscle insertions.

The *collophore* (fig. 30 A, *Col*) is a large, thick, tubular pouch of the body wall projecting from the sternal region of the first abdominal segment. In most species it ends in a bilobed terminal vesicle (B, *v*), which is ordinarily retracted but is capable of being protruded by blood pressure. The entire collophore is traversed by a pair of large muscles (*rv*) arising on the tergal region of the body and inserted on the lobes of the terminal vesicle. The structure of the collembolan collophore thus suggests that it is formed by the union of a pair of abdominal appendages resembling those of the Protura (fig. 29), though in the latter the retractor muscle (B, *rv*) arises in the base of the appendage, and the appendage itself is movable by two muscles (*I, J*) arising in the body and inserted on its base. In some of the Collembola each lobe of the vesicle is produced into a long eversible tube.

The typical spring, or leaping organ of the Collembola, known as the *furcula* (fig. 30 D), has quite a different type of structure from that of the collophore. It consists of a large median base, the *manubrium* (*mn*), and of two slender arms, each of which is subdivided into a long proximal segment, the *dens* (*d*), and a short terminal segment, or *mucro* (*m*). On the base of the manubrium are inserted flexor and extensor muscles arising in the fourth and third abdominal segments, but, as already observed, these muscles apparently belong to the system of longitudinal dorsal and ventral body muscles, and are not specifically muscles of the spring. In *Tomocerus vulgaris* (fig. 30) each of the arms of the furcula is provided with an abductor muscle (D, *ab*) and an adductor muscle (*ad*) having their origins in the manubrium. According to Quiel (1915) adductor muscles are absent in *Orchesella cincta,* though he says a few obliquely transverse fibers are present in the manubrium. It is possible that Quiel did not observe in studying sections that these transverse fibers are attached on each side to a slender adductor tendon of the dens. The structure of the furcula readily suggests that it is composed of a pair of segmental appendages united by a fusion of the coxae, which become the manubrium, while the reduced telopodites become the arms.

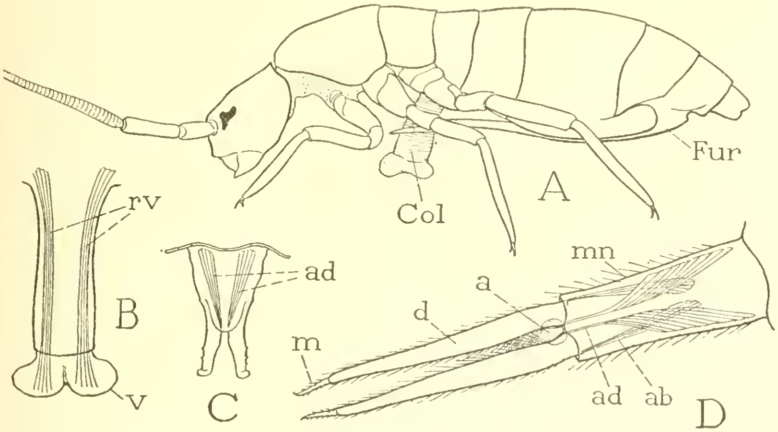

FIG. 30.—Abdominal appendages of Collembola. *Tomocerus vulgaris.*

A, lateral view of insect. B, anterior view of collophore. C, tenaculum. D, furcula.

a, aperture between bases of furcular arms receiving prongs of tenaculum; *ab,* abductor muscle; *ad,* adductor muscle; *Col,* collophore; *d,* dens; *Fur,* furcula; *m,* mucro; *mn,* manubrium; *rv,* retractor muscles of vesicle; *v,* terminal vesicle of collophore.

The minute *tenaculum* of the third abdominal segment (fig. 30 C) looks like a miniature furcula, and likewise suggests that it has been produced in the same manner by the union of the bases of a pair of appendages.

THE ABDOMINAL APPENDAGES OF THYSANURA

It is in the Thysanura that the abdominal appendages best preserve the fundamental structure characteristic of the abdominal appendages of adult Pterygota, as shown in the gonopods of the latter group; but, as will be seen later, it appears that the abdominal appendages have a more primitive form in the larvae of Ephemerida and in the larvae of certain holometabolous insects. The thysanuran appendages retain most completely their independence in the Machilidae.

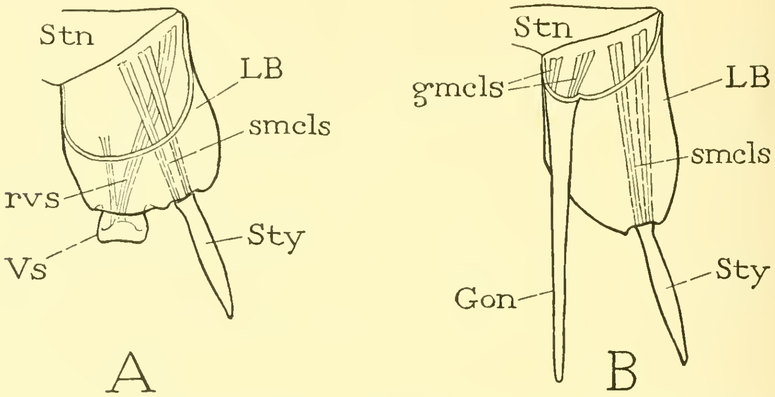

FIG. 31.—Diagrams of structure of abdominal appendages of Thysanura and Pterygota.

A, a typical pregenital appendage. B, a gonopod, or genital appendage. *gmcls,* muscles of gonapophysis; *Gon,* gonapophysis; *LB,* limb basis, usually a lobe or plate of body wall; *rvs,* retractor muscles of eversible vesicle; *smcls,* muscles of stylus; *Stn,* sternum; *Sty,* stylus; *Vs,* eversible and retractile vesicle.

The appendages of the pregenital region of the abdomen are typically developed on each of the pregenital segments except the first in Machilidae (fig. 4, II, VI), and those of each pair are distinct from the small median sternal plate (*Stn*), though their bases (*LB, LB*) are ankylosed with the latter, and are united medially with each other. Each appendage consists of a broad *basal plate* (fig. 31 A, *LB*), of a *stylus* (*Sty*) borne by the distal free margin of the basal plate, and of an *eversible sac,* or *vesicle* (*Vs*), lying mesad of the stylus and retractile into the basal plate (fig. 4, II, *Vs*). The posterior part of the basal plate projects from the ventral wall of the abdomen as a free flap with a membranous dorsal wall (fig. 32 B). Both the stylus and the eversible sac are provided with muscles arising within the basal plate (figs. 31 A, 32 B, *smcls, rvs*). The muscles of the stylus are inserted on the base of the stylus; the muscles of the vesicle traverse the latter, when the vesicle is everted, to be inserted within its distal extremity.

The appendages of the pregenital segments are never developed into any other form in the Thysanura than that which they have in the Machilidae, but they may be variously reduced, or united with the sternum. The styli and eversible sacs are sometimes absent, or either organ may occur alone (fig. 4, I, VIII). A pair of vesicles is frequently present on each basal plate, but the stylus never occurs in duplicate. In Lepismatidae the basal plates of the appendages in each segment are fused with the primary sternum to form a large zygosternum, which is the definitive sternal plate of the segment. The same is true in the Dicellura, though the regions of the limb bases may remain partially separated from the region of the primary sternum (fig. 32 C).

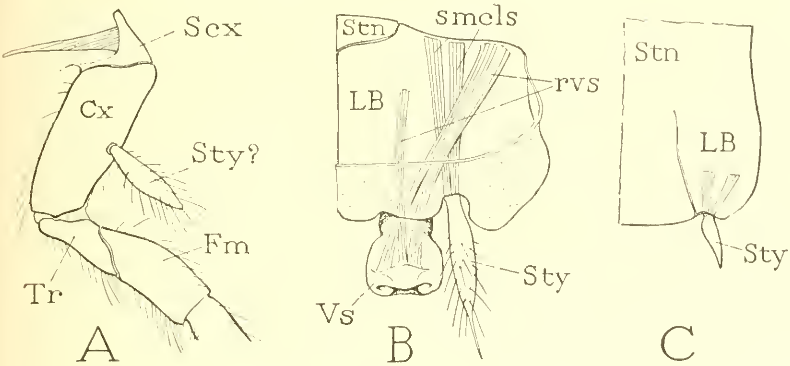

FIG. 32.—Appendages of Thysanura and Dicellura.

A, base of metathoracic leg of *Nesomachilis maoricus*, showing styliform spur on coxa. B, typical structure of a pregenital appendage of same, dorsal view. C, posterior lateral part of sternum of *Heterojapyx gallardi* with united limb basis bearing the stylus.

The basal plates of the thysanuran appendages are commonly called "coxae" (or "coxites") by American entomologists, while certain European entomologists call them "subcoxae." The idea that the plates are coxae is based chiefly on the fact that in the Machilidae stylus-like spurs occur on the coxae of the second and third pairs of thoracic legs (fig. 32 A, *Sty?*), which appear to be homologues of the abdominal styli. The question of the possible identity of the thoracic and abdominal styli will be discussed in the concluding part of this Section, but in any case the term " coxite " should not be used to designate the stylus-bearing plates, because the word can properly mean only " a part of a coxa." Since the writer is inclined to believe that the abdominal plates in question represent both the coxae and the subcoxae of the thoracic appendages, they are here termed simply the limb bases, or basal plates.

The gonopods, or appendages of the genital segments, have the same structure as the pregenital limbs in Thysanura, with the exceptions that they always lack eversible vesicles, and that typically each bears a median genital process, or *gonapophysis* (fig. 31 B, *Gon*). Two pairs of gonapophyses are regularly present in the females of Thysanura, one pair borne by the gonopods of the eighth segment, the other by the gonopods of the ninth segment. In the male, gonapophyses are known to occur on the gonopods of the eighth segment only in certain forms of *Machilis* (fig. 33 A, *1Gon*) ; they are usually present on the gonopods of the ninth segment (B, *2Gon*), but they may be absent from both genital segments (C). Each gonapophysis, when present, arises from the median, basal angle of the free dorsal surface of the stylus-bearing plate, and is provided with short muscles (fig. 31 B, *gmcls*) arising within the supporting plate and inserted on its base.

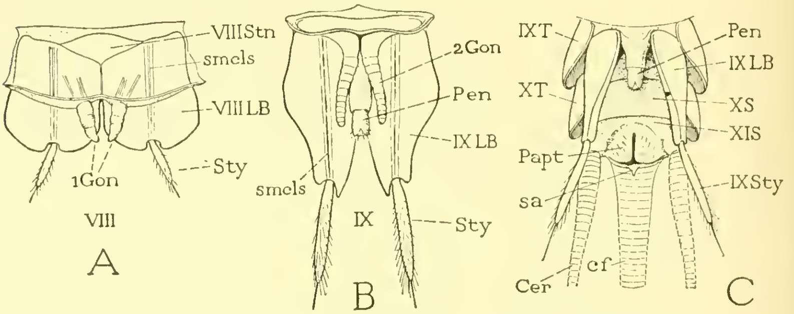

FIG. 33.—Genital and postgenital segments of Machilidae.

A, *Machilis variabilis,* male, ventral plates of eighth abdominal segment, dorsal view, with small first gonapophyses (*1Gon*). B, ventral plates of ninth segment of same, dorsal view, showing second pair of gonapophyses (*2Gon*) at sides of median penis (*Pen*). C, *Nesomachilis maoricus,* male, posterior part of abdomen, ventral view, showing absence of gonapophyses, and ventral structure of eleventh segment, bearing paraprocts (*Papt*), caudal filament (*cf*), and cerci (*Cer*).

Between the bases of the gonopods of the ninth segment in the male is a short membranous *penis* (fig. 33 B, C, *Pen*), a tubular evagination of the body wall from behind the region of the ninth sternum, having the opening of the ejaculatory duct at its extremity.

The thysanuran gonopods contain, in their simplest form, the fundamental elements of the organs of copulation and oviposition of pterygote insects. In the male the gonapophyses of the second gonopods become the so-called *parameres* of the copulatory apparatus; in the female, the first and second gonapophyses become the *first* and *second valvulae* of the ovipositor, and the basal plates of the second gonopods form the *third valvulae,* when the last are present.

The uropods, or cerci, of the Thysanura are typically long, multiarticulate filaments (fig. 7 A, *Cer*) borne by the eleventh segment (B, *XI*). In the Dicellura the abdomen contains only 10 segments, and the uropods, therefore, in this group appear to belong to the tenth segment. They are filamentous in *Campodea,* styliform in Projapygidae, and take the shape of large pinchers in Japygidae (fig. 40 C, *Cer*). The uropods differ from the preceding appendages in that they are not differentiated into a basal plate and a stylus, and they bear neither eversible sacs nor processes corresponding with the gonapophyses.

THE ABDOMINAL GILLS OF EPHEMERID LARVAE

The abdominal gills of ephemerid larvae, together with the lateral lobes of the body wall supporting them (fig. 34 A), appear to be appendages of a more primitive form than the abdominal appendages of the Thysanura. Their structure, with certain modifications, is repeated in the abdominal appendages of several groups of holometabolous larvae; but it does not furnish the basis of the structure of the gonopods in adult pterygote insects, which, as already stated, is to be derived from that of the gonopods of the Thysanura.

The ephemerid larval gills have various shapes, some being tapering stalks, either single or double, fringed with filaments (fig. 34 A, B, *Brn*), while others are expanded into broad plates; but, whatever the form, each organ is movably attached by its base to a large lateral lobe of the body wall (*LB*). The gill is movable by muscles arising in the ventral part of the supporting lobe (A, B, *bmcls*).

The gill-bearing lobes are not movable, since there are no body muscles inserted upon them. The vertical lateral muscles of the abdominal segments extend from the tergum to the edge of the sternum mesad of the gill lobes (fig. 15 A, *1l, 2l, 3l,* fig. 34 A, *l*). The gill-bearing lobes therefore have the character of limb bases implanted in the pleural areas of the segments between the tergal and sternal plates (compare *LB* of fig. 34 A with *LB* of fig. 1 A). The lateral and ventral surfaces of each lobe are often separated by a sharp fold or ridge (fig. 34 B, *LB*), and the ventral part of the lobe may be more or less united with the sternum of its segment (*Stn*). The gill (*Brn*) arises from the posterior end of the lateral surface of the supporting lobe, and is usually provided with four muscles inserted on its base (*C*). The branchial muscles, as above noted, take their origins on the ventral plate of the supporting lobe (B), and therefore not on the sternum, as stated by Dürken (1907), who did not distinguish the ventral plate of the gill basis from the true segmental sternum.

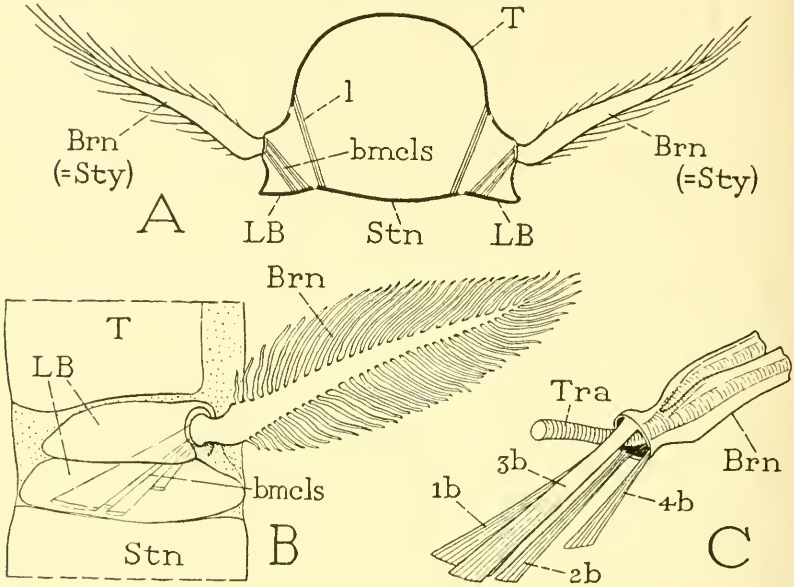

FIG. 34.—The abdominal gill-bearing appendages of ephemerid larvae.

A, diagrammatic cross section of abdominal segment, showing limb base lobes (*LB*) bearing gill appendages (*Brn*), which are evidently the styli, each movable by muscles (*bmcls*) arising in the bases; the lateral body muscles (*l*) extend from tergum to sternum.

B, external view of a gill and its supporting lobe (*LB*), in which arise the gill muscles (*bmcls*).

C, musculature and tracheation of a gill, lateral view.

The old idea that the ephemerid larval gills are appendages of the dorsum is no longer tenable. The organs are very evidently rudiments of segmental appendages, as claimed by Heymons (1896*a*, 1896*b*) and by Börner (1909), each being composed of a basis (*LB*), and of a terminal appendicular part (*Brn*) movable on the basis by muscles arising in the latter. The gill bases are interpreted by Börner as the subcoxae of the abdominal appendages, since they follow exactly in line with the subcoxal, or "pleural," plates of the thorax. The gills, therefore, Börner contends, are the equivalents of the legs, and the proximal end of each represents the coxa. On the other hand, we might assume that the gill basis includes the equivalents of both the subcoxa and the coxa of a thoracic leg, in which case the gill shaft or plate might be supposed to be the telopodite with its proximal end representing the first trochanter. The presence of the gill muscles arising in the gill basis suggests this homology, since the muscles are comparable with the trochanteral muscles of a leg (fig. 26, *O*, *Q*). But again, the gill resembles the stylus of a thysanuran appendage, and there is doubt as to whether the abdominal styli are true telopodites or secondary appendicular processes of the coxae.

Leaving aside, for the present, the question of homologies between the parts of the abdominal appendages and those of the thoracic appendages, a comparison of the abdominal appendages of the ephemerid larva with the abdominal appendages of Thysanura leaves little doubt that the gill-supporting lobes of the former are the equivalents of the stylus-bearing plates of the latter, and that the gill stalks or plates are the homologues of the styli. Neither the abdominal gills of ephemerid larvae nor the styli of *Lepisma* are present on the early postembryonic stage of the insect. In the newly hatched larva of *Ephemerella vulgata*, according to Heymons (1896), there are lateral protuberances of the abdominal segments, especially prominent on segments II and VII, which are derived during embryonic development from the embryonic limb rudiments. The gills first appear as outgrowths from these abdominal lobes about four days after hatching. The styli of *Lepisma saccharina*, Heymons (1897) says, appear likewise a considerable time after hatching, and arise from the parts of the ventral plates of the eighth and ninth abdominal segments that are derived from the "Anlagen" of the embryonic appendages.

LATERAL ABDOMINAL APPENDAGES OF SIALID AND COLEOPTEROUS LARVAE

The larva of *Sialis* (fig. 35 A) presents at least an excellent imitation of an insect that has carried the primitive polypod condition into a postembryonic stage. The long, tapering, segmented, appendicular organs, usually termed "gills," projecting from the sides of the first seven abdominal segments have a striking resemblance to legs. Each appendage (C) is a hollow process of the body wall, distinctly jointed, and composed of six segments, of which the proximal three are relatively thick, while the region of the distal three is slender and rapidly tapering to the apex.

Each appendage is supported on a lateral lobe of the body segment (fig. 35 C, *LB*). The series of lobes appears at first glance to belong to the dorsum of the abdomen, but each one, though so closely amalgamated with the tergum that the spiracle appears to be situated on its dorsal part, really occupies a pleural position between the tergum and the sternum of its segment. The lumen of each lobe is separated from the general body cavity by a vertical sheet of tergo-sternal lateral muscles, and within the lobe arise anteriorly and posteriorly muscles inserted on the base of the movable shaft of the appendage. It is clear, therefore, that we have here an organ corresponding in every respect with a gill-bearing appendage of an ephemerid larva (fig. 34 B), and that in both of these structures the basal lobe represents the stylus-bearing plate of *Machilis*, and the movable distal appendage the stylus.

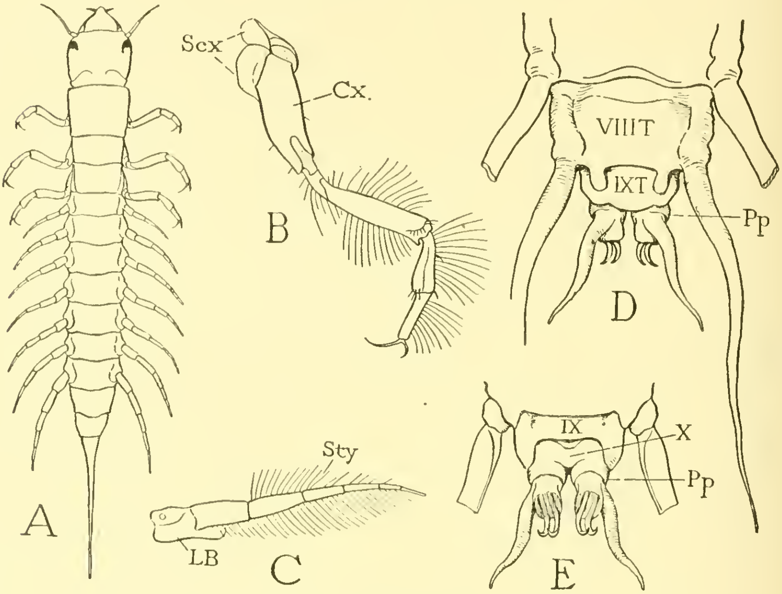

FIG. 35.—Abdominal appendages of sialid larvae.

A, larva of *Sialis*, showing jointed appendages of abdomen. B, metathoracic leg of *Sialis* larva, with subcoxal sclerites at its base. C, abdominal appendage of *Sialis* larva, showing division into basis (*LB*) and jointed stylus (*Sty*). D, posterior end of larva of *Chauliodes*, dorsal view, showing pygopods (*Pp*) of terminal segment. E, the same, ventral view.

The distinct segmentation of the abdominal appendages of the *Sialis* larva almost unavoidably gives the impression that these organs are the true telopodites of the abdominal limbs. The impression, moreover, comes close to a conviction when it is discovered that each appendage *is provided with internal muscles* in addition to those inserted on its base. The presence of these muscles was first mentioned by Heymons (1896*a*); and it can be demonstrated by dissection and staining of specimens preserved in alcohol that bundles of muscle fibers are present in at least each of the first three segments, inserted on the bases of the second, third, and fourth segments, but it is difficult to make an exact study of them without properly prepared material. The slender distal part of the shaft beyond the third segment is penetrated by a branched trachea, and this part of the appendage might serve as a tracheal gill; but the strong musculature of the proximal part of the organ, and the long hairs that fringe the segments, suggest that the abdominal appendages of the *Sialis* larva have an important locomotory function.

In the sialid genera *Chauliodes* and *Corydalus* the larvae are likewise provided with long, lateral abdominal appendages, a pair being present on each of the first eight segments, and a terminal pair on the last segment (fig. 36 B). In these genera, however, the appendages are simple, tapering, hollow processes of the integument, unsegmented, and containing no muscles. Each is supported on a lateral lobe of the body wall (*LB*).

The basal lobes of the lateral appendages of the *Corydalus* larva are large and prominent as seen in a transverse section of an abdominal segment (fig. 36 C, *LB, LB*). Each projects laterally beyond the attachments of a set of strong tergo-sternal lateral body muscles (*l*); and on the inner margin of the ventral wall of the lobe arise three muscles (D, *smcls*), one anteriorly and two posteriorly, which are inserted on the base of the distal appendicular process. Here again, therefore, we find repeated the same structures that occur in the ephemerid larval gills and in the thysanuran abdominal appendages. In the *Corydalus* larva the appendage-bearing lobes of the abdomen fall in line with the subcoxal lobes of the thoracic segments (fig. 36 A, *Scx*), rather than with the long coxae (*Cx*); but the muscles of the abdominal appendages (D, *smcls*), taking their origins in the supporting lobes, can be compared only with the basal muscles of the leg telopodite (A, *O, Q*) inserted on the trochanter. The abdominal lobes, therefore, would appear to contain both the subcoxal and the coxal parts of the limb bases.

The *Corydalus* larva differs from the *Sialis* and *Chauliodes* larvae in that the basal lobes of the first seven abdominal appendages bear each a large ventral tubercle supporting a circle of respiratory filaments (fig. 36 B, *Vs*). When the filaments are removed it is seen that each tubercle is subdivided distally into three terminal lobes (C, *Vs*), and dissection reveals the fact that the tubercle is provided with a large retractor muscle (C, D, *rvs*) arising on the dorsum of the segment and inserted by three diverging branches on the distal surfaces of the three terminal lobes of the tubercle. The gill tubercles are thus highly suggestive of the eversible sacs of the thysanuran appendages, except for the difference that their retractor muscles arise on the tergal

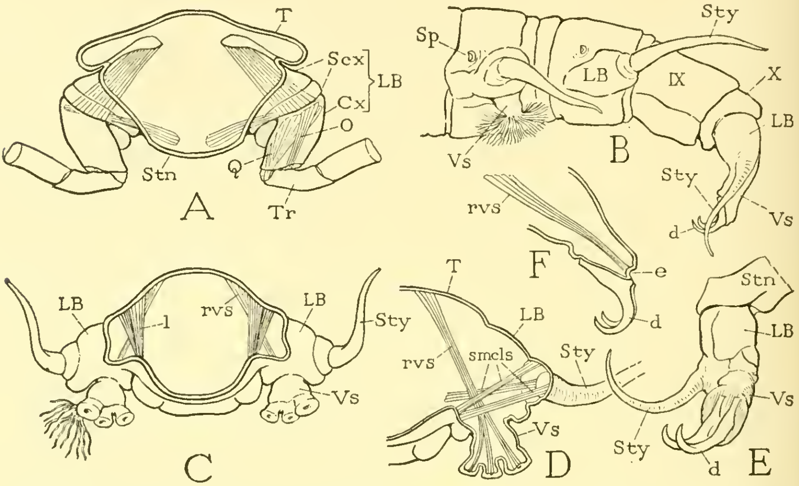

FIG. 36.—Thoracic and abdominal appendages of the larva of *Corydalus cornutus*.

A, transverse section through anterior end of metathorax, showing subcoxal lobes (*Scx*) above bases of coxae (*Cx*), and levator and depressor muscles of trochanter (*O*, *Q*) arising in coxa.

B, last four segments of abdomen, showing segmental appendages.

C, transverse section through posterior part of an abdominal segment, seen from behind, showing limb base lobes (*LB*) supporting each a stylus (*Sty*), and a retractile gill-bearing tubercle (*Vs*).

D, section through base of right abdominal appendage and gill tubercle, seen from behind, showing muscles of stylus and gill tubercle.

E, antero-mesal view of right appendage (pygopod) of tenth abdominal segment.

F, section of terminal appendage, showing insertion of retractor muscles behind bases of claws.

Cx, coxa; *d*, claws (crochets); *e*, insertion point of retractor muscles of claw-bearing tubercle (planta); *l*, lateral body muscles; *LB*, limb basis; *O*, *Q*, muscles of trochanter; *rvs*, retractor muscle of gill-bearing or claw-bearing lobe of appendage; *Scx*, subcoxa; *smcls*, muscles of stylus; *Sp*, spiracle; *Stn*, sternum; *Sty*, stylus; *T*, tergum; *Vs*, retractile lobe of appendage (retractile vesicle).

region of the body segment, instead of in the bases of the appendages, as in the Thysanura (fig. 32 B, *rvs*). On the other hand, as we shall presently see, the gill tubercles of the *Corydalus* larvae are almost identical in structure with the abdominal feet of lepidopterous larvae.

The appendages of the last abdominal segment in the larva of *Chauliodes* and *Corydalus* are remarkable structures in that they combine the characters of the preceding appendages of *Corydalus* with the features of an abdominal leg of a caterpillar. Each of these terminal appendages (figs. 35 D, *Pp,* 36 B, E) consists of a large, hollow, somewhat cylindrical lobe of the body wall. The basal part of the organ (fig. 36 B, E, *LB*) bears laterally a tapering process (*Sty*) similar to the lateral processes of the preceding appendages, and ends distally in a thick tubercle (*Vs*), which lacks gill filaments, but is armed on its terminal surface with a pair of large, curved claws (*d*). The appendage is traversed by a strong retractor muscle (F, *rvs*) taking its origin on the dorsum of the tenth segment, and having its insertion on the distal wall of the tubercle at the posterior ends of the long bases of the claws (*e*). The resemblance in structure and mechanism of these appendages to the " anal " legs of caterpillars is so striking that it is difficult to believe the likeness is fortuitous. The terminal body segment is better developed in the *Corydalus* larva (fig. 36 B, *X*) than in *Chauliodes* (fig. 35 E), in which its dorsal part is rudimentary.

Lateral appendicular processes of the abdomen, similar in every respect to those of the sialid larvae, are present also on certain aquatic coleopterous larvae, especially in the families Dytiscidae and Gyrinidae. In the gyrinid *Dineutes,* for example, the larva is provided with long, tapering processes arising from lateral lobes of the body wall on each side of each of the first eight segments, and with a pair of two-branched processes on the ninth segment. Each process is penetrated by a trachea from the lateral respiratory trunk, and is furnished with two short, antagonistic muscles arising in the supporting lobe of the body and inserted on its base. The larva of the dytiscid *Coptotomus* has the same equipment of lateral processes, but the writer did not find muscles connected with them in a specimen examined.

THE ABDOMINAL LEGS OF LEPIDOPTEROUS LARVAE

A typical abdominal leg of a caterpillar consists of three parts (fig. 37 A). At the base is a ring of flexible integument (*mb*) ; beyond this is a longer, cylindrical section (*Cx*) forming the greater part of the appendage, and frequently having a sclerotic plate in its outer wall often marked by distinctive groups of setae (fig. 3 A); distally the leg ends in a retractile lobe (*Vs*), called the *planta,* which bears the claws, or *crochets* (*d*).

Functionally the planta is the most important part of the leg, and structurally it is the most variable. The proximal parts of the appendage differ principally in relative size in different species. The planta in its more generalized condition is a short cylindrical pad with a circular distal surface, on the center of which is inserted a group of retractor muscle fibers. In such cases the crochets may be arranged in a complete circle around the distal plantar surface, with their recurved points turned peripherally and upward. With most caterpillars, however, the claws are limited to a semicircle or a small arc usually on the inner margin of the planta (fig. 37 B), and in such cases the planta itself (*Vs*) generally becomes asymmetrical by a reduction or obliteration of its outer half. The planta then assumes the form of a lobe projecting to the mesal side of the axis of the limb, marked by the insertion point of the retractor muscle (*e*), and its claws (*d*)

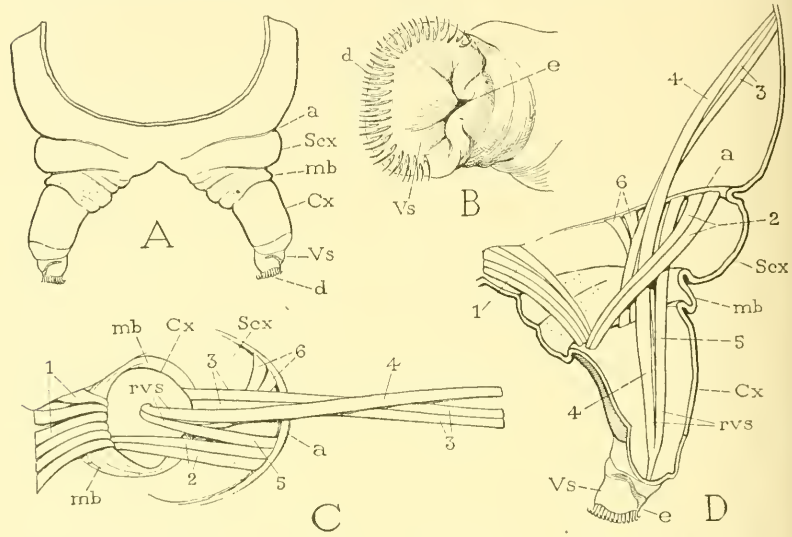

FIG. 37.—Structure of an abdominal leg of a caterpillar. *Malacosoma americana.*

A, posterior view of a pair of abdominal legs. B, ventral view of a left abdominal leg, showing crochets (*d*) turned outward, and insertion of retractor muscles (*e*) at inner margin of plantar lobe (*Vs*). C, dorsal view of leg musculature, right side. D, posterior view of musculature of a right leg.

a, dorso-pleural groove; *Cx,* coxa; *d,* crochets; *e,* insertion point of retractor muscles of planta; *mb,* membranous area between subcoxa and coxa; *rvs,* retractor muscles of planta; *Scx,* subcoxa; *Vs,* planta (retractile vesicle).

curve mesally and upward when the planta is protracted in the usual position. The various types of foot structures resulting from modifications in the form of the planta and in the arrangement of the crochets characteristic of the different groups of caterpillars have been described by Fracker (1915).

Immediately above each abdominal leg there is usually a prominent lobe or swelling of the body wall (fig. 37 A, *Scx*), separated from the latero-dorsal area of the segment by a distinct groove (*a*). Corresponding lobes are present also on the legless abdominal segments, and likewise on the metathorax and mesothorax (fig. 3 A, *Scx*). The serial identity of these suprapedal lobes of the abdomen and thorax is demonstrated by their uniform position relative to the appendages, and by the fact that in many species they bear similar or identical marks or groups of setae. In the anatomy of the caterpillar, therefore, the abdominal and thoracic appendages appear to be homodynamous structures. Eastham (1930), in his study of the embryology of *Pieris rapae,* says: "The prolegs which are retained on their segments must be regarded as true appendages. They develop in the same manner as those of the head and thorax, have the same relation to their own somites, and a musculature develops in connection with each comparable to that of the thoracic limbs though of a weaker order."

The suprapedal lobes of the caterpillar (fig. 3 A, *Scx*) are clearly the subcoxal areas of the appendages, since those of the thorax are identical with the areas which in certain other holometabolous larvae contain the pleural sclerites of the thorax (B, C, Scx_3). The free part of the abdominal appendage in the caterpillar is, therefore, apparently the coxa (fig. 37 A, *Cx*). The planta (*Vs*), then, is either a rudiment of the telopodite, or a highly specialized retractile vesicle of the coxa. Further light on the morphology of the caterpillar proleg may be obtained from a study of the musculature.

The musculature of an abdominal leg of a caterpillar is comparatively simple. It comprises two sets of muscles, those of one set being inserted on the base of the principal part of the leg (fig. 37 D, *Cx*), those of the other on the planta (*Vs*). The muscles inserted on the proximal rim of the leg include three groups of fibers represented in *Malacosoma americana* and *Estigmene acrea* as follows: (*1*) a series of median fibers (fig. 21 B, 37 C, D, *1*) arising on the midline of the venter, or also on the mesal parts of the anterior and posterior intersegmental folds, and converging to the mesal rim of the base of the principal segment (*Cx*) of the leg; (*2*) a group of two fibers (fig. 37 C, D, *2*) arising on the groove (*a*) above the suprapedal lobe of the body wall, and inserted on the mesal rim of the leg base posteriorly just ventrad of the insertions of the median muscles; (*3*) a group of two or three fibers (C, D, *3*) taking their origins on the middle of the lateral wall of the segment posterior to and a little above the level of the spiracle (fig. 21 B), and having their insertions on the outer side of the proximal rim of the leg (figs. 21 B, 37 C, D, *3*).

The muscles of the planta take their origins outside the leg from two widely separated parts of the body wall. The plantar muscles of *Malacosoma americana* (fig. 37 C, D) comprise four fibers. The principal one is a long fiber (*4*) arising on the middle of the lateral wall of the segment, close to the origins of the lateral muscles of the leg (*3*), from which point it curves downward into the leg to be inserted on the inner face of the planta. The other plantar muscles arise on the dorso-pleural groove (*a*) above the suprapedal lobe (fig. 37 D, *Scx*). One consists of a single fiber (C, D, *5*) arising posteriorly just before *2*, and entering the leg with *4*. The other includes two fibers (*6*) in *Malacosoma*, represented by a single fiber in *Estigmene* (fig. 21 B, *6*), arising anteriorly on the dorso-pleural groove, and curving posteriorly and downward into the leg to join with *4* and *5*. In the distal part of the leg (fig. 37 D) all the fibers of the plantar group unite to form a common stalk which is inserted on the inner surface of the ventral wall of the planta. In caterpillars having a disk-shaped planta, the muscle insertion is at or near the center of the latter, but with species in which the planta has the form of a mesal lobe, the muscle attachment is at the outer side of the plantar lobe (fig. 37 B, D, *e*).

On comparing, in the caterpillar, the musculature of an abdominal leg with that of a thoracic leg, it is found that though there is no exact correspondence in the number and arrangement of the fibers, there is a general similarity in the disposition of the muscles sufficient to suggest a derivation of the muscles in the two cases from one fundamental plan of musculature. Thus, in the metathorax of *Malacosoma* (fig. 38 A, B) there is a set of sternal fibers (*a*) arising anteriorly on the intersegmental fold, and inserted mesally on the rim of the coxa (*Cx*), which correspond with the median muscles of an abdominal leg (fig. 37 C, D, *1*). Likewise, there are muscles from the lateral wall of the thoracic segment inserted on the outer rim of the coxa (fig. 38 B, C, *b*), having thus the same relation to the appendage as the fibers of muscle *3* in the abdomen (fig. 37 C, D). In the thorax there are several subcoxo-coxal muscles (fig. 38 B, *c*) which have no exact counterparts in the abdomen, though in the latter there is a muscle from the groove above the subcoxal lobe (fig. 37 C, D, *2*) to the inner margin of the apparent coxal segment of the leg. The other muscles in the base of a thoracic leg (fig. 38 B, C, *d, e, f, g*) are coxo-trochanteral and coxo-femoral muscles, representatives of which are entirely absent in the abdominal legs. On the other hand, the plantar muscles of the abdomen have no evident counterparts in the thorax.

The general parallelism between the muscles of the abdominal appendages and those of the thoracic legs shows that the musculature of the prolegs in the mature caterpillar is, as Eastham says of the musculature in the embryo, " comparable to that of the thoracic limbs though of a weaker order." Moreover, if the musculature has any bearing on homologies in the segments of the appendages, it shows that the suprapedal lobes of the body wall above the abdominal limbs are the subcoxae (fig. 37 A, D, *Scx*), and that the principal parts of the legs are the coxae (*Cx*). The plantae of the abdominal appendages, however, have no evident homologues in the thoracic legs, nor do their muscles correspond with any of the muscles of the legs in the thorax.

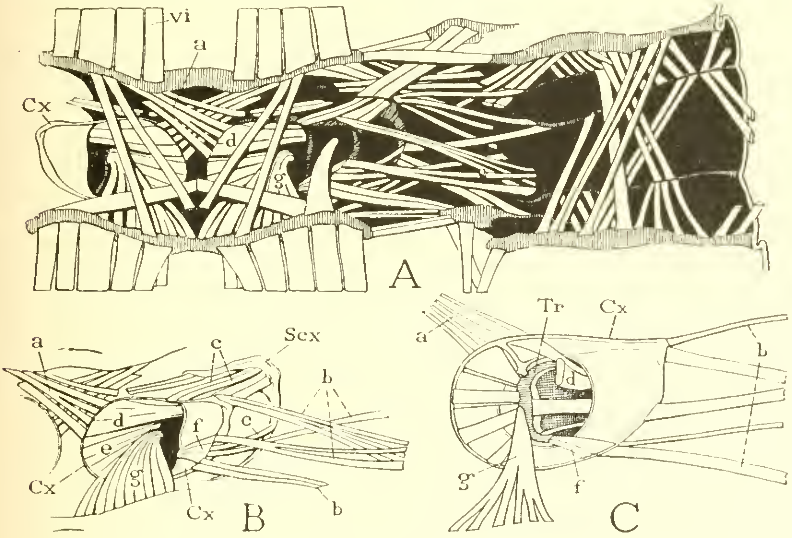

FIG. 38.—Body muscles of a thoracic leg of a caterpillar.

A, external body muscles and leg muscles of ventral area and right half of metathorax of *Malacosoma americana.* B, basal muscles of right metathoracic leg of same. C, coxal and coxo-trochanteral muscles of right mesothoracic leg of *Estigmene acraea.*

The nature of the planta becomes clear when we compare an abdominal limb of a caterpillar (fig. 37 D) with an abdominal appendage of the *Corydalus* larva (fig. 36 C, D). A striking resemblance is seen at once between the retractile planta of the former and the gill-bearing tubercle (*Vs*) of the latter. Moreover, the likeness amounts almost to a structural identity when the planta is compared with the claw-bearing lobe of one of the terminal appendages of the *Corydalus* larva (fig. 36 E, *Vs*). In each case the organ is provided with strong retractor muscles arising on the dorsum of the body segment. It is a mere detail that the muscles in *Corydalus* (fig. 36 D, *rvs*) branch to the several lobes of the gill tubercle; in the terminal appendages the bundle of retractor fibers (F, *rvs*) tapers to a narrow stalk inserted at the bases of the claws exactly as in the foot of the caterpillar (fig. 37 D). The *Corydalus* larva lacks only the accessory muscles of the planta arising in the base of the subcoxa. We can, therefore, scarcely avoid the conclusion that the planta of the caterpillar's abdominal leg is an eversible vesicle of the limb basis, here borne by the coxa, which is not consolidated with the subcoxa. The representatives of the styli, preserved in the movable distal processes of the sialid appendages (fig. 36 C, D, E, *Sty*), have been lost from the abdominal limbs of all lepidopterous larvae.

The anal legs, or appendages of the last abdominal segment of the caterpillar, differ from the legs of the preceding abdominal segments only in details of their musculature. Their structure will be described in the subsequent discussion of the terminal appendages of holometabolous larvae.

The abdominal appendages of chalastogastrous hymenopterous larvae have the same essential structure as the abdominal limbs of caterpillars, though they are not so highly organized, and the plantar lobes are reduced to terminal disks of the coxal segments (fig. 3 C).

THE GONOPODS

The appendages of the eighth and ninth segments of the abdomen are potentially gonopods because of the association of the openings of the genital ducts with these segments. They are, however, not necessarily modified for reproductive purposes, as in the males of certain Thysanura in which the appendages of the eighth and ninth segments (fig. 33 C) do not differ structurally from those of the preceding segments.

Typically a gonopod is distinguished from the pregenital and postgenital appendages by the development of a median process from the proximal part of its base. A complete gonopod, therefore, consists of a *basal lobe* or *plate* (fig. 31 B, *LB*), of a lateral, distal *stylus* (*Sty*), and of a median, proximal *gonapophysis* (*Gon*). Both the stylus and the gonapophysis may be movable on the basis by muscles arising in the latter and inserted on their bases (*smcls, gmcls*). So far as has been ascertained neither of the appendicular parts of a gonopod ever contains intrinsic muscles. In the males of some Ephemerida the genital styli are distinctly jointed and thus separated into apparent segments, though the latter are not independently movable. In the Thysanura the gonapophyses are marked by circular constrictions, varying from a few to many according to the length of the organs (fig. 33 A, B), but the resulting subdivisions have none of the characters of true segments, and are entirely comparable with the annulations of the caudal filament and cerci (C; *cf, Cer*).

In female insects the gonopods form the ovipositor, when this organ is present, and both pairs of appendages enter into its composition. In the Thysanura the gonapophyses only are involved in the ovipositor, the basal plates and the styli retaining the structure typical of these parts in the pregenital segments of Machilidae. Evidently the condition here represents a primitive stage, in which two pairs of median apophyses of the appendages of the eighth and ninth abdominal segments form a simple egg-laying organ. In female Pterygota the styli of the gonopods are usually lost, those of the first pair being always absent, and the basal plates are transformed into a suspensory apparatus for the gonapophyses. The basal plates of the first gonopods (fig. 39 A) evidently become the small sclerites known as the valvifers (B, *Vlf*), which support the first gonapophyses (*1Vl*), though there is a difference of opinion on this point. Those of the second gonopods form lobes (*IXLB*) supporting the second gonapophyses (*2Vl*), or they are drawn out into long processes that become a third pair of blades in the ovipositor (C, *3Vl*). The component blades of the adult ovipositor are commonly called *valvulae*. It is to be observed that only the first and second pairs of valvulae (B, C, *1Vl, 2Vl*) represent the gonapophyses (A, *1Gon, 2Gon*), those of the third pair (C, *3Vl*) being derived directly from the basal plates of the second gonopods, the styli of which are apparently lost.

The ovipositor is absent or rudimentary in many groups of insects, but its wide distribution throughout the orders leaves little doubt of its being a primitive structure of the Insecta. It has no homologue in other Arthropoda, and it is doubtful if the rami of the gonopods in the Crustacea are homodynamous with the gonapophyses of insects. The various theories concerning the possible homologies of the genital processes of the gonopods in insects will be considered in the closing discussion of this paper.

In male insects the history of the gonopods is much more involved than in the female, and the evolution of the genital appendages into organs of copulation has produced many different kinds of structures. It is only in certain species of *Machilis* that both pairs of gonopods bear gonapophyses (fig. 33 A, B, *1Gon, 2Gon*). In all male pterygote insects gonapophyses are lacking on the eighth segment, and the gonopods of the ninth segment only enter into the copulatory apparatus, though accessory structures of the eighth and the tenth segment may be included.

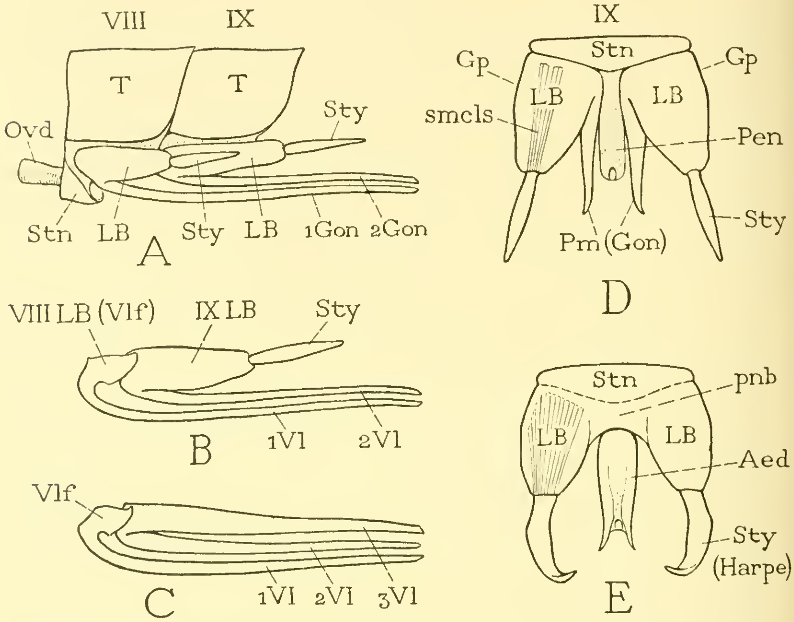

FIG. 39.—Diagrams showing the morphology of the ovipositor, and the external genitalia of the male.

A, female genital segments and generalized structure of the gonopods. B, an ovipositor with two pairs of valvulae formed of the gonapophyses. C, an ovipositor with three pairs of valvulae, the third pair (*3Vl*) formed of the basal plates of second pair of gonopods (A, *LB*).

D, generalized structure of ventral parts of ninth abdominal segment of male, showing sternum (*Stn*), gonopods (*Gp, Gp*), and penis (*Pen*). E, specialized structure of male genitalia; basal plates of gonopods (*LB, LB*) united by pons basalis (*pnb*), parameres united with penis to form an aedeagus (*Aed*), and styli (*Sty*) transformed into clasping lobes.

Aed, aedeagus; *Gon,* gonapophysis; *1Gon, 2Gon,* gonapophyses of first and second gonopods; *LB,* basal plate of gonopod; *Ovd,* oviduct; *Pm,* parameres (male gonapophyses); *pnb,* pons basalis; *smcls,* muscles of stylus; *Stn,* sternum; *Sty,* stylus; *T,* tergum, *1Vl, 2Vl, 3Vl,* first, second and third valvulae; *Vlf,* valvifer.

The basal plates of the second gonopods in the male may unite with each other and with the primary sternum of their segment, as do those of the preceding segments, to form a composite zygosternum, and in such cases the styli either retain the typical shape of styliform organs, or they are lost. The gonapophyses, usually termed the *parameres,* however, in the more generalized insects, are associated with a median intromittent organ, or penis (figs. 33 B, 39 D, *Pen*), which is a tubular evagination of the segmental wall behind the ninth sternum, bearing the opening of the ejaculatory duct at its extremity. In the higher insects the primitive penis becomes partly or entirely suppressed, and the parameres unite with it or with each other to form the secondary and often more complicated intromittent organ usually termed the *aedeagus* (fig. 39 E, *Aed*), which incloses the ejaculatory duct and bears the gonopore.

The basal plates of the gonopods of the ninth segment in the male, if not completely amalgamated with the sternum, may form free lobes of the ninth segment, or they may unite with each other, with the sternum, or with the sternum and the tergum of the ninth segment. In this way the genital segment of the male, especially in holometabolous insects, assumes a great diversity of structure, and it is often reduced to a simple continuously sclerotized annulus. The ninth segment, however, regardless of its form, always bears the aedeagus, which may be partly or wholly concealed in a *genital chamber* of its ventral part, and it generally carries clasping organs of various forms on its posterior margin. Usually, among the clasping organs of the ninth segment, or often the only structures having a clasping function, is a pair of lobes flexible at their bases and independently movable by muscles taking their origins in the basal plates of the gonopods, or in the regions of the ninth annulus derived from the gonopod bases. These movable claspers, designated the *harpes* by students of Lepidoptera, are evidently the homologues of the styli of the more generalized insects (fig. 39 D, E, *Sty*).

It is most important, now, to observe that in the fundamental organization of the gonopods there are only two sets of appendicular structures that are independently movable by muscles inserted directly on their bases. These structures are the styli and the gonapophyses. Therefore, in the ninth segment complex of the male genitalia, there will generally be two sets of appendicular structures, the *harpes* and the *parameres,* provided with muscles arising in the basal plates of the gonopods, or in the parts of the ninth segmental ring derived from the latter. By a study of the genital musculature, then, these two structures can be identified with certainty in almost all cases throughout the orders, unless one or the other or both are absent. In addition to these fundamental, musculated processes, however, there are innumerable other secondary genital processes having no necessary homology in the different orders, which may be developed on the ninth segment, on the aedeagus, or on the segments preceding and following the ninth. These structures, except in rare cases, have no muscles of their own, and are not independently movable, though some of them may be moved incidentally by the usual segmental muscles attached at their bases. The movable claspers derived from the styli, however, are sometimes divided, and each may be separated into two quite distinct parts provided individually with groups of muscle fibers. In such cases there will appear to be, as in some of the Hymenoptera, a pair of movable lobes on each side of the genital apparatus.

A more detailed analysis of the structure of the organs of oviposition and copulation, as shown in the principal orders of insects, will form the subject matter of Part II of this paper, wherein will be presented also a larger body of evidence in support of some of the statements that seem arbitrary in the brief discussion given above.

THE CERCI (UROPODS)

The prevalence of cerci in so many orders of insects, and the almost universal occurrence of the organs in the more generalized groups leave little doubt that the cercal appendages are primitive structures, and that, in some form, they must have been characteristic features of the early insect ancestors. The anatomy and structural variations of the cerci are well known; functionally the appendages are in most cases sensory organs, though they are frequently modified in form to serve mechanical purposes; morphologically they are subjects of diverse opinion among speculative entomologists. The essential facts known concerning the cerci can be briefly stated.

In the Thysanura the cerci evidently belong to the eleventh abdominal segment. The last typical segment of the body in such forms as *Nesomachilis* (fig. 7 A) is the tenth (*X*), which is a complete annulus. From within the posterior margin of this segment there project the three terminal filaments, of which the lateral pair are the cerci (*Cer*). If the group of filaments is pulled out of the tenth segment, it is seen that the three of them arise from a common basal ring (B, *XI*), which has all the aspects of a reduced segment, in this case the eleventh, normally concealed within the tenth. The eleventh annulus presents a wide dorsal region (C, *XIT*) prolonged into the median caudal filament (*cf*), a narrow ventral region (D, *XIStn*) bearing a pair of broad posterior flaps (*Papt*), and two prominent lateral lobes supporting the cerci (*Cer*). There can be little doubt, therefore, that the caudal filament and the cerci here belong to the eleventh abdominal segment. The lobes of the eleventh sternum are evidently the paraprocts (D, *Papt*). Projecting from beneath the base of the caudal filament (D, *cf*) is a small median lobe (*sa*), possibly a remnant of the true telson, represented by the lamina supra-analis of the twelfth segment, better developed in odonate larvae (fig. 12 A, *sa*).

The terminal parts of the abdomen are less simple in some other thysanurans than they are in *Nesomachilis*. In *Thermobia* (fig. 7 E, F), for example, the eleventh segment is largely obliterated except for a distinct tergal plate, or epiproct (E, *Eppt*), which is connected laterally by a pair of small sclerites with the bases of the cerci (*Cer*). The paraprocts of *Thermobia* are large sclerotic plates (F, *Papt*) supporting the cerci. They would thus appear to correspond with the lateral lobes of the eleventh segment and the median paraproct plates of *Nesomachilis* (*D*). A sternal region of the eleventh segment distinct from the paraprocts is not evident in *Thermobia*.

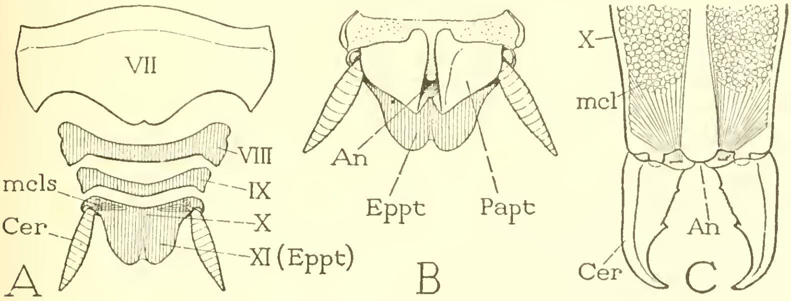

FIG. 40.—The cerci and associated parts.

A, posterior segments of *Periplaneta orientalis*, dorsal view, showing union of tenth and eleventh abdominal terga. B, ventral view of terminal segment of same. C, cerci of *Heterojapyx gallardi*, and muscles of tenth segment that move them.

In the Dicellura (Campodeidae and Japygidae) the abdominal segments beyond the tenth are obliterated, and the cerci are supported directly by the end of the tenth segment (fig. 40 C, *Cer*).

The cerci of the Pterygota most commonly *appear* to belong to the tenth abdominal segment, since they arise at the posterior edge of the latter, usually from membranous areas inclosed by the adjacent angles of the tenth tergum, the epiproct, and the paraprocts (fig. 12 A, B, *Cer*). In *Periplaneta* the cerci of the adult insect arise from between the lateral angles of the last tergal plate and the upper angles of the paraprocts (fig. 40 A, B), but the terminal plate of the dorsum is here clearly a composite sclerite formed of the united tenth tergum (A, *X*) and the epiproct (*XI*). Frequently the cerci are more closely associated with the paraprocts than with the tergal plates. In any case, however, the intermediate position of the cerci in adult Pterygota gives no positive evidence of the segmental relations of these appendages in this group of insects.

On the other hand, the ontogenetic evidence of the nature of the pterygote cerci seems to be quite definite, for it is stated by Ayers (1884), Cholodkowsky (1891), Wheeler (1893), and Heymons (1896*a*) that the cerci in the embryos of Orthoptera are formed directly from the appendages of the eleventh abdominal segment (figs. 5 A, 9 A, B, *Cer*). Heymons claims that the eleventh segment itself disappears from the adult abdomen, and that the cerci thus come to have an apparent intersegmental position between the tenth and the twelfth segments. As already shown, however, it appears more probable that the eleventh segment is usually represented in the adult by the epiproct and the paraprocts, and that it is the twelfth segment which is lacking, or reduced to a circumanal fold (fig. 12 A, *Prpt*).

The association of the cerci with the upper basal angles of the paraprocts, or their actual connection with these plates in some cases, as in *Thermobia* (fig. 7 F), has given rise to the idea that the cerci and the paraprocts have a genetic relation to each other. Thus, Crampton (1920, 1921) contends that the paraproct is the base of a segmental appendage of which the cercus is the distal part. According to Heymons (1896), on the other hand, the embryonic cercus represents the *entire* appendage of the eleventh segment, including the basis, which in the pregenital segments unites with the primary segmental sternum to become a lateral part of the definitive sternal plate. In the adult insect, Heymons says, the cercal base usually disappears as an evident lobe, though a rudiment of it is retained in young nymphs of *Gryllus* and *Decticus* as a small basal ring supporting the free part of the organ (fig. 8 B).

The musculature of the cerci, so far as it is known, is always dorsal, there being no muscles from the sternal region of the abdomen or from the paraprocts in any way associated with the cerci. The origins of the muscles present, however, give no clew to the segmental relations of the cerci, since the muscles arise either on both the tenth and eleventh terga, or on the tenth tergum alone. In her study of the abdominal muscles of Orthoptera, Ford (1923) finds that each cercus is typically provided with four muscles. Three of these muscles, distinguished as an abductor, a depressor, and an elevator muscle, take their origins on the tenth abdominal tergum; the fourth arises on the supra-anal plate or epiproct. The muscle from the epiproct, Ford says, is absent in *Gryllotalpa*, but it is present in *Gryllus*, *Neoconocephalus*, *Ceuthophilus*, and *Melanoplus*. In *Gryllus*, because of the union of the tenth tergum and the epiproct, this muscle, however, has shifted forward to the area of the tenth tergum. The writer has found only three muscles in *Dissosteira* inserted directly on the base of the cercus, two arising on the tenth tergum, and one on the epiproct.

The origin of the anterior muscles of the cerci on the tenth segment might be construed as evidence in favor of the view that the cercal appendages belong to the tenth segment; or, on the other hand, it might be taken as favoring Heymons' claim that the true eleventh segment has been obliterated. However, it is not necessary to assume that the muscles associated with the cerci are primarily muscles of these appendages. The great bundles of fibers that operate the pincer-like cerci of *Japyx* almost fill the large tenth abdominal segment (fig. 40 C, *mcl*), but they appear to be the longitudinal dorsal muscles normal to this segment, which secondarily function as cercal muscles by reason of their posterior attachments at the bases of the cerci. Ford (1923), observing that most of the cercal muscles in Orthoptera arise from the tenth tergum, asserts that these muscles are "intersegmental muscles between the tenth and eleventh segments," while the muscles from the epiproct, she says, represent "the intersegmental muscles between the eleventh and twelfth terga." (Her reference of the posterior muscles to the twelfth tergum is in accord with her acceptance of Heymons' claim that the eleventh segment has disappeared in the adult.)

Whatever may be the nature of the dorsal muscles of the cerci, the fact is significant that the organs have no ventral musculature—in this respect cerci differ from styli and gonapophyses. The absence of muscles from the paraprocts to the cerci, moreover, weakens the comparison between the paraprocts and the stylus-bearing plates of the preceding abdominal segments, since the stylus muscles always take their origin in these plates. The termination of the ventral musculature of the abdomen in the paraprocts, on the other hand, makes it almost certain that the paraprocts are terminal lobes of the eleventh sternum.

Cerci are usually absent in holometabolous insects, but cercus-like appendages occur on the eleventh abdominal segment in females of *Panorpa* (fig. 8 H, *Cer?*), and on the terminal segment of adult

Tenthredinidae, which is numerically the tenth abdominal segment. The panorpid appendages may be true cerci. Appendages occurring on an apparent tenth segment might be suspected of being cerci if there is evidence that this segment is composed of the tenth and eleventh somites, a condition which frequently occurs in orthopteroid insects, where there is no doubt that the terminal appendages are the cerci. In the Tenthredinidae, however, there is reason to believe, as will be shown later, that the terminal appendages of the adult are not the cerci, but are appendicular organs of the tenth segment corresponding with the socii of adult Lepidoptera, and that they are derived from the postpedes of the tenth somite of the larva.

THE TERMINAL APPENDAGES OF ENDOPTERYGOTE LARVAE

Appendicular organs representative of abdominal limbs are present on the last abdominal segment in some or most of the larvae of Neuroptera, Trichoptera, Lepidoptera, and chalastogastrous Hymenoptera. These larval appendages of the terminal segment have a lateral or latero-ventral position, and are movable by muscles in some cases attached on their bases, but more generally inserted within their distal parts. The appendages most resemble jointed limbs in the Trichoptera. In Neuroptera, Lepidoptera, and Hymenoptera they commonly have the structure typical of the abdominal legs of the caterpillars. Since the terminal segment in these larvae is evidently the true tenth somite of the abdomen, or the tenth and the eleventh somites combined, there is little doubt that the terminal appendages are the pygopods. The Endopterygota differ thus from the more generalized Exopterygota in that some of them retain the tenth segment appendages in postembryonic stages.

In addition to the true appendicular organs, there may be in endopterygote larvae also processes developed from the dorsum of the last segment, and lobes of various forms associated with the anal opening, or protruded from within the rectum. Processes resembling cerci occur in some coleopterous larvae, but their morphology is uncertain.

It seems probable that the pygopods of endopterygote larvae are, in certain orders, caried over to the adult stage as processes which sometimes occur on the proctiger, or terminal segment of the imago. These processes have various forms in the Trichoptera and Lepidoptera, and are termed the *socii* by students of the latter; in chalastogastrous Hymenoptera they resemble cerci, and are frequently called "cerci." Busck and Heinrich (1922) have observed that in the microlepidopteron *Ethmia machelhosiella* the anal prolegs, with their crochets, are retained in the pupa, and Bottimer (1926, fig. 3 A) shows a similar retention of the anal legs in the pupa of *Chaetocampa crotonella*. It is unfortunate that socii are absent in these species, for we might expect to find the socii developed within the anal prolegs of the pupae. More positive evidence of the identity of the terminal larval appendages with the terminal appendages of the adult is presented by Middleton (1921) in a study of the chalastogastrous Hymenoptera. Middleton claims that the anal prolegs, or postpedes, of the larva of *Pteronidea ribesii* are transformed during metamorphosis into anal lobes of the pupa, and that within these lobes are developed the so-called " cerci " of the adult sawfly. These appendages of the adult insect, he points out, are not borne by the tergum of the anal segment, but arise from a lateral membranous area of the venter of this segment, and thus morphologically have the same position as have the postpedes of the larva. The anal segment in both the larval and the adult sawfly is numerically the tenth abdominal segment, and its appendages are therefore not the true cerci in either case.

Trichoptera.—The abdomen of trichopterous larvae lacks appendages except on the terminal segment. In some forms, as in *Platyphylax designatus,* a fringe of slender setae along each side of the abdomen from the second to the end of the eighth segment (fig. 41 A, B, *a*) evidently marks the dorso-pleural line separating the dorsum of the abdomen from the region of the limb bases (*LB*), since, if the line of this fringe were carried into the thorax, it would run dorsad of the thoracic subcoxae (A, Scx_3). On the ninth segment there is nothing to mark the dorso-pleural boundary; but on the terminal segment the base of the appendage (B, *Pp*) has a lateral position corresponding with the limb base areas of the segments preceding the ninth. The terminal segment of *Platyphylax* is a hemispherical lobe with a long, median anal cleft on the ventral part of its distal surface (*An*). It is evidently the tenth somite, or pygidial segment.

The pygopods of trichopterous larvae differ considerably in different families and genera. Their principal variations have been described by Ulmer (1903) and by Krafka (1924). According to Ulmer there are two principal types of these appendages. Those of one type are short; those of the other, characteristic of Hydropsychidae and Rhyacophilinae, are long and leg-like. In both types the limb terminates in a hook-like claw. The structure of the two forms of appendages is here illustrated from *Platyphylax designatus* (fig. 41 B, *Pp*) and an unidentified species of *Hydropsyche* (F, *Pp*).

In *Platyphylax designatus* each larval pygopod together with its supporting structure (fig. 41 B, *Pp*) consists of a large basal plate (C, *b*), a smaller intermediate plate (*c*), and a free apical claw (*d*) having its point turned downward and outward. The apical claw has a movement of adduction on the middle plate, and the latter is movable on its hinge with the basal plate. The muscles of this appendage may be studied by cutting the terminal body segment into lateral halves. It is first seen that the base of the appendage is crossed internally by several slender transverse muscles attached on the segmental walls. The muscles inserted on the appendage consist of three flat groups of fibers (fig. 41 D), all arising on the anterior margin of the basal plate (*b*). Two of these muscles (*1a, 1b*) converge downward and posteriorly to a common point of insertion on the inner margin of the base of the apical claw (*d*), and thus evidently function as adductors of the latter. The third muscle is a broad sheet of fibers (*2*) lying external to the others, and inserted on the dorsal margin of the intermediate plate (*c*). Associated with the appendage is a pair of slender, vertical fibers (*5*) crossing the inner face of the basal plate and attached above and below it to the membranous walls of the

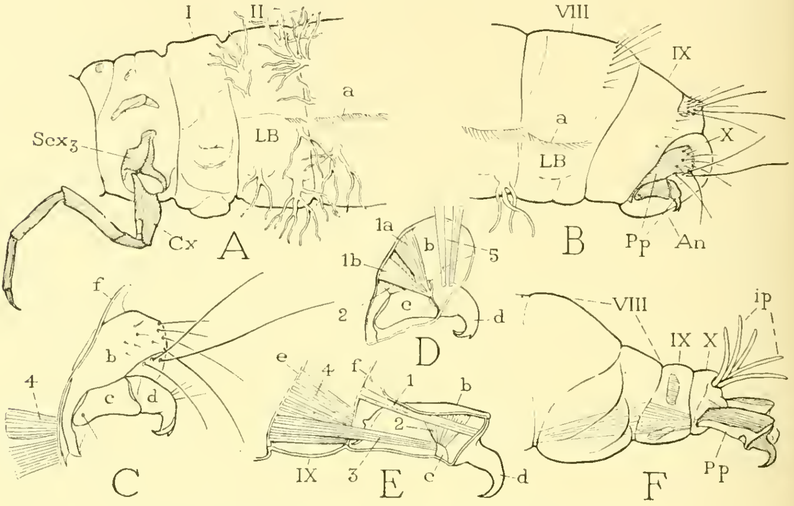

FIG. 41.—Structural details of trichopterous larvae.

A, metathorax and anterior part of abdomen of *Platyphylax designatus.* B, posterior abdominal segments of same. C, appendage of tenth segment of same. D, mesal view of right appendage, showing muscles. E, mesal view of terminal appendage of *Hydropsyche sp.*, showing muscles. F, posterior end of abdomen of same, with intestinal processes (*ip*) extruded from anus.

a, line of dorso-pleural groove; *An,* anus; *b,* proximal sclerite of appendage; *Cx,* coxa; *d,* claw of appendage; *e, f,* intersegmental folds between eighth and ninth, and ninth and tenth abdominal segments; *ip,* intestinal processes; *LB,* area of abdominal limb base; *Pp,* pygopod; *Scx,* subcoxa.

terminal body segment. The ventral muscles of the ninth body segment (C, *4*) are attached posteriorly on the intersegmental fold (*f*) just before the lower part of the basal plate of the appendage, but no muscles are inserted directly on the latter.

The terminal appendages of the larva of *Hydropsyche* (fig. 41, F, *Pp*) represent quite a different type of appendicular organ. Each pygopod here is a large, two-segmented, leglike structure projecting from the ventro-lateral part of the terminal body segment. The proximal segment of the appendage (E, *b*) is elongate and cylindrical; the distal segment (*d*) is a strong, decurved claw with a high, narrow base articulated by its dorsal end with the dorsal extremity of the basal segment. Ventrally, just before the base of the claw, there is a small triangular sclerite (*c*) in the lower, membranous wall of the proximal segment.

The musculature of the terminal appendage of *Hydropsyche* (fig. 41 E) differs in several respects from that of *Platyphylax* (D). As in the latter, however, there are no muscles inserted on the base of the organ, but there are an adductor muscle (E, *1*) inserted on the base of the apical claw (*d*), and two flexor muscles (*2, 3*) inserted on the small ventral sclerite (*c*). The adductor (*1*) arises, not in the basal segment of the appendage as in *Platyphylax* (D, *1a, 1b*), but in the proximal part of the last body segment. One of the flexor muscles (E, *2*) is a broad fan of fibers arising on the dorsal wall of the basal segment, and thus suggests an identity with muscle *2* of *Platyphylax* (D) arising on the basal plate of the appendage. The other flexor muscle is a long bundle of fibers (E, *3*) arising on the intersegmental fold (*e*) between the eighth and ninth abdominal segments along with the fibers of the ventral longitudinal muscles of the ninth segment (*4*), but separating from the latter posteriorly to enter the appendage. This muscle apparently has no representative in *Platyphylax* (D).

The relation between the two types of appendages described above is obscure. The only suggestion that can be made is that the basal plate of the *Platyphylax* appendage (fig. 41 D, *b*) corresponds with the basal segment of the *Hydropsyche* appendage (E, *b*) and that the intermediate plate of the former (*c*) is represented by the small ventral sclerite (*c*) of the latter. The apical claw (*d*) is evidently the same in both. Still more difficult is it to find possible homologies between either of these two types of trichopterous appendages and the terminal appendages of the sialid larvae, *Chauliodes* and *Corydalus* (figs. 35 D, E, 36 B, E), or the abdominal legs of lepidopterous larvae (figs. 37, 42 C). The basal plate or basal segment (*b*) in the trichopterous appendage, however, may be the limb basis of a more typical abdominal appendage, while the apical claw (*d*) and the associated middle plate (*c*) may possibly represent the stylus. Judging from the structure there is little probability that the trichopterous claw is homologous with the claws of *Corydalus* or *Chauliodes,* or with the crochets of lepidopterous larvae. The lack of similarity in the larval abdominal appendages of Trichoptera and Lepidoptera is somewhat surprising, considering the many other structural likenesses between these two orders.

Many trichopterous larvae are provided with a group of slender processes protractile through the anus (fig. 41 F, *ip*), which arise from the intestinal wall. In the species of *Hydropsyche* figured there are from four to six of these processes. The structures are hollow, thin-walled tubules containing no tracheae, and are therefore usually termed "blood gills"; but the idea of their respiratory nature is based on their structure and on the fact that they can be entirely exposed by protraction through the anus, for no one apparently has made any physiological experiments on their function. According to Branch (1922) the organs arise as diverticula of the intestinal wall produced posteriorly from the six folds of the pre-rectal part of the proctodeum, and each is provided with a three-branched muscle taking its origin on the intersegmental membrane between segments VIII and IX of the abdomen, and extending through the lumen to the tip of the processes. When retracted the processes lie in the rectum with only their extremities exposed in the anal aperture. Protraction evidently is accomplished by internal pressure resulting from a contraction of the abdominal walls.

Neuroptera.—The pygidial appendages in the larvae of the sialid genera *Chauliodes* and *Corydalus,* as already noted, are long, thick structures projecting posteriorly and ventrally from the terminal segment of the abdomen (fig. 35 D, E, *Pp,* fig. 36 B, E). Each organ consists of a large basis (fig. 36 E, *LB*), supporting laterally a flexible, tapering process representing the stylus (*Sty*), and bearing distally a short, cylindrical lobe (*Vs*) armed with two strong claws (*d*). The appendage has a striking resemblance to the typical abdominal leg of a caterpillar, except that the latter has no representative of the stylus. The distal lobe, which clearly is serially homologous with the gill-bearing tubercles of the preceding appendages in *Corydalus* (fig. 36 B, C, D, *Vs*), is remarkably like the planta of the caterpillar's leg (fig. 37 D, *Vs*). It is retracted by a strong muscle (fig. 36 F, *rvs*) arising on the dorsal wall of the terminal body segment, and inserted on the distal wall of the lobe at the posterior or upper end of the long bases of the claws. The claws themselves are in every way suggestive of the crochets of the caterpillar's foot.

Notwithstanding the general structural resemblance between the terminal appendages of *Chauliodes* or *Corydalus* and the abdominal legs of caterpillars, it can scarcely be supposed that the foot structure in either case has been derived immediately from that of the other, since the two-clawed condition would be a highly specialized one in the Lepidoptera. All that may be claimed is that the fundamental structure of the larval abdominal limbs is the same in both the Neuroptera and the Lepidoptera. The neuropterous appendage is the more primitive in that it retains the stylus, which has the form of a segmented appendage in *Sialis* (fig. 35 A, C). We may assume that the gill-bearing tubercles of the *Corydalus* larva have been formed secondarily from the foot lobes, or retractile vesicles, as a better adaptation to aquatic life in this genus, and that the vesicles have been lost from all the appendages in *Sialis,* and from all but the terminal appendages in *Chauliodes.*

Lepidoptera.—The so-called anal legs, or postpedes, of caterpillars are so similar to the legs of the preceding abdominal segments as scarcely to need a separate description. The musculature of the two sets of appendages, however, differs in some respects. The plantar lobe of each anal leg is retracted by a large dorsal muscle (fig. 42 A, B, C, *rvsd*) and a small ventral muscle (*rvsv*), both arising from the intersegmental fold (*f*) before the ninth abdominal segment. The lateral muscles of the leg are reduced to a few fibers (D, *b*) lying external to the large dorsal retractor of the planta. Between the bases of the legs there is a sheet of transverse ventral muscles (B, *tv*), which appear to belong to the wall of the last body segment rather than to the appendages.

The great development of the dorsal retractor muscles of the anal legs, the reduction of the lateral muscles, and the presence of the ventral retractors of the plantae are all features correlated with the function of the postpedes in the caterpillar, which usually have a stronger independent forward movement than do the legs of the preceding segments.

The large terminal segment of lepidopterous larvae appears to be a compound segment composed of the tenth abdominal somite, with its appendages, the pygopods, and the reduced eleventh segment, bearing the anus, but lacking cerci. Figures of the embryo of *Pieris rapae* given by Eastham (1930) show clearly a well-developed tenth abdominal segment bearing the last pair of appendages, and beyond it a large terminal lobe, containing the anus, which is evidently the eleventh somite. In the caterpillar (fig. 11) the eleventh somite is apparently represented in the terminal segment by the four postpedal lobes surrounding the anus (C, D), which may be supposed to be the epiproct (*Eppt*), the paraprocts (*Papt*), and a hypoproct (*Hypt*). There is, however, no evidence of a dual composition of the terminal segment of the caterpillar furnished by the musculature of this segment. Both the dorsal and the ventral internal longitudinal muscles (fig. 42 A, B, *di, vi*) extend continuously from the anterior intersegmental fold (*f*) to the epiproct and the paraprocts. Two large sets of internal dorsal fibers (A, *de*) arise in the notches between the epiproct and paraprocts and are inserted on the dorsal plate of the segment. The eleventh segment, therefore, if represented here at all, is reduced to the circumanal lobes; and the fibers of the longitudinal muscles of the tenth and eleventh segments have become continuous.

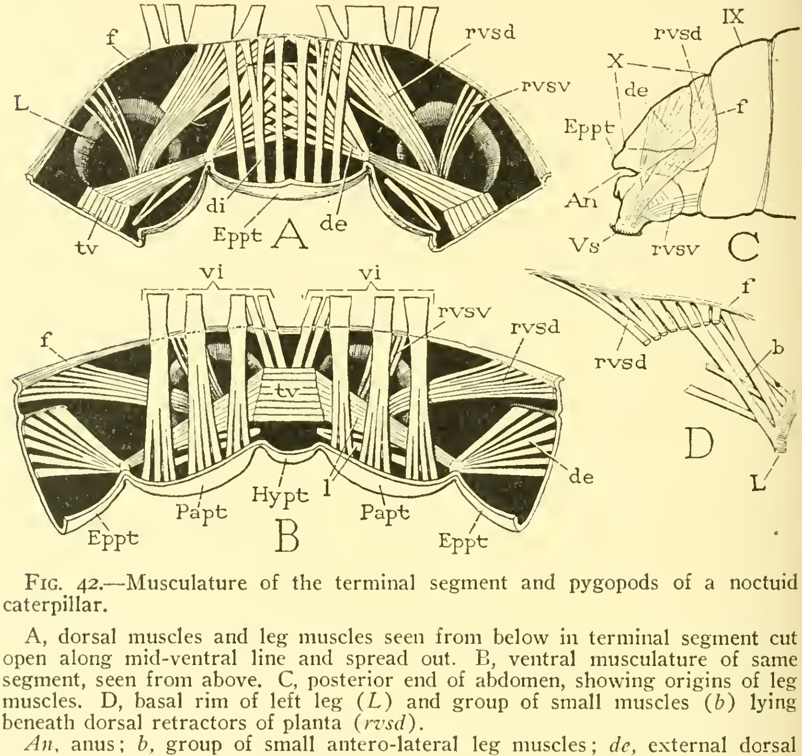

FIG. 42.—Musculature of the terminal segment and pygopods of a noctuid caterpillar.

A, dorsal muscles and leg muscles seen from below in terminal segment cut open along mid-ventral line and spread out. B, ventral musculature of same segment, seen from above. C, posterior end of abdomen, showing origins of leg muscles. D, basal rim of left leg (*L*) and group of small muscles (*b*) lying beneath dorsal retractors of planta (*rvsd*).

An, anus; *b,* group of small antero-lateral leg muscles; *de,* external dorsal muscles; *di,* internal dorsal muscles; *Eppt,* epiproct; *f,* intersegmental fold between ninth and tenth segments; *Hypt,* hypoproct; *L,* basal rim of leg; *l,* lateral muscles; *Papt,* paraproct; *rvsd,* dorsal retractor of planta; *rvsv,* ventral retractor of planta; *tv,* transverse ventral muscles; *vi,* internal ventral muscles; *Vs,* planta.

Continuity of muscle fibers is of frequent occurrence wherever the intersegmental connections are lost, or where segmental boundaries are obliterated.

Chalastogastrous Hymenoptera.—The larvae of the sawflies and horntails are provided with terminal appendicular organs of several varieties, all borne by the last abdominal segment, some arising from the dorsum, others from the venter.

On the dorsum there is in some forms, as in *Pteronidea ribesii* (fig. 43 A), a pair of small, immovable lateral processes (*a*) arising from the end of the last segment above the anal opening (*An*). These processes have been regarded as rudimentary cerci (Crampton, 1919), but they are more evidently mere cuticular outgrowths, as claimed by Middleton (1921), analogous with the urogomphi of coleopterous larvae (fig. 44 C, *ug*), since they have none of the characteristics of true cerci, and, according to Middleton, take no part in the formation of the lateral, cercus-like appendages of adult Tenthredinidae. In certain other chalastogastrous larvae a median process, or postcornu (fig. 43 C, *b*), is borne on the end of the tenth abdominal segment. This process varies characteristically in shape and size in different families, as tabulated by Middleton (1921). It occurs in larvae that bore into stems or that live in silk-spun tents or within the hollow of curled leaves.

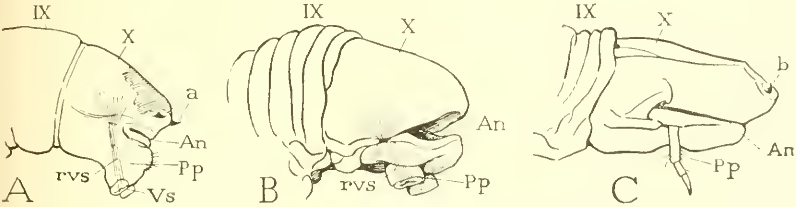

FIG. 43.—Terminal appendicular structures of larvae of chalastogastrous Hymenoptera.

A, *Pteronidea ribesii* (Tenthredinidae). B, *Cimbex americana* (Cimbicidae). C, *Cephaleis sp.* (Pamphiliidae).

a, paired processes of dorsum of terminal segment; *An*, anus; *b*, median process of dorsum of terminal segment; *Pp*, postpedes, or pygopods; *rvs*, retractor muscle of plantar lobe; *Vs*, planta.

The ventral appendages of the pygidial segment of chalastogastrous larvae likewise vary in form in different groups. Those of species that live in the open closely resemble the anal legs of lepidopterous larvae. In *Pteronidea ribesii*, for example (fig. 43 A), a ventral projection of the tenth segment beneath the anus, bearing two small terminal lobes (*Vs*), is clearly the homologue of a pair of appendages such as occur on the more anterior segments of the abdomen. The free lobes (*Vs*) are evidently comparable with the plantae of the abdominal legs of caterpillars (fig. 37 D, *Vs*), though the retractor muscles of the lobes in the sawfly larva take their origins from a point on the side of the segment just anterior to the cleft of the anal opening (fig. 43 A, *rvs*). In other forms, as in *Cimbex americana* (B), the ventral appendages (*Pp*) consist apparently of the plantar lobes only, which arise directly from the flattened venter of the pygidial segment. Again, as in the Cephidae and Pamphiliidae, typical "prolegs" are replaced on the tenth segment by slender jointed appendages (C, *Pp*); but these "arthrostyli," as they have been called (Crampton, 1919), are evidently alternative forms of the anal "prolegs," or postpedes, since they arise at approximately the same points as do the typical postpedes in other forms (A, *Pp*), and do not occur conjointly with the latter. They are not, however, provided with muscles, so far as the writer could discover; but each is penetrated by a large nerve, and bears sense organs on the distal segment having the form of minute disks, in addition to setae on the proximal and middle segments. The jointed form of the terminal appendage is, therefore, evidently an adaptation to a sensory function instead of a locomotory one.

Crampton (1919) suggests that the jointed appendages, or "arthrostyli," of chalastogastrous larvae do not represent the "prolegs" directly, but that each has the relation to the latter of a stylus, that is, it is an appendicular part of the true appendage. Middleton (1921), on the other hand, thinks that the jointed appendages are direct representatives of the unjointed postpedes, because the two organs have identical positions on the tenth segment, and do not occur together. He would attribute the difference in form to the different habits of the larvae, since those species having typical, fleshy postpedes feed in the open on leaves and grasp the edges of the latter with the terminal appendages, while those having slender, jointed postpedes, bore into the stems of plants, or live in the protection of web nests or curled leaves. To the writer it appears most probable that the two forms of appendages are identical organs, and that the jointed variety is a secondary modification of the typical postpedes for a sensory function, the jointing being a mere subdivision of the appendage and not a true segmentation.

The observation made by Middleton (1921) that the postpedes of the larva become the cercus-like appendages of the adult sawfly has been discussed in the introductory part of this section, and need be given no further attention here, except to point out its importance, if true, in establishing an identity between the terminal appendages of larval insects and the appendicular processes of the tenth segment in certain adult holometabolous insects.

Coleoptera.—In many families of the Coleoptera the abdomen of the larva is provided with a pair of appendicular processes arising from the dorsum of the ninth segment. These structures have been variously termed styli, cerci, pseudocerci, corniculi, and urogomphi.

The abdomen of the larva of *Dytiscus* ends with a transverse posterior surface of the narrow eighth segment (fig. 44 A), in the upper part of which the last pair of spiracles open through a median, vertical slit (*VIIISp*). From the membrane below the spiracular area of the eighth segment there arise laterally two slender, tapering processes (*ug?*) fringed with long hairs. Between the bases of these organs is a small, median plate (*IXT?*), which appears to be a remnant of the ninth abdominal tergum. Ventral to it is the anal opening (*An*). According to Speyer (1922, Korschelt, 1924), each of the terminal appendages of the larva of *Dytiscus marginalis* is provided with three muscles, two inserted dorsally on its base, and one ventrally, all of which arise on the tergum of the eighth segment.

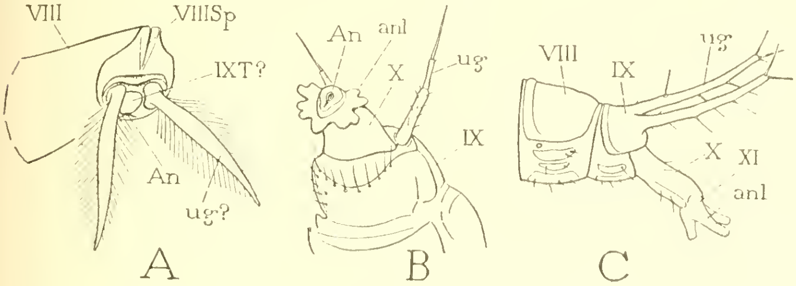

Fig. 44.—Terminal appendages of coleopterous larvae.

A, posterior end of abdomen of *Dytiscus circumcinctus* larva. B, end of abdomen of a silphid larva, *Thanatophilus sp.*, with exserted anal lobes (from Kemner, 1918). C, end of abdomen of carabid larva, *Oodes helopioides*, with exserted anal lobes (from Kemner, 1918).

An, anus; *anl*, anal lobes; *ug*, urogomph.

The morphology of the larval appendages of *Dytiscus* is difficult to determine. The apparent position of the organs on the rudimentary ninth segment makes it doubtful that they are true cerci, and the dorsal origins of their muscles is not in accord with the musculature of styli. It is claimed by Blunck (1918, Korschelt, 1924) that in all Coleoptera the first two primitive somites of the abdomen are united in the first definitive segment, and that, therefore, the segment bearing the terminal appendages is really the tenth. In this case we might regard the terminal appendages of the *Dytiscus* larva as the cerci. However, the evidence presented by Blunck of the fusion of the first and second segments of the abdomen is not generally accepted by students of Coleoptera, and is not convincing, while the fact that the segment preceding the appendicular processes bears the eighth pair of abdominal spiracles would ordinarily be taken as conclusive evidence that this latter segment is the true eighth somite of the abdomen, especially since these respiratory apertures, as described by Blunck, have the structure typical of lateral abdominal spiracles.

For the present, therefore, the nature of the terminal appendages of the *Dytiscus* larva must be left in doubt, but if the organs do not belong to the series of lateral, stylus-like appendages, fully represented in *Coptotomus* and Gyrinidae, it is possible that they are structures homologous with those dorsal processes often developed on the ninth abdominal segment of other coleopterous larvae, which appear to be mere cuticular outgrowths, though they may become movable at their bases. The muscles inserted on the processes in *Dytiscus* are evidently not specific muscles of the appendages, but groups of segmental or intersegmental fibers that, by reason of their attachments at the bases of the processes, serve to move the latter.

The abdomen of most other coleopterous larvae consists of 10 distinct segments (fig. 44 B, C). The ninth segment is usually well developed and frequently supports a pair of processes (B, C, *ug*) arising from its dorsum. These processes are termed *urogomphi* by Böving, since from their segmental position it is clear that they can not be cerci. In some species the urogomphi are fixed outgrowths of the posterior end of the ninth tergum (C) ; in others they arise from the membrane behind the ninth tergal plate (B), and are then flexible at their bases. They vary much in size and shape from short, spine-like points to long, thick processes or multiarticulate filaments, and they are sometimes distinctly jointed. The urogomphi appear to be equivalent structures in all cases, and are probably but cuticular outgrowths of the ninth abdominal tergum, which in certain species become movable by a membranization of the tergal wall at their bases. The mobile appendages of the *Dytiscus* larva, therefore, are perhaps urogomphi of the rudimentary ninth segment, secondarily movable by some of the intersegmental muscles normally extending between the eighth and ninth segments.

The tenth abdominal segment in many coleopterous larvae is a short, often tubular structure (fig. 44 B, C, *X*), at the extremity of which is a small retractile and eversible membranous pad surrounding the anus, known as the " pygopodium " (C, *XI*), which may be produced into two or more soft lobes (*anl*). It is claimed by Kemner (1918), from embryological evidence, that the so-called pygopodium is the rudimentary eleventh abdominal somite. The eversible pygopodial lobes, however, in no way represent appendicular organs, Kemner asserts, nor are they evaginations of the wall of the rectum, as they have been supposed to be; they are merely productions of the cercumanal area on which the longitudinal muscles from the tenth to the eleventh segment are attached. If the organs in question, therefore, are not of an appendicular nature, the term " pygopodia " should not be given to them, since it is convenient to apply this name specifically to the true appendages of the tenth, or pygidial, segment. The presence of a distinct though rudimentary eleventh segment in larvae of Coleoptera is of interest because of the general suppression of this segment in holometabolous insects.

TERMINAL LOBES OF THE PARAPROCTS

In a few of the lower Pterygota an appendicular lobe is borne by each of the paraprocts. These processes have been termed " paraprocessi " by Crampton (1920). Examples of paraproct lobes occur in the Odonata and in the tridactylid Orthoptera.

The paraproct processes of Odonata occur in adult Anisoptera in the form of small, seta-bearing lobes projecting posteriorly from the ends of the paraprocts. Corresponding lobes are not present in the larvae of this group of dragonflies, in which the paraprocts, together with the elongate epiproct, form the valves that close the anal opening (fig. 12 A, B). In the larvae of Zygoptera, however, paraproct lobes are highly developed as the large, flat, tracheated plates that form the lateral caudal gills (C, *paptl*). The median gill (*cf*) is a similar lobe of the epiproct (*Eppt*), and is evidently comparable with the median caudal filament of Thysanura (fig. 7 A, B, C, *cf*).

In the Orthoptera paraproct lobes are well developed in the Tridactylidae, where they have the form of long processes resembling the cerci (fig. 45 A, B, *paptl*). In some species of *Ripipteryx* those of the male are incurved at the ends and are said to be used as claspers during copulation. In *Ellipes* (fig. 45 A, B) each process is borne on a membranous area at the end of the short paraproct (*Papt*). Crampton (1918, 1921) has given considerable significance to the " paraprocessi " of the Tridactylidae, which he regards as homologous with the styli of the preceding segments, and as representatives of the exopodites of crustacean appendages (fig. 45 C, D, *expd*). Most other writers, including Walker (1919), regard the processes as secondary lobes of the paraprocts. It is highly unlikely that the structures in question are styli, since, as already shown, the paraprocts are not limb bases. Crampton's view regarding the relation of the paraproct process to crustacean exopodites will be discussed in the following Section of this paper.

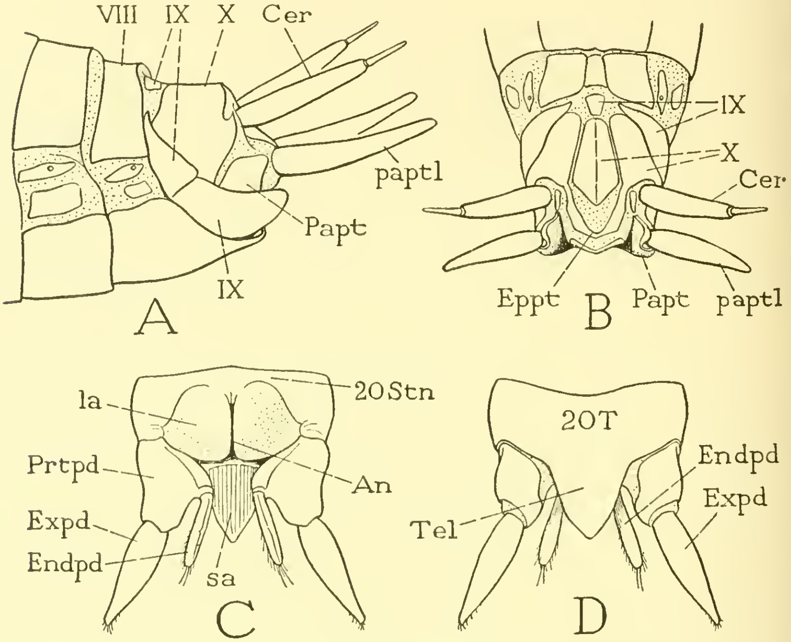

FIG. 45.—Terminal appendages of a tridactylid insect and an isopod crustacean.

A, posterior part of abdomen of *Ellipes minuta* (tridactylid orthopteron). B, the same, dorsal view. C, end of abdomen of *Porcellio* (isopod crustacean), ventral view. D, the same, dorsal view.

An, anus; *Cer,* cercus; *Endpd,* endopodite; *Eppt,* epiproct; *Expd,* exopodite; *la,* lamina sub-analis; *Papt,* paraproct; *paptl,* lobe of paraproct; *Prtpd,* protopodite; *sa,* lamina supra-analis; *Tel,* telson (fused with tergum of twentieth segment).

MORPHOLOGY OF THE ABDOMINAL APPENDAGES

There is no need at present to offer proof of the serial identity of the appendicular organs of the insect abdomen with the segmental appendages of the thoracic and cephalic regions of the body. Embryologists have amply demonstrated the continuity of appendage rudiments on the entire series of primitive somites, at least 20 in all, leaving only a prostomial lobe and a periproctial region devoid of true limb structures. To determine the homologies of the parts of the abdominal appendages with the parts of the better developed appendages on the anterior regions of the body, or with those of theoretically more generalized appendages, is quite another matter.

Theoretical Structure of Arthropod Appendages.—At the outset of an attempt to study the morphology of the rudimentary abdominal appendages of insects a difficulty is encountered arising from the lack of uniform opinion as to the structure of a generalized but fully segmented arthropod limb. Particularly is it necessary in a study of rudimentary appendages to know the structure of the basal part of a primitive appendage. In the thorax of modern insects the functional base of a leg is the coxa, and yet, it seems almost certain that at an earlier stage the true basis of the limb must have included the subcoxal region now forming the so-called pleuron and in some cases a lateral part of the definitive sternal plate of the supporting body segment. Then, the further question arises as to whether the subcoxa was once a free segment of the appendage, or whether it has been evolved secondarily by a differentiation of the primitive limb basis into subcoxal and coxal parts. Differences of opinion on such questions as these have led immediately to different interpretations of the basal parts of the abdominal appendages, and consequently to different views concerning the nature of the distal parts.

A simple condition of the limb base occurs throughout the Arachnida, which is well shown in any one of the legs of a phalangid (fig. 46 A). It is to be seen here that the leg is supported on a large basal segment (*LB*) that occupies the lateral wall of a segmental area of the body, and that it turns slightly forward and rearward on a dorsoventral axis (*a-b*) extending from the tergum above to the sternum below. To this large basal segment the telopodite is articulated by a dicondylic hinge on a horizontal axis (*f-g*). The first segment of the telopodite is a trochanter (*1Tr*).

In the majority of the Crustacea the proximal region of the leg has the same structure as in the Arachnida, there being a single basal segment, the coxopodite (fig. 46 B, C, *LB*), implanted directly in the ventro-lateral wall of the supporting body segment, and often articulated dorsally (*a*) with the tergal plate (B, *T*). The basis, however, is not prolonged ventrally as in the phalangid (A), and is inclined to be cylindrical (C). The telopodite articulates with the basis by its proximal segment (the first trochanter, or basipodite, B, C, *1Tr*) on a horizontal, dicondylic hinge (*f-g*) having the same type of structure as that in the arachnid (A).

If, now, we look at a typical thoracic leg of an insect (fig. 46 D), it is seen that the proximal joint in the appendage corresponding structurally and functionally with the joint between the basis and the telopodite in the phalangid or crustacean leg (A, B, C, *f-g*) is that between the coxa and the trochanter (D, *f-g*). The coxa (*Cx*), however, is separated from the tergum (*T*), and often from the sternum (*Stn*), by a sclerotization, known as the " pleuron " (*Scx*), occupying the position in the lateral wall of the supporting body segment that is occupied by the limb basis in the phalangid and crustacean (A, B, C, *LB*). In other words, the basal region of the appendage in the case of the insect leg (D, *LB*) is composed of two parts (*Scx, Cx*) corresponding with the single plate or segment (coxopodite) forming the basis of the arachnid and crustacean appendages illustrated (A, B, C). A condition similar to that in the insect thorax is found, however, in the thoracic region of the decapod crustaceans, where a large pleural plate occurs on each side of the body intervening between the coxae and the tergum. This plate is clearly a composite structure, the segmental areas of which are evidently derived from the subcoxal parts of the leg bases, because they support the gills of the

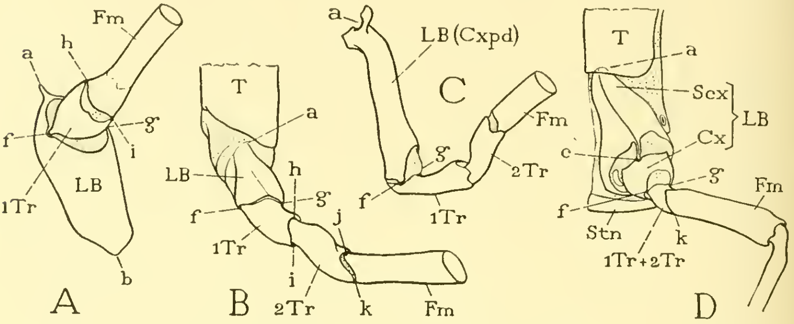

Fig. 46.—Basal parts of arthropod legs.

A, third right leg of a phalangid, *Liobunum*, showing limb basis (coxopodite) elongate ventrally (*LB*), turning antero-posteriorly on dorsoventral axis (*a-b*), with telopodite movable dorsoventrally on horizontal axis (*f-g*).

B, last right ambulatory leg of a crustacean, *Anaspides tasmaniae*, with small basis, or coxopodite (*LB*), on which the telopodite turns dorsoventrally on horizontal axis (*f-g*) of first trochanter, or basipodite (*1Tr*).

C, leg of an isopod crustacean, *Porcellio*, with elongate basis, or coxopodite (*LB*), to which the telopodite is articulated by a horizontal hinge (*f-g*) as in A and B.

D, mesothorax and middle leg of a young acridid nymph, *Melanoplus*, showing region of limb basis (*LB*), between the horizontal baso-telopodite hinge (*f-g*) and the tergum (*T*), subdivided into subcoxa (*Scx*) and coxa (*Cx*).

a, dorsal articulation of limb basis with body; *a-b*, axis of articulation of limb basis with body; *c*, dorsal subcoxo-coxal articulation; *Cx*, coxa; *Cxpd*, coxopodite (limb basis); *f-g*, axis of baso-telopodite hinge; *Fm*, femur (meropodite); *h-i*, axis of hinge between first and second trochanters; *j-k*, axis of trochantero-femoral hinge; *LB*, limb basis (coxopodite); *Scx*, subcoxa; *Stn*, sternum; *T*, tergum; *1Tr*, first trochanter (basipodite); *2Tr*, second trochanter (ischiopodite).

branchial chamber. Subcoxal sclerites occupying the lateral walls of the body segments are again found in the Chilopoda (fig. 27 A, *Scx*), and in the last leg-bearing segment they are here united with the coxa to form a single basal plate (*LB*) of the appendage, occupying the pleural region of the segment.

From comparative studies such as those just cited, the writer has come to regard the pleural subcoxa, or sclerotic area of the lateral body wall supporting the free part of an appendage, as the proximal part of the primary limb basis secondarily separated, wherever it occurs, from the distal part of the basis, which becomes the movable coxa, or functional base of the limb. On the other hand, many students of Arthropoda regard the subcoxa as a primitive limb segment, which has become suppressed or fused with the coxa wherever traces of it are not to be found in modern forms. The entire absence of a subcoxa in all Arachnida and in the majority of Crustacea, however, is against this view; and the lack of uniformity in the subcoxocoxal musculature, when a subcoxa is present, suggests that the subcoxo-coxal joint is a recent division of the limb basis that has occurred principally in the Chilopoda and the Hexapoda. If the subcoxa is a secondary formation, then it must be assumed that the subcoxo-coxal muscles likewise are secondary, and that, as the subcoxa became differentiated from the coxa, most of the primitive basal muscles of the appendage were transferred to the coxa.

The subcoxa in its more primitive condition is best seen in the Chilopoda and in the thoracic segments of apterygote Hexapoda. It here consists of a circular fold or slight elevation of the body wall supporting the leg, containing one or more small sclerites, particularly in the region above the coxa. The large " pleura " of the thoracic region of pterygote insects, or the pleural plates of the branchial chambers of decapod crustaceans, undoubtedly represent highly specialized developments of the subcoxae, adapting the latter to uses quite independent of any function connected with the legs. The subcoxal plates in the thorax of holometabolous insect larvae, however, are relatively small and are closely associated with the coxae (figs. 3 B, C, 41 A, Scx_3). The region of the subcoxa *surrounds* the base of the coxa, but its ventral arc is reduced to a fold, which generally in the thorax of adult insects unites with the sternum. The sclerotized area of the subcoxa may be broken up into several small sclerites; in the thorax of pterygote insects there is typically a large supracoxal plate known as the " pleuron."

In a former paper the writer (1928) has given reasons for believing that the body of a gnathal appendage represents the basis of a leg. It is similarly divided secondarily into two parts (cardo and stipes), though it is not clear that the two parts exactly correspond with the subcoxa and coxa of a thoracic leg. The palpi, however, are thus seen to be the telopodites of the head appendages. If the interpretation concerning the primary segmentation of a gnathal or a thoracic appendage into basis and telopodite is now carried to the appendages of the abdomen, the basal plates or basal lobes of the latter become the true limb bases, and the telopodites should be freely movable appendicular processes of the bases.

In general, then, it appears that the arthropod limb is divided by a joint near its base into a proximal part, the primary *limb basis,* and into a distal part, or *telopodite.* The baso-telopodite joint is the coxo-trochanteral joint of a fully segmented limb, which is the joint between the coxopodite and the basipodite in terms usually employed by carcinologists. The use of the term "basipodite" by Börner (1904, 1921) to designate the subcoxo-coxal base of the limb creates a duplication in nomenclature that is likely to be confusing. The movement of the telopodite on the basis is typically in a vertical plane, produced by levator and depressor muscles arising in the basis (fig. 25 A, *O, Q*).

On the assumption that the basal mechanism of all the limbs is fundamentally the same in all groups of arthropods, we can imagine a simple primitive condition in the arthropodan ancestors in which the entire series of appendages had a uniform line of flexure near the body, along which the distal parts of the limbs, or telopodites, were movable in a vertical plane on their bases. The bases, on the other hand, turned forward and rearward on the axes of their attachments on the body. Wherever the basis is differentiated into a coxa and a subcoxa, the primitive basal movement of the appendage on the body is lost, but is replaced by a vertical axis of promotion and remotion between the subcoxa and the coxa, as the latter becomes secondarily the functional base of the limb. Finally, if the limb becomes rudimentary and loses its basal musculature, the basis might become transformed to a simple immovable lobe or plate of the wall of the supporting body segment, with the telopodite reduced to an appendicular process movable by muscles arising in the basis.

Other Theories on the Morphology of the Abdominal Appendages.—The principal problem encountered in a study of the abdominal appendages of insects is that of determining the homologies of the parts of the appendages with those of a generalized limb. The basis, the stylus, the gonapophysis, the eversible vesicle, each raise questions as to its nature and derivation.

Discussions on the morphology of the abdominal appendages of insects, and speculations on their possible homologies with the limbs of Crustacea have continued for half a century without leading to definite conclusions. They began at least with Wood-Mason (1879), who, in a paper on the origin of insects, interpreted the stylus-bearing plates of the abdomen of *Machilis* as the protopodites of primitively biramous appendages, of which the endopodites are represented by the gonapophyses, and the exopodites by the styli. The eversible vesicles, Wood-Mason suggested, may be homologues of nephridia, those of the eighth and ninth segments being converted into the genital ducts.

Diversities of opinion soon followed the publication of a more widely read paper by Haase (1889) on the morphology of the segmental appendages, containing not only a clear exposition of the appendicular nature of the stylus-bearing plates in the abdomen of Thysanura, but also a demonstration of the triple origin of the definitive abdominal sterna of insects in general from the union of the rudimentary embryonic limbs with the median sternal area in each segment. The styli, Haase claimed, are not the leg rudiments, but secondary structures of the nature of hairs, which have been converted into locomotory organs from sensory organs. The eversible vesicles he believed function as blood gills, but are to be traced back in all cases to coxal glands.

Wheeler (1893) and earlier students of the embryology of insects regarded the gonapophyses of the genital segments as the direct representatives of the appendages of these segments. Considering the late development of the gonapophyses, however, and their invariable median position on the body of the insect, Heymons (1896*a*) contended that the genital processes are secondary integumental outgrowths having no relation to the appendages, and that the latter are preserved in the styli and cerci. Heymons' heterodox opinion brought a severe criticism from Verhoeff (1896), who defended the limb nature of the gonapophyses as an established fact, and maintained that the identity of the abdominal styli with the thoracic styli of *Machilis* could not be disputed, and that therefore both are merely appendicular processes of the legs. In reply to Verhoeff, Heymons (1896*b*) emphasized his former statements in evidence of his view concerning the nature of the appendicular parts of the abdomen, pointing out that, during embryonic development of the Orthoptera, the abdominal appendages disappear, and the gonapophyses are later formed quite independent of the limbs. He argued that if the gonapophyses are the limbs, intermediate stages should be found some-where between gonapophyses and legs. The styli, Heymons reasserted, are direct derivatives of the abdominal appendages, and occur in primitive forms such as *Campodea* and *Japyx* in which gonapophyses are lacking. From the abdominal limb rudiments of the embryo, Heymons showed, are produced not only the typical styli, but also the cerci, and the lateral gills of the larvae of Ephemerida and *Sialis*.

Since Heymons' views are based on embryological studies they deserve more attention than purely theoretical considerations. In his studies of the development of the appendages of *Periplaneta, Ectobia,* and *Mantis,* Heymons (1896*a*) observes that each limb rudiment of the ninth segment is early marked by a circular constriction, which divides the appendage into a broader proximal part and a slenderer distal part. The proximal part flattens out and finally is incorporated in the definitive sternal plate of the segment, while the distal part becomes longer and slenderer and develops directly into the stylus. The gonapophyses, on the other hand, Heymons claims, are secondary outgrowths of the sterna in the Orthoptera. Concerning them he says: "In Gryllus there can be no doubt of the nature of the gonapophyses. Abdominal extremities are present in the embryo on the eighth and ninth segments, but they later degenerate, and in old embryos as well as in young larvae leave not the slightest rudiments. It is only later, in older larvae, that the gonapophyses appear, and they are therefore undoubtedly to be regarded as secondary integumental outgrowths." Thus, according to Heymons, the stylus and not the gonapophysis is the representative of the telopodite in an abdominal appendage.

It must be conceded that the facts of embryonic development do not necessarily recapitulate phylogenetic evolution, since we can never be sure that the early stage of an organ reproduces the primitive form of that organ, and this must be particularly true of a rudimentary structure. Thus, if the telopodite of a limb bearing a basal exite process has long been lost, the limb rudiment in the embryo might be supposed to consist of the limb basis and the accessory process, and to lack the telopodite element entirely. Hence, while Heymons' evidence of the nature of the styli is highly suggestive that the styli are the rudiments of the telopodites, it does not demonstrate the point. On the other hand, Heymons' line of reasoning concerning the gonapophyses makes it seem almost certain that the genital processes are not the telopodites of the gonopods, but the facts of development can scarcely be taken as evidence that the gonapophyses do not belong to the genital appendages. It is amply proven in the Thysanura that the gonapophyses are processes of the gonopods, and in the Orthoptera they are undoubtedly outgrowths of the parts of the definitive sterna derived from the bases of these appendages.

Verhoeff (1903), retaining his former views on the homologies between the abdominal and thoracic appendages, but going more into detail, proposed, on theoretical grounds, that the stylus-bearing plates of the insect abdomen represent the coxae, which in the abdomen he distinguished as "coxites," or in the genital segments as "gonocoxites." According to Verhoeff's theory, the telopodites are lost from all the abdominal appendages except those of the eighth and ninth segments, where they become the gonapophyses; the styli are secondary lateral outgrowths of the coxae, equivalent to the coxal spurs of the thoracic legs of *Machilis;* and the eversible vesicles are median coxal structures comparable with the coxal glands of Diplopoda.

Börner, though at first taking Heymons' view of the nature of the gonapophyses, later (1904) agrees with Verhoeff that the genital processes represent the telopodites of the abdominal appendages, preserved only on the gonopods. Regarding the supporting plates, however, Börner differs from Verhoeff in that he identifies them as "basipodites," meaning by this term that each plate is the equivalent of the coxa and subcoxa of a thoracic leg. (The same idea concerning the nature of the basal plates is followed in the present paper, but Börner's term "basipodite" is replaced with "limb basis" to avoid confusion with the more usual application of the other word to the first trochanter.)

Silvestri (1903, 1905) regards the basal segment of an arthropod limb as being in all cases a subcoxa (including the so-called coxopodite of Crustacea), and he would divide the appendage into a basis (subcoxa) and a telopodite at the subcoxo-coxal joint. Applying this interpretation of the basal structure of the limb to the abdominal appendages of insects, Silvestri (1905) identifies the stylus-bearing plates of the Thysanura with the subcoxae. The styli he regards as the rudiments of the telopodites, with their bases representing the coxae. Silvestri, therefore, admits no homology between the abdominal styli and those of the thorax in *Machilis;* the leg styli he claims are secondary outgrowths of the coxal integument. Verhoeff (1903) had figured a coxal muscle attached to the leg stylus of *Machilis,* but this supposed muscle Silvestri shows does not exist—an observation in accord with statements by earlier as well as by subsequent writers, and one easily verified.

The most interesting feature in Silvestri's interpretation of the morphology of the abdominal limbs is his proposal that the genital apophyses are serially homologous with the eversible sacs of the pregenital segments. Silvestri argues as follows: On the first abdominal segment of *Projapyx* and *Anajapyx* there are borne on each subcoxa (stylus-bearing plate) a typical stylus and, mesad of it, a cylindrical or conical process. In *Machilis* and *Nicoletia* each subcoxa of the first segment has a retractile vesicle, and in *Campodea* only a cylindrical process. The following six segments of Machilidae bear on the subcoxae both styli and vesicles, but on the next two, the genital segments, each subcoxa has a stylus and, in some genera, mesad to it a genital process. Thus Silvestri contends that the gonapophysis is evidently an eversible sac *permanently everted*. Muscles he observes are attached to each appendage, though he does not point out that those of the gonapophysis are inserted on the base of the process, while those of the vesicles traverse the organ to be inserted in its extremity.

The abdominal appendages of insects have not lacked attention from students of arthropod phylogeny, because their several parts make up a composite limb pattern that may be supposed to conform with the biramous structure of crustacean appendages, and thus indicate either that insects are closely related to the Crustacea, or that the primitive arthropod limb was a biramous structure. Writers who espouse the idea of a crustacean ancestry for insects, following Wood-Mason (1879), interpret the stylus as the exopodite, and find the homologue of the endopodite in the gonapophyses of the genital appendages. The theory must assume that the endopodites have been suppressed on the pregenital segments, since the eversible vesicles are eliminated as possible telopodite homologues by the fact that they sometimes occur in duplicate.

The theoretical possibilities of aligning the appendages of insects with those of Crustacea have been exhaustively searched by Crampton. In a study of the terminal appendages of the tridactylid orthopteron, *Ellipes,* Crampton (1921) adduces evidence that he takes to be conclusive of the biramous nature of insect appendages. The dorsal pair of terminal appendicular processes in the Tridactylidae are undoubtedly the cerci (fig. 45 A, B, *Cer*); the ventral pair (*paptl*) are the lobes of the paraprocts ("paraprocessi"). After removing the end of the abdomen and spreading the parts out from below until they lie in one plane, Crampton makes a comparison of the tridactylid appendages in this position with the uropods of an isopod crustacean in the normal position (fig. 45 C, D), and arrives at the conclusion that the cerci of the former correspond with the endopodites of the latter, and that the paraproct lobes of *Ellipes* represent the exopodites of the isopod. The paraprocts themselves Crampton regards as the protopodites (i. e., combined coxopodites and basipodites) of the terminal appendages. The interpretation of the paraproct lobes as exopodites is consistent with other evidence that the styli are exopodites, for the paraproct lobes fall in line with the styli, or would do so if styli were present in the tridactylids, and the abdominal styli are serially continuous with the thoracic styli of *Machilis,* which appear to have an exopodite status, and therefore suggest that the entire series of styliform organs are exopodites.

There are several weak places in the above line of reasoning. In the first place, the writer fails entirely to get Crampton's view from the comparison between the tridactylid and the isopod, since, with the terminal parts of both in the normal condition (fig. 45 B, D), the cercus of the insect (*Cer*) surely has the position of the exopodite (*Expd*) of the crustacean uropod, while the paraproct lobe (*paptl*) corresponds in position with the small endopodite (*Endpd*) borne by the basal plate of the uropod (C). In the second place, a more careful examination of details shows that the cercus (B, *Cer*) has no anatomical relation with the paraproct (*Papt*), being situated dorsad of the latter in a position corresponding with that of the base of the crustacean uropod (D). Furthermore, as has already been shown, there is no evidence whatever to support the idea that the paraprocts of insects are parts of the appendages. Their musculature indicates that they are mere lateroventral, subanal lobes of the eleventh abdominal sternum. The cerci have no muscles arising in the paraprocts. Finally, the embryological evidence concerning the nature of the cerci appears to show definitely that the cerci are the *entire* appendages of the eleventh segment, and that their bases, if present at all, are retained in a basal ring of each organ. Hence, until some radically new information comes to light concerning the cerci, there is no question of exopodite or endopodite connected with them. Our present information is to the effect simply that the *cerci are the appendages of the eleventh abdominal segment.*

The lobes of the paraprocts, whether the "paraprocessi" of the tridactylids, the small lobate ends of the paraprocts of the Anisoptera, or the lateral gill plates of the Zygoptera, have no validated claim to an appendicular origin. They must, then, for the present be regarded as secondary outgrowths of the subanal lobes of the sternum of the eleventh abdominal segment, comparable to the various median outgrowths of the supra-anal plate of the same segment.

The most nearly convincing evidence of the biramous nature of insect appendages is, admittedly, the presence of styliform processes on the mesothoracic and metathoracic legs of *Machilis* closely resembling the styli of the abdomen. Without this coincidence, or if *Machilis* and its coxal spurs had not survived to modern times, it is doubtful if entomologists would ever have thought of regarding the abdominal styli or the cerci as other than direct rudiments of legs.

Conclusions.—The abdominal appendages of insects are rudimentary limbs. Each consists of a basis and usually one or more distal appendicular parts, including a stylus, an eversible or retractile vesicle, and a gonapophysis. From the facts known of the comparative structure of the abdominal appendages, and from theoretical considerations we may draw the following tentative conclusions relative to the homologies of the parts of the appendages, but it must be admitted that the evidence at hand is not sufficiently definite to establish any particular view concerning them.

The *limb bases* of the abdominal appendages are the lobes or plates of the walls of the body segments that support the appendicular processes. They are usually well developed in larval insects, but in most adults they are partially or wholly united or blended with the sternum, or in the male genital segment fused also with the tergum; in the eleventh segment they are reduced to small basal rings of the cerci, or entirely obliterated. Generally there is no distinction between coxal and subcoxal regions in the limb bases of the abdomen. In position on the body the abdominal limb bases usually fall in line with the subcoxae or pleural areas of the thorax. But since there is no apparent reason for the development of large subcoxal plates on the abdominal segments, such as those of the pterygote thorax, it is not to be supposed that the limb bases of the abdomen represent the subcoxae alone. It is more probable that their principal parts are derived from the flattened coxae, or that the structures in most cases may represent primitive limb bases undifferentiated into coxae and subcoxae. In the caterpillars and sawfly larvae, however, the principal segment of each abdominal leg appears to be the coxa, which is quite distinct from a subcoxal lobe of the wall of the body segment to which it is attached. The abdominal limb bases are seldom movable on the body, since they commonly lack muscles corresponding with the basal muscles of the gnathal and thoracic appendages arising on the body wall. Exceptions to this rule are found in the male genital segment, where the bases of the gonopods are occasionally provided with muscles and are independently movable; but in such cases it is to be suspected, at least, that the muscles are secondary developments.

The *styli*, or other homologous appendicular processes of the abdomen, are of wide occurrence in insects, and serve a variety of functions, to which they are adapted by structural modifications. The styliform type is not necessarily the primitive form of the organs. The abdominal styli may be serially homologous with the thoracic coxal styli of *Machilis,* or the latter may be merely large spurs resembling the abdominal styli, from which they differ in lacking muscles. The abdominal styli are individually movable on the limb bases by muscles arising in the latter. If they are not the rudimentary main shafts of the abdominal limbs, they are exite lobes of the coxae analogous with the epipodites of crustacean appendages. They are not comparable with the exopodites of Crustacea, because the exopodite branch of a typical biramous limb is an exite of the first trochanter, or basipodite.

There are many reasons for regarding the abdominal styli or their derivatives in insects as the rudimentary telopodites of the abdominal appendages. The styli seldom lose their muscles, except when they are immovably united with the bases; in some insects they take an active part in locomotion; they may be jointed in a manner suggesting at least a true segmentation, and in the larvae of *Sialis* they have intrinsic muscles in their basal segments. The styli of the gonopods in male pterygote insects, especially in the holometabolous orders, are commonly modified to serve as grasping or clasping organs during copulation. The styli are the most generally persistent of the distal parts of the abdominal appendages. If it were not for their likeness in apterygote and orthopteroid insects to the coxal spurs of *Machilis,* it seems doubtful if the abdominal styli would ever have been regarded as anything else than the rudimentary telopodites of the abdominal appendages, represented in a similar form by the cerci on the eleventh segment.

The *vesicles* of the abdominal appendages of Apterygota, the *gill tubercles* of the larva of *Corydalus,* and the *plantar lobes* of the larval abdominal legs of Lepidoptera and chalastogastrous Hymenoptera are all organs of a similar and unique type of structure. They are essentially exserted or invaginated lobes of the coxal areas of the limb bases lying mesad of the bases of the styli, and are retractile by muscles inserted within their distal parts. In the case of the Apterygota the muscles arise in the limb bases; in the others they arise from the lateral walls of the body. We might, with Verhoeff, regard these sacs as derivatives of coxal glands, since integumentary glands sometimes take the form of eversible and retractile pouches. The coxal vesicles, however, serve a variety of purposes, and they are more simply explained as endite lobes of the coxae, which in some cases have become normally invaginated. They may thus be likened to the endite lobes of the gnathal appendages, and, as the latter, they sometimes occur in duplicate on each appendage.

The *gonapophyses* are hollow, median outgrowths of the bases of the gonopods, developed in both male and female insects during postembryonic stages. They are movable by muscles arising in the limb bases, or in areas of the genital segments derived from the latter, except where they are operated by the segmental muscles of the body. Theoretically the gonapophyses may be supposed to be either the telopodites (endopodites) of the gonopods, or endite lobes of the bases of these appendages. There are several objections to the first view. The gonapophyses, for example, are never truly segmented, and never have a form suggestive of a leg structure; they occur only on the appendages of the genital segments, unless the cylindrical processes of the first abdominal segment in certain Dicellura are homologous structures; and finally, they serve only in a particular capacity in connection with oviposition and copulation, except in insects where they are secondarily adapted to form a stinging organ. These facts, together with the invariable median position of the gonapophyses on the gonopod bases, suggest that the gonapophyses are basal endites of the gonopods, movable by muscles arising in the basis, as such endites usually are, and specially adapted to the reproductive functions. The genital apophyses might then be regarded as serially homologous with the eversible or retractile vesicles of the pregenital appendages and certain larval pygopods, in which case Silvestri's idea that they represent " permanently everted eversible vesicles " is better stated in the reverse, namely, that the eversible vesicles are inverted gonapophyses. However, the vesicles do not occur at points on the gonopod bases corresponding with the origins of the gonapophyses, and the musculature of the two sets of organs is characteristically different. It is perhaps possible that the gonapophyses are subcoxal endites, and the vesicles coxal endites.

If none of the appendicular processes of the abdominal limbs can be satisfactorily identified with the telopodite of a primitive appendage, we must conclude that the abdominal telopodites have been lost from all but the terminal segment, where they form the cerci, and that the various persisting appendicular structures are accessory processes of the limb bases. Otherwise, we must choose between the gonapophyses and the styli as possible representatives of the telopodites. Of the two, the styli certainly present better credentials, considering their occurrence on many segments of the abdomen as contrasted with the segmental localization of the gonapophyses, their structural and functional versatility by comparison with the limitations of the genital apophyses in form and use, and their leglike relations to the limb bases as opposed to the median, proximal origins of the gonapophyses. All these points qualify the abdominal styli for true limb rudiments, and give the genital processes the status of basendites specially developed for reproductive purposes. The pretensions of the abdominal styli to telopodite origin are opposed only by their similarity to the thoracic styli of *Machilis;* but there is nothing to show that these leg structures are not mere coxal spurs resembling in form but fundamentally unlike the musculated appendages of the abdomen, the styliform shape of which is but one of their many structural adaptations.

A discussion of the phylogeny of insects, or particularly of the possible origin of insects from any other group of existing arthropods is beyond the intended scope of the present paper. A recent work by Tillyard (1930) on the evolution of the Insecta, though somewhat partisan in favor of myriapodan descent, gives many reasons for believing that insects are not directly related to the Crustacea. And yet, the weight of evidence, whether put forth by claimants of a myriapodan or a crustacean ancestry for insects, seems to depend largely on minimizing or disqualifying the evidence on the other side. However, if we were to give equal weight to arguments on both sides of the question, the insects would be cut off from all ancestral ties, and thereby deprived of a respectable pedigree—unless they are able to take care of themselves through all the unknown ages of time before they are first known to us as fully-winged hexapods in the Carboniferous deposits. To the writer it appears that all the principal arthropod groups must represent independent lines of descent from some remote ancestral forms embodying the potentialities of a spider, a crab, a centipede, or an insect. It has recently been emphasized by Clark (1930) that the chronic inability of the evolutionary theory in its usual form to explain the lack of intermediates between the major groups of animals constitutes a real weakness of the theory, which calls for a new concept of the method by which distinct types of organisms have been produced. The condition to which Clark refers is well exemplified within the Arthropoda, where connective forms between the classes are unknown. Moreover, it is impossible to construct imaginary arthropods that will fill the blanks, as, for example, the three-cornered gap between the crustaceans, the myriapods, and the insects. Considering that embryos develop before our eyes by ways that are still inscrutable, it takes a strong faith in established ideas to believe that organic evolution has proceeded entirely by the means we have furnished for its guidance.

ABBREVIATIONS USED ON THE FIGURES

a-a, dorso-pleural groove.
a-b, axis of articulation of limb base on body.
ab, abductor muscle.
Ac, antecosta.
acs, antecostal suture.
ad, adductor muscle.
Aed, aedeagus.
An, anus.
Ap, apodeme.
Apd, segmental appendage.
Apt, sternal apotome.

Bnd, basendite.
Brn, branchia (gill).
brncls, branchial muscles.
Bspd, basipodite (first trochanter).

c-d, axis of subcoxo-coxal joint.
Cer, cercus (uropod).
cf, caudal filament.
Col, collophore.
Con, nerve connective.
ct, coxo-trochanteral joint.
Cx, coxa.
Cxpd, coxopodite.

D, dorsum.
d, dorsal muscles.
del, lateral external dorsal muscles.
dem, median external dorsal muscles.
dil, lateral internal dorsal muscles.
dim, median internal dorsal muscles.
dl, dilator muscle.
dm, median dorsal muscles.
DMcl, longitudinal dorsal muscles.
DTra, dorsal longitudinal tracheal trunk.

Endpd, endopodite.
Eppt, epiproct.
Expd, exopodite.

f-g, axis of baso-telopodite joint.
Fm, femur (meropodite).
ft, femoro-tibial joint.
Fur, furcula.

gmcls, muscles of gonapophysis.
Gng, ganglion.
Gon, gonapophysis.
Gp, gonopod.
GSeg, genital segment.

Hpn, hypandrium.
Ht, heart.
Hypt, hypoproct.

I, tergal promotor muscle of appendage.
ip, intestinal process.
Isg, intersegmental fold.
Ist, intersternite.

J, tergal remotor muscle of appendage.

k, interfurcal sternal ridge.

L, leg.
l, lateral body muscles.
la, lamina subanalis.
LB, limb basis.
le, external lateral muscles.
li, internal lateral muscles.
lStn, last pregenital sternum.
lT, last pregenital tergum.
LTra, lateral longitudinal tracheal trunk.

Mb, intersegmental membrane (conjunctiva).
mb, membrane.
Mcl, longitudinal muscles.
mcls, muscles.
mn, manubrium.

NlG, neural groove.

O, levator muscle of first trochanter.
Ovd, oviduct.

p, paratergal muscle.
Papt, paraproct.
paptl, lobe of paraproct.
patg, paratergite.
Pc, precosta.

Pen, penis.
Ph, phragma.
Pl, pleuron.
pl, pleurite.
Pm, paramere (male gonapophysis of ninth segment).
PN_3, meta-postnotum (precosta of first abdominal segment).
pnb, pons basalis.
Pp, pygopod.
Prpt, periproct.
Prtpd, protopodite (united coxopodite and basipodite).
Ptar, praetarsus (dactylopodite).

Q, depressor muscle of first trochanter.

rvs, retractor muscles of vesicle of leg base, or of its derivatives.
rvsd, dorsal retractor of planta.
rvsv, ventral retractor of planta.

S, definitive sternum (usually including limb bases).
SA_3, metasternal apophysis.
sa, lamina supra-analis.
Scx, subcoxa.
Sp, spiracle.
s-p, sterno-pleural muscle.
smcls, muscles of stylus, or of its derivatives.
Stn, primary segmental sternum.
Sty, stylus of leg base, or its derivatives.

T, tergum.
Tar, tarsus (propodite).
Tb, tibia (carpopodite).
td, dorsal transverse muscles.
Tcl, telson.
Tlpd, telopodite.
t-p, tergo-pleural muscle.
Tr, trochanter.
1Tr, first trochanter (basipodite).
2Tr, second trochanter (ischiopodite).
Tra, trachea.
t-s, tergo-sternal muscle.
tv, ventral transverse muscles.

ug, urogomph.

V, venter.
v, ventral muscles.
vel, lateral external ventral muscles.
vem, median external ventral muscles.
vil, lateral internal ventral muscles.
vim, median internal ventral muscles.
Vl, valvula.
Vlf, valvifer.
VMcl, ventral longitudinal muscles.
VNC, ventral nerve cord.
Vs, vesicle of limb base, or its derivatives.

1-3, thoracic segments.
I-XII, abdominal segments.

REFERENCES

Ayers, H. (1884). On the development of Oecanthus niveus and its parasite Teleas. *Mem. Boston Soc. Nat. Hist.* **3**: 225-281, pls. 18-25.

Backhoff, P. (1910). Die Entwicklung des Copulationsapparates von Agrion. *Zeitschr. wiss. Zool.* **95**: 647-706, 29 text figs., pl. 21.

Bauer, A. (1910). Die Muskulatur von Dytiscus marginalis. *Zeitschr. wiss. Zool.* **95**: 594-646, 19 figs. Also in Korschelt (1924), Chapter 12.

Becker, E. (1926). Zur phylogenetischen Entwicklung des Skeletts und der Muskulatur der Ateloceraten (Tracheaten). I. Das Tergalskelett und die Dorsalmuskulatur von Chilopoden. *Revue Zool. Russ.* **6**: 3-67, 4 pls. (In Russian and German.)

Berkeley, Alfreda A. (1928). The musculature of Pandalus danae Stimson. *Trans. R. Canadian Institute* **16**: Pt. 2: 181-231, pls. 1-8.

Berlese, A. (1906). Sopra una anomalia negli organi sessuali esterni femminei di Locusta viridissima L. *Redia* **3**: 305-314, 7 figs.

——— (1909). Gli insetti, Vol. 1. Milan.

——— (1910). Monografia dei Myrientomata. *Redia* **6**: 1-182, pls. 1-17.

Betts, Annie D. (1923). Practical Bee Anatomy. 76 pp., 12 pls. The Apis Club.

Blunck, H. (1918). Die Entwicklung des Dytiscus marginallis L. vom Ei bis zur Imago. 2 Teil. Die Metamorphose (der Habitus der Larve). *Zeitschr. wiss. Zool.* **117**: 1-129, 57 figs.

Börner, C. (1904). Zur Klärung der Beingliederung der Ateloceraten. *Zool. Anz.* **27**: 226-243, 5 figs.

——— (1909). Die Tracheenkiemen der Ephemeriden. *Zool. Anz.* **33**: 806-823, 4 figs.

——— (1921). Die Gliedmassen der Arthropoden. In Lang's *Handbuch der wirbellosen Tiere* **4**: 649-694, 57 figs. Jena.

Bottimer, L. J. (1926). Notes on some Lepidoptera from eastern Texas. *Journ. Agr. Research* **33**: 797-819, 3 figs.

Böving, A. G. (1914). On the abdominal structure of certain beetle larvae of the campodeiform type. A study of the relation between the structure of the integument and the muscles. *Proc. Ent. Soc. Washington* **16**: 55-61, 8 figs.

Branch, Hazel E. (1922). A contribution to the knowledge of the internal anatomy of Trichoptera. *Ann. Ent. Soc. America* **15**: 256-275, pls. 14-18.

Breed, R. S. (1903). The changes which occur in the muscles of a beetle. Thymalus marginicollis Chevr., during metamorphosis. *Bull. Mus. Comp. Zool.* **40**: 317-382, pls. 1-7.

Brocher, F. (1922). Étude experimentale sur le foncionnement du vaisseau dorsal et sur la circulation du sang chez les insectes. 5. La Periplaneta orientalis. *Ann. Soc. Entom. France* **91**: 156-164, 1 fig.

Busck, A., and Heinrich, C. (1922). Life history of Ethmia machelhosiella Busck. (Lep.). *Proc. Ent. Soc. Washington* **24**: 1-9, pls. 1-3.

Calvert, P. P. (1911). Studies on Costa Rican Odonata. I. The larva of Cora. *Ent. News* **22**: 49-64, pl. 3.

——— (1915). Studies on Costa Rican Odonata. VII. The waterfall dwellers: The internal organs of Thaumatoneura larva and the respiration and rectal tracheation of Zygopterous larvae in general. *Ent. News* **26**: 385-395, 435-447, pls. 15-17.

Campbell, F. L. (1929). The detection and estimation of insect chitin; and the irrelation of "chitinization" to hardness and pigmentation of the cuticula of the American cockroach, Periplaneta americana L. *Ann. Ent. Soc. America* **22**: 401-426.

Carlet, G. (1890). Sur les muscles de l'abdomen de l'abeille. *Ann. Sci. Nat. Zool.*, 7 sér., **9**: 1-17, pl. 1.

Cholodkowsky, N. (1891). Die Embryonalentwicklung von Phyllodromia (Blatta) germanica. *Mém. Acad. Sci. St. Petersbourg*, 7 sér., **38**, No. 5, 120 pp., 6 pls.

Clark, A. H. (1930). The New Evolution. Baltimore.

Craighead, F. C. (1916). The determination of the abdominal and thoracic areas of the cerambycid larvae as based on a study of the muscles. *Proc. Ent. Soc. Washington* **18**: 129-142, pls. 7-9.

Crampton, G. C. (1918). A phylogenetic study of the terminal abdominal structures and genitalia of male Apterygota, ephemerids, Odonata, Plecoptera, Neuroptera, Orthoptera, and their allies. *Bull. Brooklyn Ent. Soc.* **13**: 49-68, pls. 2-7.

——— (1919). The genitalia and terminal abdominal structures of males, and the terminal structures of the larvae of "chalastogastrous" Hymenoptera. *Proc. Ent. Soc. Washington* **21**: 129-151, pls. 9-12.

——— (1920). Remarks on the basic plan of the terminal abdominal structures of the males of winged insects. *Canad. Ent.* **52**: 178-183, pl. 6.

——— (1921). A comparison of the terminal abdominal structures of insects and Crustacea. *Ent. News* **32**: 257-264, pl. 5.

Dirkes, L. (1928). Das larvale Muskelsystem und die Entwicklung der imaginalen Flugmuskulatur von Psychoda alternata Say. *Zeitschr. Morph. Ökol. Tiere* **11**: 182-228, 14 text figs.

Du Porte, E. M. (1920). The muscular system of Gryllus assimilis Fabr. *Ann. Ent. Soc. America* **13**: 16-52, pls. 1-7.

Dürken, B. (1907). Die Tracheenkiemenmuskulatur der Ephemeriden unter Berücksichtigung der Morphologie des Insektenflügels. *Zeitschr. wiss. Zool.* **87**: 435-550, 29 text figs., pls. 24-26.

Eastham, L. E. S. (1930). The embryology of Pieris rapae.—Organogeny. *Phil. Trans. Roy. Soc. London*, ser. B, **219**: 1-50, pls. 1-9.

Ferris, G. F., and Chemberlin, J. C. (1928). On the use of the word "chitinized." *Ent. News* **39**: 212-215.

Florence, Laura (1921). The hog louse, Haematopinus suis Linné: its biology, anatomy, and histology. *Cornell Univ. Agric. Exp. Sta., Memoir* **51**: 641-725, pls. 58-66.

Forbes, W. T. M. (1914). A structural study of the caterpillars: III, the somatic muscles. *Ann. Ent. Soc. America* **7**: 109-124, pls. 17-25.

——— (1916). On certain caterpillar homologies. *Journ. New York Ent. Soc.* **24**: 137-142, 1 fig.

Ford, Norma (1923). A comparative study of the abdominal musculature of orthopteroid insects. *Trans. Roy. Canadian Institute* **14**: 207-319, pls. 7-23.

Fracker, S. B. (1915). The classification of lepidopterous larvae. *Illinois Biol. Monographs* **2**, No. 1, 169 pp., 10 pls.

Grassi, B. (1887). Anatomia comparata dei Tisanuri e considerazioni generali sull' organizzazione degli insetti. *Atti de' Lincei, Mem. Cl. Sci. Fis.*, Ser. 4, **4**: 543-606, 5 pls.

Haase, E. (1889). Die Abdominalanhänge der Insekten mit Berücksichtigung der Myriopoden. *Morphol. Jahrb.* **15**: 331-435, pls. 14, 15.

Hansen, H. J. (1930). Studies on Arthropoda. III. On the comparative morphology of the appendages in the Arthropoda, 376 pp., 16 pls. Copenhagen.

Hewitt, C. G. (1914). The house fly, Musca domestica Linn., 382 pp., 104 figs. Cambridge Zoological Series.

Heymons, R. (1892). Die Entwicklung der weiblichen Geschlechtsorgane von Phyllodromia (Blatta) germanica L. *Zeitschr. wiss. Zool.* **53**: 434-536, pls. 18-20.

——— (1895). Die Segmentirung des Insektenkörpers. *Abhandl. Akad. Wiss. Berlin* **1895**, 39 pp., 1 pl.

——— (1896). Über die Lebensweise und Entwicklung von Ephemera vulgata L. *Sitzungs-Ber. Gesell. Naturf. Fr. Berlin* **1896**: 82-96.

——— (1896 a). Zur Morphologie der Abdominalanhänge bei den Insekten. *Morph. Jahrb.* **24**: 178-204, pl. 1.

——— (1896 b). Über die abdominalen Körperanhänge der Insekten. *Biol. Centralb.* **16**: 854-864.

——— (1897). Entwicklungsgeschichtliche Untersuchungen an Lepisma saccharina. *Zeitschr. wiss. Zool.* **62:** 583-631, 2 pls.

——— (1899). Der morphologische Bau des Insektenabdomens. *Zool. Centralb.* **6:** 537-556.

——— (1901). Die Entwicklungsgeschichte der Scolopender. *Zoologica. Orig-Abhandl. Gesamtg. Zool.* **33,** 244 pp., 8 pls.

——— (1904). Die Hinterleibsanhänge der Libellen und ihrer Larven. *Ann. K. Naturhist. Hofmuseums, Wien* **19:** 21-58, pl. 1.

Hopkins, A. D. (1909). The genus Dendroctonus. U. S. D. A., Bur. Ent., Tech. Ser., No. 17, Part 1, 164 pp., 8 pls.

Imms, A. D. (1908). On the larval and pupal stages of Anopheles maculipennis, Meigen. *Parasitology* **1:** 103-133, pls. 9, 10.

Jeziorski, Lucie (1918). Der Thorax von Dixippus morosus (Carausius). *Zeitschr. wiss. Zool.* **117:** 727-815, pls. 17-19.

Kemner, N. A. (1918). Vergleichende Studien über das Analsegment und das Pygopodium einiger Koleopterenlarven, 104 pp., 44 figs. Uppsala.

Korschelt, E. (1924). Bearbeitung einheimischer Tiere. Der Gelbrand Dytiscus marginalis L., Vols. 1 and 2. Leipzig.

Krafka, J., Jr. (1924). Morphology of the prolegs of trichopterous larvae. *Ann. Ent. Soc. Amer.* **17:** 70-103, pls. 16, 17.

Künckel d' Herculais, J. (1875). Recherches sur l'organisation et le développement des Volucelles, 208 pp., 26 pls. Paris.

Kunike, G. (1926). Chitin und Chitinseide. *Kunstseide,* **8,** 182, 183.

Lankester, E. R. (1909). A treatise on zoology, pt. 7, fasc. 3 (Calman, W. T.). London.

Lubbock, J. (1859). On the arrangement of the cutaneous muscles of the larva of Pygaera bucephala. *Trans. Linn. Soc. London* **22:** 173-191, pls. 34, 35.

——— (1873). Monograph of the collembola and thysanura, 276 pp., 78 pls. London.

Lyonet, P. (1762). Traité anatomique de la chenille qui ronge le bois de saule, 616 pp., 18 pls.

Miall, L. C., and Hammond, A. R. (1900). The structure and life history of the harlequin fly (Chironomus), 196 pp., 129 figs. Oxford.

Middleton, W. (1921). Some notes on the terminal abdominal structures of saw-flies. *Proc. Ent. Soc. Washington* **23:** 139-144, pl. 11.

Morison, G. D. (1927). The muscles of the adult honey-bee (Apis mellifera L.). *Quart. Journ. Micr. Sci.* **71:** 395-463.

Nelson, J. A. (1915). The embryology of the honey-bee, 282 pp., 95 text figs., 6 pls. Princeton Univ. Press.

——— (1924). Morphology of the honey-bee larva. *Journ. Agric. Research* **28:** 1167-1213, 5 text figs., 8 pls.

Paterson, Nellie (1930). Bionomics and morphology of the early stages of Paraphaedon tumidulus Germ. (Chrysomelidae). *Proc. Zool. Soc. Lond.* **1930,** pt. III: 627-676.

Prell, H. (1913). Das Chitinskelett von Eosentomon. *Zoologica. Orig.-Abhandl. Gesamtg. Zool.* **25,** 58 pp., 6 pls.

Quiel, G. (1915). Anatomische Untersuchungen an Collembola. *Zeitschr. wiss. Zool.* **113:** 113-164, pls. 6, 7.

Riester, A. (1931). Muskulatur von Copilia Dana. *Zool. Jahrb., Anat.* **53:** 317-404, 50 figs.

SAMTLEBEN, B. (1929). Anatomie und Histologie der Abdominal- und Thoraxmuskulatur von Stechmückenlarven. *Zeitschr. wiss. Zool.* **134**: 180-269, 18 figs.

SCHMIDT, E. (1915). Vergleichende Morphologie des 2. und 3. Abdominalsegments bei männlichen Libellen. *Zool. Jahrb., Anat.* **39**: 87-200, 25 text figs., pls. 9-11.

SCHMIDT, W. (1915). Die Muskulatur von Astacus fluviatilis (Potamobius astacus L.). Ein Beitrag zur Morphologie der Decapoden. *Zeitschr. wiss. Zool.* **113**: 165-251, 26 figs.

SEDGWICK, A. (1909). A student's text-book on Zoology, Vol. 3. London.

SILVESTRI, F. (1903). Classis Diplopoda, Vol. 1, Anatome, 272 pp., 345 figs., 4 pls. Portici.

——— (1905). Thysanura. *Zool. Jahrb.,* 3, Suppl. **6**: 773-806, pls. 38-44.

SNODGRASS, R. E. (1924). Anatomy and metamorphosis of the apple maggot, Rhagoletis pomonella Walsh. *Journ. Agric. Research* **28**: 1-36, 6 pls.

——— (1925). Anatomy and physiology of the honey-bee, 327 pp., 108 figs. New York.

——— (1928). Morphology and evolution of the insect head and its appendages. *Smithsonian Misc. Coll.,* **81**, No. 3, 158 pp., 57 figs.

SPEYER, W. (1922). Die Muskulatur der Larve von Dytiscus marginalis L. Ein Beitrag zur Morphologie des Insektenkörpers. *Zeitschr. wiss. Zool.* **119**: 423-492, 21 figs., pl. 7. Also in Korschelt (1924), Chapter 13.

STEINER, L. F. (1929). Homologies of tracheal branches in the nymph of Anax junius based on their correlation with the muscles they supply. *Ann. Ent. Soc. America* **22**: 297-308, 1 pl.

STRAUS-DÜRCKHEIM, H. (1828). Considérationes générales sur l'anatomie comparée des animaux articules, auxquelles on a joint l'anatomie descriptive du Melolontha vulgaris, 434 pp., 10 pls. Paris, Strasbourg, Bruxelles.

TIEGS, O. W. (1922). Researches on the insect metamorphosis. *Trans.* and *Proc. Roy. Soc. S. Australia* **46**: 319-527, pls. 15-30.

TILLYARD, R. J. (1917). The biology of Dragonflies, 396 pp., 188 figs. Cambridge.

——— (1930). The evolution of the Class Insecta. *Roy. Soc. Tasmania, Papers* and *Proc.* **1930**: 89 pp., 19 figs.

ULMER, G. (1903). Über die Metamorphose der Trichopteren. *Abh. Gebiete Naturwiss. naturwiss. Verein Hamburg* **18**, 154 pp., 4 pls.

VERHOEFF, K. W. (1896). Zur Morphologie der Segmentanhänge bei Insecten und Myriopoden. *Zool. Anz.* **19**: 378-383, 385-388.

——— (1903). Zur vergleichenden Morphologie der Coxalorgane und Genitalanhänge der Tracheaten. *Zool. Anz.* **26**: 60-77, 15 figs.

VOSS, F. (1905). Über den Thorax von Gryllus domesticus. II. Die Muskulatur. *Zeitschr. wiss. Zool.* **78**: 355-521, 14 figs.

WALKER, E. M. (1922). The terminal structures of orthopteroid insects: a phylogenetic study. Part II. *Ann. Ent. Soc. America* **15**: 1-76, 11 pls.

WALLENGREN, H. (1914). Die Atmung bei den Arthropoden. II. Die Mechanik der Atembewegunden bei Aeschnalarven. *Lunds Univ. Årrskrift,* N. F. **10**: 1-24, 1 pl.

Weber, H. (1928). Skelett, Muskulatur und Darm der schwarzen Blattlaus Aphis fabae Scop. *Zoologica. Orig.-Abhanal. Gesamtg. Zool.* **28,** 120 pp., 12 text figs., 12 pls.

Whedon, A. D. (1919). The comparative morphology and possible adaptations of the abdomen in the Odonata. *Trans. Amer. Ent. Soc.* **44:** 373-437, pls. 21-29.

Wheeler, W. M. (1893). A contribution to insect embryology. *Journ. Morph.* **8:** 1-160, pls. 1-6.

Wood-Mason, J. (1879). Morphological notes bearing on the origin of insects. *Trans. Ent. Soc. London* **1879:** 145-167, 9 figs.

SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 85, NUMBER 7

EFFECTIVENESS IN NATURE OF THE SO-CALLED PROTECTIVE ADAPTATIONS IN THE ANIMAL KINGDOM, CHIEFLY AS ILLUSTRATED BY THE FOOD HABITS OF NEARCTIC BIRDS

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ERRATA

Page 56. In the table Identifications of Lepidoptera, the middle column is a relic from a set of calculations of the percentages of identifications among all insects. The appended figures are to be substituted as representing the percentages of identifications among all Lepidoptera. In explanation of the third column in this table, it may be said that it differs from others given further on in the work by omission of figures for families not represented among the food identifications.

Percentage of identifications among all Lepidoptera
2.6992
.0270
.0270
.8060
.0919
.2055
.0108
.0270
.0108
.0108
.4706
.0324
.9412
.0378
.6383
6.1015
.0216
.3678
.3570
.1568
.8438
11.4458
25.3306
.0487
.0054
.3101
.0054
.0108
.2218
.6112
.7248
68.5670
1.2279
3.5376

Page 86. The figure 1 before the decimal in the entry for the family Diopsidae should be deleted.

Pages 102-105. Insert the word "aquatic" after the word "all" in the heading for the middle column on each of these pages, with the exception of that at the bottom of page 105.

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U. S. DEPARTMENT OF AGRICULTURE

CONTENTS

SMITHSONIAN MISCELLANEOUS COLLECTIONS, VOL. 85, NO. 7.

INTRODUCTION

In a previous paper[1] the writer set forth reasons for believing that the results of experimental tests of the effectiveness of the so-called protective adaptations in protecting animals from their enemies are not trustworthy indications of what occurs under natural conditions. In the present contribution he proposes to show just what insects and other animals are actually preyed upon by wild birds of the United States, Canada, and Alaska, giving also incidental notes on other enemies. This evidence reflecting food habits under natural conditions goes far to show how little the alleged protective devices have to do with choice of food by vertebrates.

Judging from the literature of the subject since 1912, the contentions of the article on the experimental study of the food habits of animals seem to have been generally admitted, or at least regarded as too well supported to be lightly attacked. Only one essay has been seen by the writer, that seems in any way a reply, namely an account of "Experiments and Observations Bearing on the Explanation of Form and Colouring,"[2] by C. F. M. Swynnerton, who refers to my criticism of the experimental method as "rather over-vigorous." The vigor of the criticism is admitted but in view of the absurdity of the arguments against which it was directed, it can hardly be considered

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[1] The experimental method of testing the efficiency of warning and cryptic coloration in protecting animals from their enemies. Proc. Acad. Nat. Sci. Philadelphia, June 1912, pp. 281-364 (Sept. 6, 1912).

[2] Journ. Linn. Soc., Zool., vol. 33, pp. 203-385, London, June 30, 1919.

excessive. Undeniably selectionists have been absurd in their disquisitions on adaptations; for instance "eye-spots" on a butterfly's wings are to direct the attack of enemies to a nonvital spot, while "eye-spots" on a caterpillar are "terrifying" and prevent even a touch where merely a touch would be fatal; in numerous species of birds the male is colored red and black or orange and black, characteristics that selectionists say have been developed by sexual selection as an attraction to the opposite sex, yet the females of these birds are supposed to be repelled by the same colors in possible insect prey; red insects are said to be warningly, red fruits invitingly colored, and so on. A popular foible of similar type is that of sportsmen who hold up to admiration the marvelous protective coloration of game birds, and in the next breath complain of severe depredations on these birds by "vermin."

But this is digressing and the writer is glad to acknowledge that if all of the experimenters had been as critical of their methods and conclusions as Mr. Swynnerton, the tone of his former paper would have been quite different. For instance Mr. Swynnerton carried on more experiments than any of the authors reviewed in the previous communication, before he, according to his own confession, learned how to experiment. This in itself confirms the writer's charges that the experiments he reviewed were both inadequate and misinterpreted. It may further be stated that the principal conclusions Mr. Swynnerton draws from his experiments and observations would have been agreed to in advance by anyone experienced in the study of bird food. Thus he concludes that birds show preferences among the food items available to them, and that predatory animals of various groups show more or less agreement in preferences. From his general experience with birds he decides also that "Unless through sheer impossible hardness, size, etc., there is practically no such thing as 'inedibility,'"[1] and he appreciates that a group of insects, limited in numbers as are butterflies, will not be taken by insectivorous birds out of proportion to their abundance as compared to all insects available.

These things did not require experimental test for they are corroborated in every thorough report on the natural feeding habits of birds. What can not be admitted, however, is that preferences of birds learned by feeding them upon some certain group of insects to an extent far greater than the birds ever prey upon them in nature, reflect normal feeding habits, nor that there is evidence of intensive enough feeding by discriminating enemies upon any group of insects

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[1] A brief preliminary statement of a few of the results of five years' special testing of the theories of mimicry. Proc. Ent. Soc. Lond., 1915, pp. xxxii-xliii.

to meet the requirements of the selection theories. We further can not admit what the experimenters imply, namely, that the analyses of the stomach contents of birds fail to reveal the approximate numbers present of certain insects (such as butterflies) which they believe are eaten to a considerable extent. This point will be discussed later.

So much for what has happened between the previous paper and the present, which as stated, will be devoted chiefly to an exposition of the animal food of nearctic birds, with special reference to the so-called protective adaptations.

PROTECTIVE ADAPTATIONS

The characteristics of animals that are usually classed as protective adaptations include resemblance to generalities or details of the environment, whether through color or other modification of the animal itself or utilization by it of materials from the environment for concealment, the possession of protective bristles, spines, hard integuments, stings, poisonous bites, and the like, and nauseous or irritating odors or tastes. There are animals with actually poisonous properties among many of the phyla including species with poison glands and special organs for using the poison in offense or defense, among Coelenterata, Echinodermata, Arachnida, Insecta, and Pisces; others with poison glands connected with the mouth organs among worms, spiders, other arachnids, mites, myriapods, chilopods, insects, fishes, and reptiles; animals with unarmed poison glands among coelenterates, echinoderms, myriapods, insects, mollusks, amphibians; and others poisonous in a variety of ways so that practically all phyla are represented. The colors of the animals possessing dangerous qualities in many cases are said to be warning in nature, and the colors of animals which resemble them but lack the disagreeable qualities are termed mimetic. The subject of protective adaptations has very largely become one of coloration especially as associated with the qualities of animals from the supposed point of view of possible predators.

A statement of the various classes of color adaptations is here quoted from Prof. E. B. Poulton, the leading advocate of the view that these adaptations are really protective and that they have been developed by natural selection.

> *Protective and Aggressive Resemblance.*—By far the most widespread use of colour is to assist an animal in escaping from its enemies or in capturing its prey; the former is *Protective,* the latter *Aggressive.* It is probable that these were the first uses to which non-significant colours were put. The resemblances are of various kinds; the commonest cases are those of simple concealment. The animal passes undetected by resembling some common object which is of

no interest to its enemies or prey respectively, or by harmonising with the general effect of its surroundings; the former is *Special,* the latter *General Resemblance,* and both may be *Protective* or *Aggressive.* Among the most interesting *Special Aggressive Resemblances* are the cases of *Alluring Colouring,* in which the animal, or some part of it, resembles an object which is attractive to its prey.[1]

Protective and Aggressive Mimicry.—Mimicry is in reality a very important section of *Special Resemblance.* The animal gains advantage by a superficial resemblance to some other, and generally very different, species which is well known and dreaded because of some unpleasant quality, such as a sting or an offensive taste or smell, &c., or it may even be protected from the animal it resembles: this is *Protective Mimicry.* When, however, the animal resembles another so as to be able to injure the latter or some other form which accompanies it or is not afraid of it, the *Mimicry* is *Aggressive.*[2]

Warning Colours.—When an animal possesses an unpleasant attribute, it is often to its advantage to advertise the fact as publicly as possible. In this way it escapes a great deal of experimental "tasting." The conspicuous patterns and strongly contrasted colours which serve as the signal of danger or inedibility are known as *Warning Colours.* In other cases such colours or markings enable individuals of the same species easily to follow those in front to a place of safety, or assist them in keeping together when safety depends upon numbers. It is these *Warning Colours* which are nearly always the objects of *Protective Mimicry.*[3]

Following is a copy of Poulton's table [4] classifying color adaptations:

I. *Apatetic colours.*— Colours resembling some part of the environment or the appearance of another species.		II. *Sematic colours.*—Warning and signalling colours.	III. *Epigamic colours.*—Colours displayed in courtship.
A. *Cryptic colours.*—Protective and Aggressive Resemblances.	B. *Pseudosematic colours.*—False warning and signalling colours.		
1. *Procryptic colours.*—Protective Resemblances.	1. *Pseudaposematic colours.*—Protective Mimicry.	1. *Aposematic colours.*—Warning colours.	
2. *Anticryptic colours.*—Aggressive Resemblances.	2. *Pseudepisematic colours.*—Aggressive Mimicry and Alluring Colouration.	2. *Episematic colours.*—Recognition Markings.	

Having presented the foregoing outline of protective color and other adaptations, references to them in succeeding pages will be made without further explanation of the terms involved.

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[1] The colours of animals, pages 19-20, 1890.

[2] Idem, p. 20.

[3] Idem, p. 21.

[4] Idem, p. 338.

ANIMALS EATEN BY NEARCTIC BIRDS

Data Cited and How Obtained

The main body of data used herein consists of the records of animals identified in the contents of the stomachs of about 80,000 nearctic birds examined in the United States Biological Survey since 1885. These stomachs represent a wide range of species of all of the families of birds occurring in the region; the birds were collected at all seasons and in practically all parts of nearctic America. While not evenly distributed in any of these senses, the collection is very satisfactory for the purpose in hand, and yields a mass of precise information on bird food that far surpasses anything of the kind available elsewhere.

A word about the methods of investigating bird food may be desirable. The gizzards of birds, together with the gullets or crops when they contain food, are received chiefly from persons collecting birds for some other scientific purpose, although in some cases they are especially obtained to throw light on the relations of birds to some crop, or useful or injurious animal. They are preserved usually with formalin in the field and in alcohol after receipt at the laboratory. Contents of a stomach being examined are removed either wet or dry as best fits the particular case and transferred to watch glasses or small white blotters for sorting and identification of the material under compound binocular dissecting microscopes. A great deal of the analysis is done at a magnification of 8 diameters but special study of difficult subjects is continued when necessary under higher powers.

At this point it may be well to comment on the popular misconception that anything found in a bird's stomach necessarily is ground up and in all but unrecognizable state. As a matter of fact the reverse is true. Most birds swallow their food whole; consequently in any collection of birds a certain proportion will have swallowed some food items just before death. These things often are in perfect condition; they may be, and sometimes are, used for cabinet specimens. The nearly or quite whole objects usually furnish clues to the fragmentary material, and in the great majority of cases it is possible to sort out completely all components of the food. It is the exception when the finely ground food remains defy separation and identification. Determinations are carried as far as practicable; each member of the staff of analysts is a specialist in some line and they cooperate freely; specimens defying their combined efforts, if in fair or better condition, are submitted to advanced investigators elsewhere. The records quoted in the following pages include more or less of the handiwork of practically every prominent American systematic zoologist of the period. Nevertheless everything is not identified, far from it; expert assistance has not been available in some cases when needed, too far digested residues sometimes occur, and rarely we find also well-preserved but puzzling objects that indefinitely defy classification.

These, however, are but minor flaws in the system; the groundwork of our faith in the results of stomach analysis is the law of averages. Given good distribution geographically and seasonally, which necessarily follows from miscellaneous collecting carried on for so many years, the reliability of results varies directly with the number of stomachs. The collection (80,000) here reported upon is believed sufficient to furnish fairly dependable data, although additions are made almost daily to the list of animals identified from bird stomachs.

The total number of identifications of animals from these stomachs, counting those of whatever degree, once for each time identified irrespective of the number of individual specimens concerned, is 237,399.[1]

It was impracticable to compute the total number of individual animals concerned for the reason that these were not counted in all cases. Moreover this figure would not have been especially useful in the absence of estimates for comparison of the actual animal population of significant areas. In casting about for a standard which would afford some idea of the frequency of occurrence of animals of various groups, the estimated number of species therein proved to be the only one available for the whole range of the animal kingdom. That the number of species in taxonomic groups bears a general relation to the number of individuals can not be questioned. It is easy to point out exceptions, but remember we can only deal with this problem in an approximate way, and it goes without saying that on the average a group more numerous in individuals will have developed more species than one less numerous. The correspondence is not exact, but it is sufficient to give a fair working idea of the position of the various groups in the scale of frequency of occurrence, the

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[1] The tabulation necessary to yield this figure was an immense one (covering nearly a thousand typewritten pages) and has been found, it is not surprising, to contain some errors. These are so small, however, that rectification of them would not cause changes of more than a fraction of one per cent in any part of the results, except in the table for Coleoptera, pp. 65-67. Hence they do not invalidate the figures at all for the purpose here used of showing in a general way the tendencies exhibited by our birds in their choice of animal food.

very standard we wish for comparison with frequency of identification in the stomachs of collected wild birds. The general correlation of these factors to be noted in the tables presented in subsequent pages increases confidence in the value of the method.[1]

IDENTIFICATIONS OF ANIMAL FOOD

To illustrate the way in which data was assembled, that for the phyla may be given in rather more detail than is planned for the balance of the report. The figures for number of species in the various phyla are compiled from various estimates[2] of this nature; the facts that these are not strictly up-to-date nor anything like exact are of no consequence in a field where only approximations may be hoped for.

The subjoined table shows the estimates used for the number of described species in each phylum and the percentage that figure bears to the total number of animals known.

Phyla of Animals and the Number and Percentage of Species in Each

Phylum	Estimated number of species known	Percentage of species in this phylum among the whole number
Protozoa	8,000	1.4272
Porifera	2,500	.4460
Coelenterata	4,500	.8028
Platyhelminthes	5,000	.8920
Nemathelminthes	1,500	.2676
Trochelminthes	500	.0892
Molluscoida	1,700	.3032
Echinodermata	4,000	.7136
Annulata	4,000	.7136
Arthropoda	418,250	74.6188
Mollusca	61,000	10.8828
Chordata	49,565	8.8427
Totals	560,515	99.9995

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[1] Here may be mentioned the law demonstrated by Olaf Arrhenius (Journ. Ecol., vol. 9, no. 1, p. 99, Sept., 1921) that among plants "The number of species increases continuously as the area increases." Since as a rule the number of individuals also increases with the area, the parallelism between the number of individuals and that of species is further confirmed.

[2] Pratt, H. S., On the number of known species of animals. Science, vol. 35, pp. 467-468, March 22, 1912.

Henshaw, H. W., Number of species of living vertebrates. Science, vol. 36, pp. 317-318, Sept. 6, 1912.

Handlirsch, A., Die fossilen Insekten, pp. 1182-1188, 1908.

Classifying the 237,399 identifications of the animal food of nearctic birds and calculating the percentage of the determinations, by phyla, we reach the results shown in the next table, the percentage of species in each phylum among the whole number of known species being repeated for ease in comparison.

Identifications of Animal Food by Phyla

Phylum	Number of identifications	Percentage of identifications among those of all animals	Percentage of species in this phylum among the whole number of animal species known
Protozoa	12	.0050	1.4272
Porifera	2	.0008	.4460
Coelenterata	122	.0514	.8028
Nemathelminthes	24	.0101	.2676
Molluscoida	134	.0564	.3032
Echinodermata	125	.0526	.7136
Annulata	1,131	.4764	.7136
Arthropoda	210,752	88.7751	74.6188
Mollusca	11,771	4.9583	10.8828
Chordata	13,326	5.6133	8.8427

Without going into details, it is apparent that the percentage of identifications preserves very well a relative ratio to that of the number of species and presumably, therefore, to the abundance of individuals in the phyla. What variations there are seem obviously due to differences in the availability to birds of the differing types of animals.

Taking up the phyla in order, we begin with the

PROTOZOA (ONE-CELLED ANIMALS)

Protective adaptations.—Judging from what is asserted about other phyla, phosphorescence and the possession of bright colors in some groups and of silicious or calcareous, often tuberculate or spinose, tests or shells or of exoskeletons formed of foreign bodies in others, are characters that would be deemed of protective significance in Protozoa.

Bird enemies.—Protozoa are too small to engage the attention of birds, those found in stomachs being Foraminifera strained from water or mud, or picked up as gravel by ducks. It is probable also that protozoa are consumed, along with the stems and leaves of aquatic plants upon which they often are abundant, by wild ducks which feed upon such vegetation. Stomach analysis, however, has not been directed toward the recognition of such minute material.

Number of identifications, 12; percentage of identifications among those of all animals, .0050; percentage of species in this phylum among the whole number of animal species known, 1.4272.

Other enemies.[1]—Protozoa are the prey of others of their kind—of bacteria, of rotifers, of flatworms, of amphipods and other small crustacea, and of mollusks; they are eaten also by the young of numerous species of fishes, by the adults of specialized forms (menhaden, gizzard shad), and by the larvae of batrachians.

Discussion.—Protozoa, because of their minute size and general inaccessibility to birds, would not be expected to enter largely into the food of this class. The forms eaten by birds are among the best "protected" protozoa, but the possession of shells can hardly be considered as an adaptation for protection from enemies in the case of animals so small as to be easily devoured by almost any carnivorous animals encountering them and which exist in such enormous numbers that vast areas of sea bottom are covered with remains of their shells. In this case as in many others, numbers are so large and reproduction so great that the inroads of all enemies are fully discounted. Losses to predatory enemies are only a fraction of the total death rate.

PORIFERA (SPONGES)

Many sponges are pervaded by calcareous or silicious spicules which may render them more or less undesirable as food for predatory animals. Some are brightly colored and some phosphorescent. "Sponges do not appear to be edible by Fishes or even the higher Crustaceans or Molluscs. Countless lower animal forms, however, burrow in their substance, if not for food, at least for shelter, and the interior of a sponge is frequently found to be teeming with small Crustaceans, Annelids, Molluscs and other Invertebrates."[2]

Sponges have been identified from only 2 stomachs of nearctic birds (Canada goose and lesser scaup) and from their low degree of accessibility to birds, not many cases of feeding upon them would be expected.

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[1] Entries under this head for the various groups treated are intended as suggestive rather than as exhaustive. A list of papers from which much of this information has been gleaned forms the special bibliography on pp. 145-201. Notes on the food of reptiles, amphibians, and mammals are mostly from analyses of stomach contents in the Biological Survey.

[2] Parker, T. J., and Haswell, W. A., A text-book of zoology, vol. I, p. 126, 1910.

Number of identifications, 2; percentage of identifications among those of all animals, .0008; percentage of species in this phylum among the whole number of animal species known, .8028.

Discussion.—Information at hand seems to indicate that sponges are used very little as food by other animals; sea-urchins, marine worms, amphipods, and mollusks, however, are recorded as predators. Fresh water sponges are eaten to some extent by fishes. Whether this is credited to their "protective adaptations" is of little moment as the fact remains that sponges do not multiply excessively nor overrun the earth as forms that lack enemies are in theory supposed to do.

Sponges have bright and varied colors and one case of mimicry has been pointed out.[1] If it be true as apparent from observations thus far, that they have few or no enemies, natural selection can not be advanced as an explanation of their color phenomena. If sponges without enemies have adaptations of the same character as other groups with numerous enemies, it would seem evident that selection by predatory animals has no necessary connection with the adaptations.

COELENTERATA (HYDRAS, JELLYFISHES, SEA-ANEMONES)

Protective adaptations.—Some coelenterates have a chitinous cuticle, others have a calcareous skeleton, and many of them have nematocysts or stinging cells. Numbers of them are brilliantly colored or phosphorescent but it must be noted also that many are transparent or nearly so, showing that possession of protective devices (as the nematocysts) is not always accompanied by the development of "warning colors."

Bird enemies.—The Coelenterata most often found in bird stomachs are the Hydrozoa (such as *Abietinaria*, *Sertularella*, and *Thuiaria*). They have been identified 113 times from the stomachs of 13 species of ducks, 2 of gulls, and one each of murre, murrelet, and shearwater. Sea-anemones (*Anthopleura*, *Aulactinia*) have been identified four times from stomachs of a scoter, an eider, an oyster-catcher, and a gull, Alcyonaria from two ducks, and coral from one.

Number of identifications, 122; percentage of identifications among those of all animals, .0514; percentage of species in this phylum among the whole number of animal species known, .8028.

Other enemies.—Hydroids are eaten by marine worms, by sea-urchins and sea-anemones, and also by fishes, as the cod, haddock.

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[1] McIntosh, W. C., The coloration of marine animals. Ann. Mag. Nat. Hist. 7th ser., vol. 7, p. 223, Mar., 1901.

sand launce, lump sucker, cunner, scup, filefish, and flatfishes; ctenophores are eaten by the spiny dogfish, flatfishes, whiting, and cod; sea-anemones are eaten by cod,[1] haddock, tilefish, flatfishes, the sunfish *Mola,* spiny dogfish, whiting, and by the so-called jellyfishes and by whales. Holothurians and some fishes (*Scarus*) feed on corals.

McIntosh notes that the brightly colored jellyfishes " have precisely the same habits as the uncoloured and transparent," which raises doubt as to the validity of the selectionist interpretation of the facts. The brightly hued and the translucent forms are equally palatable to whales and other animals using jellyfishes as food. He adds with regard to sea-anemones that " the view that the gaudy colors . . . . act as a warning is not borne out by the eagerness with which the cod swallows the brightest, such as *Stomphia,* while the smaller flatfishes fill their stomachs with *Edwardsiae.*" (Ann. Mag. Nat. Hist. 7th ser., vol. 7, pp. 224-225, 1901.)

Discussion.—Coelenterates are another group of animals but slightly available to birds and seem to be taken in full proportion to the degree of availability. The nematocysts seem a futile defense against animals of the groups here mentioned as coelenterate enemies, and must be also in the case of the myriads of crustacea (possible enemies) all of which have a chitinous exterior and which moreover manipulate their food in the chelae before chewing it, a process that would result in the harmless discharge of the stinging cells. It is alleged that hermit crabs have a commensal relation with certain hydroids which grow upon the shells they inhabit and that they are protected from their enemies by the presence of the inedible stinging hydroids.[2] This is not the case where the bird enemies are concerned, as the sea ducks which are the principal bird enemies of hydroids, often swallow the hermit crab, shell, hydroids and all. Many of the examples identified from bird stomachs came from precisely this source. With respect to the practical aspect of the case, it would appear that in its shell retreat and its own strong claws the hermit crab has much more efficient defenses than the nettlelike hydroids. It seems more likely that the latter merely grow on mollusk shells as a convenient substratum. From the habit some hermit crabs have of frequently changing their abode, the advantage held by a "commensal" hydroid may be lost at any moment.

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[1] McIntosh notes that sea-anemones are a valued bait for cod.

[2] Parker and Haswell, Zoology, vol. 1, p. 144, 1910.

PLATYHELMINTHES (FLATWORMS, FLUKES)

The majority of organisms of this phylum are parasitic and therefore not available to predatory animals. Perhaps some of the fresh-water planaria and the marine nemerteans have been found but not identified in the stomachs of shore birds, but so far we have no positive determination of a worm of this phylum as bird food. Forbes reports a small catfish (*Noturus*) feeding on fresh-water planaria. McIntosh says that marine planarians of both plainly and brightly colored forms are eaten by sea-anemones and fishes. Fresh-water planarians also are eaten by fishes. Stiles intimates that carp destroy large numbers of the liver fluke (*Fasciola hepatica*) in the cercaria stage.

NEMATHELMINTHES (THREADWORMS, ROUNDWORMS)

Again a vast number of worms of this phylum are parasites, abundantly so, in fact, of birds themselves. In order to reckon as food only those so taken, all nematodes other than Gordiidae have been kept out of the computations. The records for Gordiidae number 24, the percentage of these identifications among those of all animals is .0101, and the percentage of known species[1] of Nemathelminthes among all animals according to the estimates used in the present paper, .2676. The nematodes have a tough cuticle but no special defenses; nevertheless they certainly are not eaten out of proportion to their numbers, but considering availability to birds, they may possibly be eaten somewhat in ratio to the frequency with which they are encountered. They are eaten also by flatworms and by various fishes.

TROCHELMINTHES (ROTIFERS)

None of these have yet been identified as food of nearctic birds, though possibly rotifers taken in with foliage of aquatic plants may have been overlooked. Rotifers are eaten by the young of a number of fishes.

MOLLUSCOIDA (CORALLINES, LAMPSHELLS)

Protective adaptations.—Except for the shells of the brachiopods, and cuticular walls of some bryozoa, no special protective features have been developed by the Molluscoida.

Bird enemies.—Only three brachiopods have as yet been identified from the stomachs of nearctic birds—not a matter for surprise in

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[1] An enormous number of Nematodes await description.

view of the small number and marine habitat of the species of these animals. The other Molluscoida that have been found in bird stomachs include Cyclostomata (having calcareous zooecia), Cheilostomata (with calcareous or chitinous zooecia), and Phylactolaemata. Large numbers of the statoblasts of the latter group, the fresh-water bryozoa, have been disclosed in the stomachs of wild ducks.

Number of identifications of Molluscoida, 134; percentage of identifications among those of all animals, .0564; percentage of species in this phylum among the whole number of animal species known, .3032.

Discussion.—Considering their low availability to birds, animals of this phylum probably are taken in due proportion. Fresh-water bryozoans have been recorded from stomachs of many species of fishes, and the marine forms from a smaller number. Marine bryozoans are preyed upon by worms, amphipods, decapods, and starfishes.

ECHINODERMATA (SEA-CUCUMBERS, SEA-URCHINS, STARFISHES)

Protective adaptations.—All of the echinoderms have a calcareous exoskeleton and in many the surface is beset with tubercles or spines. The starfishes and sea-urchins are armed also with pedicellariae or grasping organs, which in some cases in the latter group are said to be poisonous. Some sea-cucumbers have the " Cuvierian organs " which throw out long viscid filaments. Starfishes, especially the brittlestars and many crinoids, have the supposedly protective faculty of snapping off their arms or portions thereof. The colors of echinoderms are often conspicuous and in certain cases have been termed warning.

Bird enemies.—Starfishes have been identified 28 times in the stomachs of nearctic birds here reported upon; sea-urchins (*Strongylocentrus*, *Echinarachnius*) 92 times; and sea-cucumbers, 3 times. The birds (19 species) eating them were chiefly ducks collected in northern seas.

Number of identifications, 125; percentage of identifications among those of all animals, .0526; percentage of species in this phylum among the whole number of animal species known, .7136.

Other enemies.—Starfishes and sea-urchins prey upon one another, and are very commonly eaten by cod, haddock and other species of *Gadus,* by argentines, dragonets, rocklings, wolffishes, rays, sharks, tautog, scup, smelt, flatfishes, and others. Sea-cucumbers are less commonly taken by the same predators. Blue foxes on the Pribilof Islands feed on sea-urchins in winter. Sea-urchins and starfishes are consumed also by crabs, sea-anemones, and marine worms.

McIntosh comments interestingly on the enemies of echinoderms: "The colours of Echinoderms are often most conspicuously bright," but *Hippasterias*, which is brilliant orange-red, is eaten by gulls, cod, catfishes and by other starfishes. "The sand-stars (e. g. *Ophiura lacertosa*) are often tinted of a hue resembling their surroundings, yet they and the more brightly tinted forms are common in the stomachs of fishes and are eagerly devoured by gulls when stranded on the beach." "The brown and purple hues of sea-cucumbers may in some way subserve protection . . . . yet both they and the transparent forms are found in the stomachs of fishes." (Ann. Mag. Nat. Hist. 7th ser., vol. 7, pp. 225-226, 1901.)

Discussion.—Echinoderms have a number of protective devices but also it would appear, numerous and effective enemies. Birds prey upon this group to fully as large an extent as could be expected, considering the slight degree to which they come in contact with echinoderms.

It should be noted that while practically all starfishes and sea-urchins have similar protective adaptations, some are very gaudily, others modestly colored; in one case or the other, the natural selection theory as to the connection between special defenses and coloring is untenable. The sea-urchins with calcareous tests, abundant spines, and pedicellariae seem unusually well defended, but that this does not mean freedom from enemies is shown by the great fecundity of sea-urchins, individuals of some species, e. g., *Echinus esculentus*, yielding 20,000,000 eggs per season.

ANNULATA (WORMS)

Protective adaptations.—The chaetopods including the most common marine worms and the majority of earthworms have chitinous setae on all segments of the body. The earthworms are habitual burrowers, and some of both fresh- and salt-water annelids live in tubes. A few in each group are phosphorescent, and many of the marine worms are highly colored. A. R. Wallace says:[1] "Among the creatures which probably have warning colors as a sign of inedibility are . . . . those curious annelids the *Nereis* and the *Aphrodite* or sea-mouse."

It should be noted however that many of the brightly colored forms live in burrows or tubes, thus taking care not to advertise their "inedibility." Leeches sometimes have strongly contrasting color, as for example greenish with red and black spots.

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[1] Darwinism, p. 266, 1896.

Bird enemies.—The identifications of Annulata from nearctic birds are: 690 for the Polychaeta, chiefly Nereidae, which have been found in the stomachs of more than 70 species of birds and in numbers up to 500 in a single stomach; 428 for the Oligochaeta or earthworms from 44 species of birds; and 11 of Hirudinea or leeches from 10 species. The robin (*Planesticus migratorius*) feeds habitually and voraciously upon earthworms and the woodcock (*Philohela minor*) makes about half of its diet of these annelids.

Number of identifications, 1131; percentage of identifications among those of all animals, .4764; percentage of species in this phylum among the whole number of animal species known, .7136.

Other enemies.—Studies that have been made of the food of fishes indicate that a very large number of marine fishes prey upon the Nereidae and other annelids. They are eaten also by other worms, starfishes, sea-urchins, sea-anemones, gastropods, and crabs. Fresh-water oligochaetes form a steady contribution to the diet of the fishes of their environment. Earthworms are eaten by predacious beetles, by most batrachians, by some turtles, snakes and by various mammals including shrews, skunks, and the armadillo, but especially by the moles (*Parascalops breweri,* 26 per cent of the food; *Scalopus aquaticus,* 31 per cent; *Scapanus townsendi,* 40 per cent; *Condylura cristata,* 50 per cent.) Leeches are eaten by a variety of mammals, birds, reptiles, amphibians, fishes, crustaceans, snails, and insects.

Discussion.—Both of the annelids (*Nereis* and *Aphrodite*) Wallace mentions as being warningly colored are eaten by birds and fishes, *Nereis* frequently and in large numbers. Considering the aquatic habits of most of the annelids it would appear that they are taken by birds as often as could be expected. It is evident furthermore that they have numerous other predatory foes and that they probably contribute their full quota of food toward the dietary requirements of the animal kingdom.

ARTHROPODA (JOINTED ANIMALS)

As recorded previously in the table of phyla, the Arthropoda, including the exceedingly numerous class of insects, furnish, as would be expected, a very large preponderance of the animals eaten by birds.

Number of identifications, 210,752; percentage of identifications among those of all animals, 88.7551; percentage of species in this phylum among the whole number of animal species known, 74.6188. The disproportion of the percentage of capture to that of frequency reflects the relatively greater availability to birds of arthropods over the other phyla.

Since arthropods are by far the most important phylum of animals as bird food and since it is with reference to the included class of insects that the theories of protective adaptations have been most highly elaborated, it is desirable to subdivide the phylum for the purposes of the present discussion.

The tabulation below shows the number of identifications and their percentages for the four classes of Arthropoda that are available for food to nearctic birds.

Arthropoda

Class	Number of identifications	Percentage of identifications among those of all arthropods	Percentage of species in this class among the whole number of arthropod species known
Crustacea	6,086	2.8877	3.8254
Myriapoda	2,862	1.3530	.4781
Insecta	190,919	90.5891	91.8589
Arachnida	10,885	5.1648	3.8254

It is evident that the percentage of identifications for each class corresponds very well with the frequency of such animals as indicated by the number of species. The validity of such comparisons used throughout this paper thus receives further corroboration.

CRUSTACEA (CRABS, SHRIMPS, SOWBUGS)

Protective adaptations.—The exoskeleton of crustacea is either chitinous or much thickened or calcified. Several groups have bivalved carapaces in which the animal is nearly or entirely enclosed. The barnacles have a more complicated covering of calcareous plates, sometimes thick and hard. Most of the decapods have strong grasping forelegs, and have furthermore the faculty of snapping these off when properly stimulated. Some crustacea have burrowing habits (Hippidae) and others (hermit crabs) use the shells of univalves for shelter, while the terrestrial sowbugs roll themselves up into a ball when disturbed.

As to color, some of the smaller aquatic forms are translucent or transparent; the ostracods are said to assimilate with the general color of their environment, while some copepods and decapods are brilliantly colored. As to form, Mortensen says: "The typical cases of adaptation to life among algae are especially found among the Caprellids; they might be said to represent the Phasmids and Geometrid larvae, among marine animals" (p. 77). "*Idothea marina* and related species . . . . bear a striking resemblance to the plants (especially *Zostera* leaves) on which they are found" (p. 78).[1]

"Many Crustacea," according to Parker and Haswell, "present instances of protective and aggressive characters, i. e., modifications in form, colour, etc., which serve to conceal them from their enemies or from their prey. Probably the most striking example is that of certain crabs (*Paramithrax*) which deliberately plant Sea-weeds, Sponges, Alcyonarians, Zoophytes, etc., all over the carapace, and are thus perfectly concealed except when in motion."[2]

Poulton expresses the same view in the following language: "Certain palatable animals make use of the Special Defence and Warning Colours of other forms. Thus, the common English hermit-crab, *Pagurus bernhardus,* commonly carries on its borrowed shell the conspicuous stinging sea-anemone *Sagartia parasitica;* while another English species, *Pagurus prideauxii,* inhabits a shell which is invariably clothed by the flattened *Adamsia palliata.* Two crabs (*Polydectus cupulifer* and *Melia tessellata*), from Mauritius, described by Mobius, invariably held a sea-anemone in each claw. Two other groups of animals, sponges and Ascidians, in addition to sea-anemones, are avoided by enemies of the Crustacea, and these are also employed by the latter. Thus the British hermit-crab *Pagurus cuanensis* is found in shells which are covered with a (generally) brightly-coloured sponge (*Suberites domuncula*). Mobius also describes a Mauritian hermit-crab (*Ascidiophilus caphyraeformis*) which lives in a case formed by an Ascidian."[3]

Bird enemies.—Most of the leading subdivisions of the Crustacea contribute to the food of birds, apparently about in proportion to their accessibility. The tabulation of numbers of species of Crustacea used for comparison with those of percentages of identifications was made from "A list of the Crustacea of New Jersey including the adjacent region or that of the Middle Atlantic States,"[4] the only check list available for any considerable area of our region.

The Anostraca (fairy shrimps) are locally eaten more extensively than indicated above and the fact is an illustration of the principle

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[1] Mortensen, T. H., Observations on protective adaptations and habits, mainly in marine animals. Vidensk. Meddel. fra Dansk. naturh. For. Kjob., bd. 69, 1920.

[2] Zoology, vol. 1, p. 601, 1910.

[3] Poulton, E. B., Essays on evolution, pp. 356-357, 1908.

Thomas Scott records a copepod (*Acidicola rosea*) which lives within the branchial sac of an ascidian as having been eaten by a sole *Pleuronectes microcephalus.* (20th Ann. Rep. Fishery Bd. Scotland, p. 525, (1901) 1902.)

[4] Fowler, H. W., Ann. Rep. N. J. State Mus., pp. 463-598 (1911), 1912.

that in natural history as elsewhere sweeping statements based on partial or negative evidence are dangerous. No exception may be noted for one which claims that "enemies play no part in keeping down the numbers of *Artemia* (brine shrimps), or of *Ephydra* (alkali flies) in the larval stage."[1] Dr. Alexander Wetmore, of the Smithsonian Institution, who has had considerable experience about Great Salt Lake to which locality the quoted assertion relates, has pointed out[2] that *Artemia* and *Ephydra* are by no means free from enemies. Shovellers, lesser scaups, golden-eyes, green-winged teal, Wilson's and northern phalaropes, avocets, and black-necked stilts all feed extensively upon both of these animals. But for the fact that stomach analyses have not been made of other birds collected at the same place, it would undoubtedly be possible to add the names of a number of species to this list. Doctor Wetmore states that "the toll taken by birds from the brine shrimp and alkali fly larvae and pupae during the course of a season constitutes a mass of individuals almost beyond comprehension . . . . The immense numbers of these creatures . . . . must be attributed to the large number of offspring produced rather than to an absence of enemies." The number of records for the minute Cladocera is fully up to expectations. Among other items of this group the egg capsules or ephippia of *Daphnia* have been found in numerous stomachs of grebes and wild ducks, and in number up to 250 in a single stomach.

Identifications of Crustacea

Group	Number of identifications	Percentage of identifications among those of all Crustacea	Percentage of species in this group among those of all Crustacea of the Middle Atlantic States
Unidentified	573	9.4150	...
Anostraca	28	.4601	1.3667
Cladocera	90	1.4788	4.1002
Ostracoda	207	3.4012	3.8724
Copepoda	13	.2136	18.2232
Cirripedia	401	6.5888	5.9225
Isopoda	385	6.3259	14.3508
Amphipoda	986	16.2010	9.3394
Cumacea	...	...	3.1891
Stomatopoda	...	...	.9112
Schizopoda	48	.7887	1.1389
Decapoda	3355	55.1260	37.5853

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[1] Vorhies, Charles T., Notes on the fauna of Great Salt Lake. Amer. Nat., vol. 51, pp. 494-499, Aug., 1917.

[2] Amer. Nat., vol. 51, pp. 753-755, Dec., 1917.

The ostracods have been identified chiefly from the stomachs of 15 species of wild ducks, and no fewer than 1,200 have in two instances been taken from a single stomach. Most of the barnacles were found in the stomachs of 22 species of ducks, gulls, and shorebirds from northern waters. Amphipods were eaten by more than 80 species of birds, largely shorebirds, ducks, and other waterfowl; nearly 70 species of amphipods were identified and the number of individuals taken by single birds ran up as high as 2,500. The isopods were consumed by more than 75 species of birds, the land-forms or pillbugs alone by about half that many; the greatest number of individuals of terrestrial sowbugs found in a single stomach was 60, of aquatic forms, 256. In the Decapoda it may be of interest to note that 392 of the identifications were of shrimps, hundreds of individuals being present in some stomachs; 1,592 of Astacidae (crawfishes), the greatest number taken by one bird being 49; and 794 of crabs of various kinds. Among groups of crabs represented, there were the following numbers of captures, the figures in parentheses in each case denoting the largest number of individual crabs found in a single stomach: Sand crabs or sandbugs, Hippidae, 61 (14); stone crabs, Lithodidae, 90 (16); hermit crabs, Paguridae, 35 (40); mud crabs, Pilumnidae, 186 (36); swimming crabs, Portunidae, 39 (16); edible crabs, Cancridae, 41 (18); shore crabs, Grapsidae, 180 (26); and fiddler crabs, Ocypodidae, 272 (19).

Number of identifications 6,086; percentage of identifications among those of all arthopods 2.8877; percentage of species in this group among the whole number of arthropod species known, 3.8254.

Other enemies.—Crabs of various genera (including hermits) are a staple item of food for many fishes, such as the dogfish, rays, eels, sea bass, squeteague, scup, tautog, swellfish, toadfish, tilefish, hake, cod, haddock, sculpins, and flounders. Crawfishes are relished by fresh-water fishes and are eaten also by snakes, turtles, and various mammals such as the muskrat, raccoon, skunks, mink, and otter. Such large and powerful forms as lobsters are eaten by sea bass, rockfish, tautog, sharks, dogfish, rays, and skates. Amphipods are captured by the plant *Utricularia,* by insects, hydras, sea-anemones, and starfishes. Practically all adult fresh-water fishes eat amphipods and isopods, and when young prey upon Cladocera, Copepoda and Ostracoda. Starfishes and bony fishes such as Coregonus, Salvelinus, Alosa, herring, sticklebacks, and roaches continue feeding on these small forms when adult. Marine fishes take similar crustacea available to them, particularly the abundant shrimps and Mysidacea. Whales and seals consume enormous quantities of isopods and Euphasiacea. Caprellids are eaten by fishes as well as by birds. Cladocera and Copepoda are eaten freely by larval salamanders and to a lesser extent by recently transformed frogs. They and all other small fresh-water crustaceans fall a prey to Hydra and aquatic insects. Small marine forms are engulfed even by protozoans. Barnacles are eaten by the tautog, and by sea-anemones and sea-urchins. More than 80 kinds of crustacea have been identified from stomachs of haddock taken in waters about Scotland (Thomas Scott). Crustacea have parasites from among their own ranks, and from among the worms.

Discussion.—Most of the small crustacea are translucent or transparent but this does not save them from their foes. Practically all aquatic animals "get their start" by feeding on these crustacea, the list including a great variety of insects, fishes, and batrachians. Many of them continue feeding upon crustacea when adult, and so common is this habit that in many cases small crustacea are the animal basis of the food for the entire fauna of certain waters. This is true of the Artemia of Great Salt Lake, previously discussed, and conspicuously so of the Mysidacea, Amphipoda, Isopoda, Euphasiacea and Macrura of northern oceans, where everything from other crustacea, through fishes and birds up to whales preys incessantly upon them. There is no question of special protection here but solely of numbers and fecundity.

The protection that crustacea might be supposed to derive from their more or less indurated exoskeleton is discounted by the fact that in most cases there are plenty of enemies large enough to swallow them whole. Of what avail for instance is the bivalved shell of the almost microscopic Ostracoda? The same principle applies all along the line up to and including the crabs, for most crab-eaters swallow their prey entire; however there are some crabs that grow so large they are possibly almost free from enemies when adult.

The claws of the large decapods naturally are of little avail against enemies so voracious as to swallow the crustaceans whole and there is no evidence known to the writer that the self-mutilation practiced by decapods results in enemies swallowing the claw and letting its owner escape.

Birds find the Hippidae or sandbugs, despite their burrowing habits, and hermit crabs, adopted shell and all, are freely eaten by birds and fishes. In numerous cases the hermit crabs found in bird stomachs were those with hydroids and bryozoa growing on their carapaces or shelters. Why should it even be supposed that such combinations of animals are protective when the enemies of one of them are in most cases enemies of all? For instance the diving ducks and fishes which relish crabs, including hermits, also eat mollusks, bryozoa, and hydroids. What difference is it to them that a mollusk shell contains a hermit crab rather than its original occupant, or that hydroids are growing on it when these animals are browsed from rocks, etc., elsewhere? McIntosh has brought up this same point with regard to species of *Hyas* which become covered with a growth of algae and invertebrates, yet covered with parasites as they are, abound in stomachs of the cod.[1] They are eaten by other fishes and by birds also. Conclusions of a similar nature undoubtedly must be drawn in the case of those crabs associating sea-anemones and ascidians with themselves. Both of these classes of animals have their enemies which probably would engulf crab and all in cases where the animals were together.

The caprellids noted by Mortensen as resembling algae and by Parker and Haswell as so closely assimilated in form and color to Hydrozoa and Polyzoa as to be difficult of detection nevertheless are detected and eaten by some birds and by numerous fishes, and the protectively formed and colored isopods of the genus *Idothea* are represented by 51 records for 6 species in stomachs of 18 kinds of birds.

The fiddler crabs (*Uca*), so abundant and conspicuous on the mud flats of the southeastern coast of the United States, have one claw enormously developed, thus having the principal characteristics of the so-called protected species, a special mode of defense, and living exposed and conspicuously in large numbers. They are freely eaten by birds however and for this single genus of a few species, we have 271 records from 24 species of birds.

MYRIAPODA (THOUSANDLEGS, CENTIPEDS)

Protective adaptations.—The centipeds and millipeds exhibit differences that would warrant their being treated as separate classes; customarily, however, they are considered together. The following remarks on their protective adaptations are quoted from F. G. Sinclair.[2]

> The means of defence possessed by these animals . . . . differ very much in the different species of Myriapods. In the Centipedes the animals are provided with a powerful weapon in the great poison claws which lie just beneath the mouth, and which are provided with large poison glands, which supply a fluid which runs through a canal in the hard substance of the claw and passes into the wound made by the latter. The effect of this fluid is

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[1] Ann. Mag. Nat. Hist. 7th ser., vol. 7, p. 229, Mar., 1901.

[2] Cambridge Nat. Hist., vol. 5, pp. 36-37, 1910.

instantaneous on the small animals which form the food of the Centipedes. I have myself watched *Lithobius* in this country creep up to a blue-bottle fly and seize it between the poison claws. One powerful nip and the blue-bottle was dead, as if struck by lightning. I have also seen them kill worms and also other *Lithobius* in the same way. When another *Lithobius* is wounded by the poison claws it seems to be paralyzed behind the wound. The Millepedes, on the other hand, have no such offensive and defensive weapon. They rely for protection on the fluid secreted by the *stigmata repugnatoria* (or *glandulae odoriferae*) mentioned before. This fluid has been shown to contain prussic acid, and has a very unpleasant odour. Most of the Millepedes are provided with these glands; but in the cave Myriapods mentioned before, the animals have not to contend against so many adversaries, and these glands almost disappear. Other Myriapods defend themselves by means of the long and stiff bristles with which they are provided, e. g., the little *Polyxenus*.

Bird enemies.—Centipeds have been identified 236 times from the stomachs of 65 species of nearctic birds, and millipeds 2,598 times from 98 species. The latter were identified more than 50 times in the case of each of 12 species of birds. The highest number of millipeds found in a single stomach—that of a starling—was 40. More than a tenth of the starling's annual food in the United States consists of millipeds.

Number of identifications, 2,862; percentage of identifications among those of all Arthropoda, 1.3580; percentage of species in this class among the whole number of arthropod species known, .4781.

Other enemies.—A. H. Kirkland in his report on the "Usefulness of the American toad"[1] states that 10 per cent of the food of 149 individuals examined consisted of millipeds and that as many as 77 were found in a single stomach. Myriapods are eaten also by frogs, salamanders, lizards, snakes and turtles. Among mammals the common mole (*Scalopus*), armadillo (*Tatu*) and civetcat (*Bassariscus*) (and the mongoose as introduced into Trinidad) are known to feed on centipeds, and Brewer's mole (*Parascalops*) and the armadillo on millipeds; shrews prey upon both groups. Centipeds are eaten by predacious beetles, frequently prey upon each other, and it appears that often the male is consumed by the female following pairing. Millipeds are the chief food also of certain Lampyrid larvae, are eaten by ground beetles, and are parasitized by phorid flies.

Discussion.—There is a more or less prevalent belief that myriapods are "specially protected" animals. This idea is reflected in an article on "The hothouse milliped as a new genus," in which the author,

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[1] Farmers' Bull. 196, U. S. Dep. Agr., 16 pp., 1904.

O. F. Cook, says:[1] "Prussic acid and other corrosive secretions . . . . render . . . . the millipeds distasteful to birds and other animals that might prey upon them." This statement implies that millipeds have no natural enemies, an Utopian condition that probably no animal enjoys. In fact the evidence here adduced shows that millipeds and centipeds as well, have numerous effective bird enemies, which together with special enemies in other groups, no doubt prey upon them about in proportion to their availability. From the comparatively small numbers of myriapods and their secretive habits, it could not be expected that they form a very high percentage of the food of carnivorous animals. This reasonable expectation certainly is fully satisfied by the showing here made of the activities of their natural enemies.

INSECTA (INSECTS)

From tabulations appearing earlier in this article, it will have been noted that arthropods contribute more than 88 per cent of all the records of the animal food of nearctic birds and insects more than 90 per cent of the arthropods. To repeat the figures for the latter group, insects furnish 190,919 identifications, which is 90.5891 per cent of those of all arthropods. The percentage of species of the class Insecta among the whole number of arthropod species known is 91.8589.

Not only are insects the most numerous class of jointed animals, and the most important item of the animal food of birds, but they are also the group about which most has been written in a theoretical way as to protective adaptations (especially color) and as to the relation of these adaptations to predatory foes. On all these accounts it is desirable to discuss the insects in greater detail, certainly in most cases by orders and in some instances by families. Tabulations have been prepared, therefore, showing numbers of identifications by orders and families, with their relative percentages. The first of these is a distribution of the total number of identifications by orders.

The reader may have wondered why some of the tabulations as to relative numbers of insects have not been based on the inventories of some of the larger museums. However, this matter has been considered and the invalidating factor in such statistics is that such collections are always more or less specialized either as a result of policies of the museum or of the receipt of collections from specialists. Thus among insects, such favorite groups of the amateur as

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[1] Proc. U. S. Nat. Mus., vol. 40, p. 625, 1911.

Lepidoptera and Coleoptera are always copiously represented, while such orders as Thysanura and Thysanoptera in most cases are obviously neglected. However, one museum tabulation with percentage designations added, is herewith appended as a further demonstration (notwithstanding the defects just pointed out and the approximate nature of some of its figures) that multiplicity of species is more or less closely correlated with abundance of individuals. This table is adapted from one presented by Dr. J. M. Aldrich in the Smithsonian Report for 1919 (1921), p. 373.

Summary of U. S. National Museum Collection, June 1919

Order	Named species	Total specimens	Percentage of species in this group	Percentage of specimens in this group
Thysanura	[1] 100	[1] 700	.1010	.0329
Odonata	705	16,642	.7120	.7821
Isoptera	173	[1] 100,000	.1747	4.7000
Ephemerida	647	14,721	.6534	.6918
Plecoptera				
Corrodentia				
Mecoptera				
Trichoptera				
Neuroptera				
Mallophaga	[1] 125	[1] 1,250	.1262	.0587
Dermaptera	180	1,098	.1818	.0516
Orthoptera	2,556	25,988	2.5815	1.2214
Hemiptera	[1] 3,876	244,637	3.9147	11.4979
Lepidoptera	30,653	275,920	30.9595	12.9682
Diptera	10,253	210,880	10.3555	9.9113
Siphonaptera	[1] 130	[1] 432	.1313	.0203
Coleoptera	[1] 32,500	[1] 738,000	32.8250	34.6860
Hymenoptera	17,638	493,757	17.8143	23.2065
Thysanoptera	200	750	.2020	.0352
Strepsiptera	159	414	.1605	.0194
Total	98,925	2,125,189		

[1] Estimated.

Identifications of Insects

Order[1]	Number of identifications	Percentage of identifications among those of all insects	Percentage of species in this group among the whole number of insect species known
Aptera	5	.0026	.1691
Odonata (further unidentified)	2,082	1.0905	...
Zygoptera	245	.1283	.2603
Anisoptera	707	.3703	.3383
All Odonata	*3,034*	*1.5891*	*.5986*
Agnatha	484	.2535	.1041
Plecoptera	80	.0419	.0780
Isoptera	129	.0677	.0911
Dermaptera	18	.0094	.1301
Cheleutoptera	26	.0136	.6507
Diphtheroptera	5,695	2.9829	.7809
Orthoptera (Sens. str.)	6,280	3.2893	.8589
Paleoptera	117	.0613	.3123
Dictyoptera	58	.0304	.2082
Saltatoria (further unidentified)	6,450	3.3784	...
Orthopteroidea (further unidentified)	359	.1880	...
All Orthopteroidea	*19,003*	*9.9534*	*2.9410*
Corrodentia	17	.0089	.0780
Mallophaga	6	.0031	.3383
Siphonaptera	1	.0005	.0130
Heteroptera	11,530	6.0392	4.9457
Homoptera	5,215	2.7315	3.6442
Hemiptera (further unidentified)	5,650	2.9594	...
All Rhynchota	*22,395*	*11.7300*	*8.5899*
Neuroptera (Sens. lat.)	119	.0623	...
Megaloptera	167	.0875	.0156
Rhaphidioidea	54	.0283	.0104
Neuroptera (Sens. str.)	108	.0566	.3383
Phryganoidea	866	.4536	.3644
All Neuropteroidea	*1,314*	*.6882*	*.7187*
Lepidoptera	18,487	9.6831	15.6180
Coleoptera	85,322	44.6899	46.2032
Mecaptera	5	.0026	.0260
Diptera	10,836	5.6757	11.4432
Hymenoptera	27,025	14.1551	17.1798
Unidentified	2,676	1.4016	...

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[1] The arrangement of the orders of insects in this tabulation is a compromise among several systems.

There are no accounts given of Platyptera (embiids), Zoraptera, Notoptera (grylloblattids), Siphunculata (body lice), Apocoleoptera (beaver beetles), and Suctoria (fleas) because we have no records of bird enemies.

Total number of identifications, 190,919; percentage of identifications among those of all arthropods, 90.5891; percentage of species in this class among the whole number of arthropod species known, 91.8589.

APTERA (WINGLESS INSECTS)

Protective adaptations.—The springtails and their allies appear to have few adaptations such as are commonly called protective, their defense being agility in some cases, and secretive habits in others. Some species have coxal glands supposed to be repugnatorial.

Bird enemies.—While only five records of Thysanura are included in the tabulations here reported upon others have been made since and it seems probable that birds which feed about small pools, on the quiet surface of which Collembola sometimes abound, or on the edges of snowfields, will be found to pay due attention to thysanurans.

Total number of identifications, 5; percentage of identifications among those of all insects, .0026; percentage of species in this group among the whole number of insect species known, .1691.

Other enemies.—In reports of the Pennsylvania Department of Agriculture and others treating the same groups of animals, seven species of salamanders, four of frogs, and one toad are recorded as feeding on Thysanura. Hamilton, reporting on 400 stomach contents of young toads, says: "Collembola comprised 6.2 per cent of the diet. The springtails sometimes occurred in large numbers in the stomachs examined, and together with thrips appeared to be an important food of all small anurans" (Copeia, 1930, p. 45). Forbes reports them being eaten by a Coccinellid beetle[1] and a small fish[2] (*Labidesthes sicculus*), Needham, by the brook trout,[3] and Pearce by two species of fishes, a killifish and the mudminnow.[4] They are known to be preyed upon also by aquatic hemiptera, and are cannibalistic.

Discussion.—Thysanura are chiefly minute insects, many of which spend their whole lives in well-concealed places. The forms which live more or less exposed appear to have enemies among animals interested in such small morsels of food. However information on the subject thus far is inadequate and no doubt will be increased by more intensive investigation of potential predators.

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[1] Bull. Ill. State Lab. Nat. Hist., vol. 1, no. 6, p. 52, May, 1883.

[2] Op. cit, vol. 2, p. 525, 1888.

[3] Bull. 68, N. Y. State Mus., p. 205, 1903.

[4] Bull. U. S. Bur. Fisheries, vol. 35, p. 285 (1915-16), 1918.

ODONATA (DRAGONFLIES, DAMSELFLIES)

Protective adaptations.—Dragonflies are fairly large, powerful, predacious insects with remarkable ability for flight. They are held in fear by illiterate people, a feeling possibly inspired by the large mobile head consisting chiefly of eyes, and the strikingly contrasted color-pattern of many of them. A dark ground color with vivid spots of green or yellow, answering to the description of warning color, is common among dragonflies; some also have brilliant red, blue, and metallic colors.

On the other hand, members of the order known as damselflies in general are weak on the wing and of slighter and more delicate structure. Some of them also are brightly colored but many are dull. The immature stages of both dragonflies and damselflies are aquatic, and predacious, and invariably inconspicuously colored.

Bird enemies.—It might perhaps be expected that damselflies would be more frequently captured by birds than dragonflies, but this does not seem to be the case, the determinations for these groups so far standing at 245 damselflies and 707 dragonflies. However, 2,082 identifications do not indicate which suborder is concerned. About 200 species of birds are known to eat Odonata, and nymphs as well as adults are freely taken. No fewer than 100-125 nymphs have been taken from the gullet and gizzard of individual ducks, yellow-legs, and magpies. Regarding the adults, Needham says: "It is doubtful whether anything that flies is able to capture in flight one of the swiftest dragon flies."[1] However, we have records of birds eating *Epiaeschna heros,* one of the largest and swiftest of the dragonflies of the United States, and *Anax junius,* another of the giant species, is commonly eaten by the pigeon hawk. No fewer than 28 individuals of Anax were found in a single stomach of this falcon, and adult dragonflies, mostly *Anax junius,* were found in 120 out of 181 stomachs of the species. In a lot of dragonfly wings, picked up under the home of a colony of purple martins at West Chester, Pa., were represented about 63 individual dragonflies, largely *Epiaeschna heros,* but including also, *Anax junius, Libellula pulchella,* and *Anax longipes.*

Number of identifications, 3,034; percentage of identifications among those of all insects, 1.5891; percentage of species in this group among the whole number of insect species known, .5986.

Other enemies.—Odonata are notoriously cannibalistic both in the nymphal and adult stages. Diving beetles, water scorpions and other

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[1] In Ward and Whipple, Fresh-water biology, p. 890, 1918.

aquatic hemiptera, salamanders, frogs, turtles, and many kinds of fishes prey upon the nymphs. Ants, spiders, robber flies, chipmunks, snakes, frogs, toads, and fishes feed to some extent also on adult dragonflies, obtaining most of them no doubt when teneral. They are parasitized by nematodes, mites, and flies.[1]

Discussion.—Odonata, both immature and adult, are freely preyed upon by a variety of enemies and no special defense can be assumed except the great expertness in flight of some of the dragonflies. This we have seen does not foil various birds nor of course predators from their own ranks. All in all it would seem that Odonata are preyed upon fully in proportion to their abundance.

AGNATHA (MAYFLIES)

Protective adaptations.—The nymphs that live in water are plainly colored; some cling closely to various objects in their environment, while others swim in a rapid darting manner. The adults also are usually inconspicuously colored.

Bird enemies.—Our tabulation shows mayflies to have been identified from the stomachs of 108 species of nearctic birds. A nighthawk has been known to contain 400 adults at one time or many thousands of eggs, the remains of the digestion of adults. As many as 250 nymphs have been found in a godwit's stomach. Mayflies periodically are exceedingly abundant and then are preyed upon by practically all kinds of insectivorous birds. An interesting account of the behavior of birds in the presence of a swarm of ephemerids is given by Dr. S. D. Judd in his "Birds of a Maryland Farm";[2] on this occasion 40 species of birds were observed eating mayflies. This list adds nine to the species of birds known from stomach examination to feed upon mayflies.

Number of identifications, 484; percentage of identifications among those of all insects, .2535; percentage of species in this group among the whole number of insect species known, .1041.

Other enemies.—Mayfly nymphs are eaten by the nymphs of stoneflies and dragonflies, by water bugs, most fresh-water fishes, and to some extent by salamanders and turtles; the adults are preyed upon by fishes and adult dragonflies, spiders, toads, and bats.

Discussion.—Mayflies are good food for predacious animals and are eaten freely, so much so as to cause David Sharp to remark:[3] "That

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[1] For full discussion of dragonfly enemies, see Bull. U. S. Bur. Fisheries, vol. 36, pp. 209-211 and 222-232 (1917-18), 1920.

[2] Bull. 17, U. S. Biol. Survey, pp. 22-24, 1902.

[3] Cambridge Nat. Hist., vol. 5, p. 442, 1910.

insects so fragile, so highly organized, with a host of powerful enemies, but themselves destitute of means of attack or defense, should contrive to exist at all, is remarkable." Doctor Sharp here falls into the same error the selectionists often do, namely, of taking the struggle for existence too seriously. While mayflies are a favorite food of many predators, the evidence does not indicate that they are eaten out of proportion to their numbers. They are also very fecund, practically the whole body content of a female mayfly consisting of the two egg masses. The annual occurrence of swarms covering the foliage along streams (dating back as far as such things were recorded) is proof enough that enemies do not permanently reduce the numbers of mayflies, and furthermore that the so-called defenses or protective adaptations, of which mayflies are so nearly destitute, are not essential to the maintenance of species in large, even overwhelming numbers.

PLECOPTERA (STONEFLIES)

Protective adaptations.—The stoneflies are mostly plainly colored but some are rather bright yellow; they are poor fliers but some of them are said to emit a liquid from the basal articulations of the legs, a performance usually classed as protective. The nymphs are aquatic in habit, good swimmers, and obscure in color.

Bird enemies.—Stoneflies have been identified in the stomachs of 41 species of nearctic birds, usually in no very large numbers. The total number of identifications is 80; the percentage of identifications among those of all insects, .0419; and the percentage of species in this order among those of all insect species known, .0780.

Other enemies.—Dragonfly nymphs prey upon those of stoneflies, and a few fishes, salamanders, frogs, and turtles feed upon these insects, either in the immature or mature condition according to availability. Needham says: "Hudson has demonstrated the importance of stoneflies as fish food in the mountain streams of New Zealand" (Fresh-water Biology, 1918, p. 884), and Muttkowski reports that 90 per cent of the food of trout in Yellowstone National Park consists of them.

Discussion.—The Plecoptera are a small group of insects of restricted habitat, one we should therefore not expect to find preyed upon extensively. They are eaten by various enemies, however, more or less in proportion to their abundance, and the evidence does not seem to indicate that special defenses of any kind enter into the equation.

ISOPTERA (TERMITES)

Protective adaptations.—Termites pass most of their lives concealed in galleries in wood or underground or in well-built nests. They have strong jaws, a caste of soldiers especially well-armed in this respect, and they emit a corrosive secretion. The color is usually yellowish to brownish, but some species have the body reddish and the wings dark, nearly black, thus having a coloration approaching that termed warning.

Bird enemies.—Stomach examination has revealed termites in the dietary of 38 species of nearctic birds. The occasions when termites are available to most birds are infrequent, but when they come, the insects usually are in great abundance. Accordingly large numbers are eaten, and single stomachs have yielded as many as 215 termites in the case of a nighthawk, 400 in that of a pileated woodpecker, and 1,100 in that of a flicker. The writer has twice observed numbers of English sparrows gobbling up termites upon emergence and Hagen has recorded [1] a case in which 15 species of birds were in attendance on a swarm of white ants, the robins among them so gorging themselves that their bills stood open.

Number of identifications, 129; percentage of identifications among those of all insects, .0677; percentage of species in this group among the whole number of insect species known, .0911.

Other enemies.—Termites are as much sought after by some other animals as they are by birds and even are eaten by man. It has been said that in the Tropics "The flight of the winged termites is a great event in the animal year." [2] In India cockroaches, frogs, lizards, rats, bats, jackals, mongooses, jungle cats, and dogs have been observed [3] preying upon them. In the United States, besides wild birds and domestic fowls, salamanders, frogs, toads, lizards, spiders, centipeds, crickets, robberflies, ants, and beetle larvae prey upon termites. The insects have parasites also among the fungi, protozoa, nematodes, and mites.[4]

Discussion.—The enemies of termites are comparatively well-known, not wholly because they are numerous or active, but also because termites are "economic" insects and have therefore been the subject of considerable study from many points of view. Although

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[1] Hagen, H., Proc. Boston Soc. Nat. Hist., vol. 20, p. 118, (1878-1880) 1881.

[2] Longstaff, G. B., in Shelford, R., Naturalist in Borneo, p. 37, 1916.

[3] Rothney, G. A. J., Proc. Ent. Soc. London, 1918, pp. lxiv-lxvi.

[4] For an account of these miscellaneous enemies, see Snyder, T. E., U. S. Nat. Mus. Bull. 108, pp. 116-118, 1920.

they have protective adaptations of various kinds, termites are eaten freely by numerous animals. Birds prey upon them eagerly when occasion offers, but on the whole not out of proportion to the abundance of the insects.

ORTHOPTEROIDEA

Group	Number of identifications	Percentage of identifications among those of all Orthopteriodea	Percentage of species in this group among the whole number of nearctic Orthopteroidea [1]
Unidentified	6,809	35.8310	...
Dermaptera	18	.0947	1.8494
Paleoptera	117	.6157	4.4194
Dictyoptera	58	.3052	2.1136
Cheleutoptera	26	.1368	1.4531
Diphtheroptera	5,695	29.9688	69.3525
Orthoptera	6,280	33.0472	20.7397

DERMAPTERA (EARWIGS)

All earwigs have pincer-like appendages at the end of the abdomen, the function of which is little understood. One suggestion is that they are for defense, but in what way they might serve for this purpose is not clear. Many earwigs have glands producing a fetid secretion. These insects in general are inconspicuous but a few have brilliant colors. Earwigs are seldom met with in the United States and the record of their bird enemies is short—18 identifications in the stomachs of 15 species of birds. Percentage of identifications among those of all insects, .0094; percentage of species in this group among the whole number of insect species known, .1301. That this result is merely a reflection of the infrequency of earwigs is indicated by the fact that in Great Britain where these insects are much more common, the records of birds eating them are proportionately higher. Thus Robert Newstead,[2] treating of a mere fraction of our number of stomach examinations gives records for seven species of birds and notes that 23 earwigs were found in the stomach of a green woodpecker and 40 in that of a whimbrel. F. V. Theobald and William McGowan in their report[3] on "The Food of the Rook, Starling and Chaffinch," note that each of these birds prey upon earwigs, and

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[1] Computed from Scudder, S. H., Catalogue of the described Orthoptera of the United States and Canada, Proc. Davenport (Iowa) Acad. Nat. Sci., vol. 8, 101 pp., 3 pls., 1900.

[2] Suppl. Journ. Board Agr. [London], vol. 15, no. 9, Dec., 1908.

[3] Suppl. Journ. Board Agr. [London], vol. 15, no. 15, May, 1916.

W. E. Collinge records[1] five species of birds as feeding on these insects. Among other enemies of earwigs are batrachians, of which 6 species of salamanders, and 16 of frogs have been recorded in the United States as feeding on Dermaptera. The earwigs are neither an extensive nor an abundant group of insects and we should not expect to find them preyed upon by insectivorous animals to any marked degree.

CHELEUTOPTERA (WALKINGSTICKS)

Protective adaptations.—As their vernacular names, stick and leaf insects imply, these insects bear resemblances to objects in the vegetable kingdom that have caused them to be considered as having reached the very acme of protective adaptation. "Some," says David Sharp,[2] "look like sticks, or stems of grass; some have a moss-like appearance, while others resemble pieces of lichen-covered bark. The members of the tribe Phyllides are leaf-like. A certain number . . . are covered with strong spines, like thorns. Some, if not all, of the Phasmidae," he adds, "have the habit of ejecting a stinking fluid that is said to be very acrid" (264). The eggs of walkingsticks are peculiar in shape and sculpturing and many of them resemble seeds.

Bird enemies.—Records of walkingsticks in the identifications of bird food here discussed total 26, and pertain to 18 species of birds. The crow blackbird heads the list with seven captures.

Percentage of identifications among those of all insects, .0136; percentage of species in this group among the whole number of insect species known, .6507.

Other enemies.—Predacious hemiptera, mantids, lizards, and spermophiles may be mentioned among the enemies of stick-insects, and ichneumon flies are said to parasitize both adults and eggs.

Discussion.—The apparent discrepancy in the indices of frequency of occurrence of stick-insects in bird food and in nature is to be explained by the relatively poor representation of this group in the United States, we having but 11 species. If we grant that the form, color, and sluggishness of these insects has a protective value in relation to predators, we must admit that these qualities facilitate also the destruction of the walkingsticks by grazing animals, which engulf indiscriminately huge mouthfuls of browse together with any insects thereon that are not agile enough to beat an instantaneous retreat. In the same way if the resemblance of the eggs to seeds is to be

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[1] The food of some British wild birds, 1913.

[2] Cambridge Nat. Hist., vol. 5, p. 260, 1910.

regarded as significant, it would appear to put these objects in jeopardy, as the proportion of the food of birds and other animals made up of seeds is immensely greater than that composed of insect eggs. Judged as a protective adaptation, therefore, this case would seem to fit the old adage of "out of the frying-pan into the fire." Two authorities who have paid special attention to the subject, however, conclude that the resemblance to seeds of these eggs has no bionomic importance.[1]

SALTATORIA (GRASSHOPPERS, LOCUSTS, CRICKETS)

Owing to the facts that identifications in hundreds of cases were not carried as far as they might have been, and that it is impracticable to tabulate them by families, we put all the leaping orthoptera together, rather than consider separately the two orders into which these forms are usually grouped.

For convenience part of the tabulation of identifications is here repeated in revised form.

Identifications of Saltatoria

Group	Number of identifications	Percentage of identifications among those of all Saltatoria
Diphtheroptera		
(Grasshoppers, locusts)	5,695	30.3185
Orthoptera (Sens. str.)		
(Green grasshoppers, katydids, crickets).	6,280	33.4328
Saltatoria		
(Further unidentified)	6,450	34.3378
Orthopteroidea		
(Further unidentified, no doubt Saltatoria)	359	1.9112
All Saltatoria	18,784	

Protective adaptations.—A. R. Wallace says:[2] "The whole order of Orthoptera, grasshoppers, locusts, crickets, etc., are protected by their colours harmonising with that of the vegetation or the soil on which they live, and in no other group have we such striking examples of special resemblance."

With special reference to American insects, A. P. Morse makes the following statement:[3] The coloration

> is, with few exceptions, highly sympathetic in character, harmonizing with or resembling very closely, often to a marvelous degree, the background of the

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[1] Sharp, D., Willey Zool. Results, Cambridge, 1898, p. 75-94.

Severin, H. H. P., Ann. Ent. Soc. Amer., vol. 3, pp. 83-92, 1910.

[2] Natural selection and Tropical nature, p. 46, 1891.

[3] Proc. Boston Soc. Nat. Hist., vol. 35, no. 6, p. 244, 1920.

insect's environment. Earth tints, rock and sand textures, the infinitely varied browns, greens, and grays of living and dead vegetation, yellow, orange, rose, and silvery white are all represented in spots and streaks, the effect being to merge the insect indistinguishably into its background while at rest, thus shielding it in a very high degree from the observation of its foes. These colors are of great protective value at the present time, natural selection continually acting to preserve and perfect them, but though highly protective in character, they are without doubt primarily due to physiological processes and influences as yet imperfectly understood.

This type of coloration is admirably illustrated among New England species by the Seaside Locust and Sand Locust which live on sandy backgrounds, the Snapping and the Ledge-loving Locusts on rock habitats, the Coral-winged and the Clear-winged Locusts in fields; and in the plant-perching species the Pine-tree Locust with its background of lichened pine bark, the Red-legged and the Two-striped Locusts among the yellowish green of herbage, and other species of *Melanoplus*,—*M. mancus, M. fasciatus*, etc.,—whose darker tints resemble those of fallen leaves from the *Vaccinium* thickets amid which they live.

One who has not watched these creatures out of doors can appreciate to but a slight degree the effectiveness of sympathetic coloring as a means of concealment. Let him but try to pick out from its background immobile grass-green Cone-head, leaf-brown Shield-backed Grasshopper, or any of the Locusts just mentioned, and he will realize as never before the importance to the defenceless insect of Mother Nature's protective mantle of invisibility.

The wing-covers of certain katydids and allied forms are very leaflike, the resemblance being carried so far in certain cases, it is said, that the spots like those due to fungi and the tracks of leaf-mining insects are closely imitated.

The leaping powers of the Saltatoria, remarkably developed in some forms, must be classed as defensive; most of these insects have powerful mandibles also, a few of them indeed being markedly carnivorous.

Locusts of the subfamily Oedipodinae, especially, have another adaptation some consider protective. For instance E. B. Poulton says:[1] " The brightly coloured hind wings of many moths (*Catocala*, *Tryphaena*, etc.) and grasshoppers (*Oedipoda*, etc.) which flash out conspicuously when the insect becomes active, and disappear equally suddenly when it alights, probably serve, as Lord Walshingham has suggested [Proc. Ent. Soc. Lond. 1890, pp. l-liii], to confuse a pursuing enemy." It may be noted that Morse considers these colors as recognition markings.

Finally, among protective adaptations, certain Orthoptera are said to mimic other insects, as for instance Membracidae, Phasmidae, ants,

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[1] Essays on evolution, p. 303, 1908.

and beetles, though we have none of these forms in the United States; the mole crickets and a few other forms have special fetid secretions, and the brown drop that so many orthoptera exude from the mouth when captured is said to be a protective device.

Bird enemies.—Nearly a tenth of all the identifications of insects in bird stomachs are of leaping orthoptera. To name the birds that eat grasshoppers is to name all birds not strict vegetarians. When these insects are abundant, birds of all sizes turn their attention to the Orthoptera and for the time being make them a staple food. As a constant article of diet also, they are important to many birds. The number of identifications of Saltatoria from stomach contents was 50 or more in the case of over 20 species of birds, more than 100 in 22 additional species, more than 200 in 10 other species, in excess of 1,000 in two cases, namely, of the common crow, and the meadowlark, and more than 1,500 for the starling and crow blackbird. Expressed in proportions of the annual subsistence of certain birds most fond of the insects, we find according to Biological Survey records that Saltatoria compose 21.29 per cent of the food of the western bluebird (based on the examination of 217 stomachs), 22.01 per cent for the eastern bluebird (855); grasshopper sparrow (170), 23 per cent; the eastern and western meadowlarks combined (1,514), 26.08 per cent; the Arkansas kingbird (109), 27.76 per cent; Franklin's gull (93), 43.43 per cent; and the scissor-tailed flycatcher (129), 46.07 per cent.

These are illustrations of the relations of birds to leaping orthoptera under normal conditions. When species of these insects become excessively abundant as they frequently do, the gathering of the bird clans to feed upon them is proverbial. No instance is more celebrated than that studied by Prof. Samuel Aughey during an invasion of the Rocky Mountain locust in Nebraska. He found locusts in the stomachs of no fewer than 172 species of birds varying in size from the tiny hummingbirds up to the largest hawks, and including such usually exclusively vegetarian birds as the passenger pigeon and mourning dove. Professor Aughey was eye-witness also to 33 additional species of birds preying upon the locusts.[1]

For a modern illustration of the same phenomenon, we may cite a brief investigation made by the Biological Survey during a grasshopper outbreak in South Dakota in 1920. Out of the 26 species of birds collected, representatives of 24 had been eating the hoppers; of 19 species every bird collected had taken grasshoppers, and for the

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[1] Notes on the nature of the food of the birds of Nebraska. First Ann. Rep. U. S. Ent. Comm. (1877), App. II, pp. [13]-[62], 1878.

species eating them, the insects composed from 40 per cent to 90 per cent of the total food.

In another study of the effect of birds upon a severe irruption of grasshoppers in California, H. C. Bryant estimated that birds were destroying *daily* more than 120,000 grasshoppers per square mile in the infested area.[1]

In countries, notably Africa, where migrations of large numbers of locusts are of regular occurrence, various species of birds have more or less specialized in following these flights and feeding on the migrants, so much so, in fact, as to earn for themselves the name of locust birds.[2]

Number of identifications of Saltatoria, 18,784; percentage of identifications among those of all insects, 9.6506; percentage of species in this group among all insect species known, 1.6398.

Other enemies.—All stages of the Saltatoria are much sought for by various animals. The larvae of Cantharid beetles and of bee flies (Bombyliidae) subsist upon the eggs, as do also certain mites, and the egg masses of some species are dug up and devoured by various mammals, as moles, mice, spermophiles, and skunks. The nymphs and adults fall a prey to vertebrates of nearly all sizes and descriptions, ranging from bears, through coyotes, foxes, badgers, skunks, civetcats, weasels, wood rats, squirrels, spermophiles, moles, shrews, and mice, to lizards, tortoises, snakes, salamanders, frogs, and toads. If any seek to escape their land enemies by jumping into the water, they are snapped up by fishes. The adults are destroyed in large numbers by parasitic diptera and hymenoptera. Most of the predatory invertebrates are fond of grasshoppers, this being particularly true of dragonflies, tiger beetles, ground beetles, robber flies, digger wasps, and spiders. In the case of the latter, S. W. Bilsing found grasshoppers in 20 per cent of the webs of *Epeira trifolium*, in 35 per cent of those of *Argiope riparia*, 44 per cent of those of *A. trifasciata*, and in 53 per cent of those of *Agalena naevia*. Grasshoppers are parasitized by nematodes and protozoa and are subject to bacterial and fungal diseases, which last are said sometimes to destroy them " in myriads."

Discussion.—The Saltatoria or leaping Orthopteroidea are prominent in the insect world more through average large size and the

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[1] Univ. California Publ. Zool., vol. 11, no. 1, pp. 16-17, Nov. 1, 1912.

[2] See Badenoch, L. N., True tales of the insects, pp. 127-128, 1899; La Baume, W., Beihefte z. Tropenpflanzer, vol. 11, no. 2, pp. 65-128, Apr., 1910; Agr. Journ. Cape of Good Hope, vol. 18, pp. 820-833, 1901; vol. 19, pp. 99-106, 165-171, 248-262, 1901; vol. 28, pp. 364-366, 1906; Trans. South African Phil. Soc., vol. 1, p. 193, 1880.

abundance of individuals rather than through abundance of species. Almost everywhere in the United States that herbage is plentiful, grasshoppers in the late summer rattle away from the approaching pedestrian in such numbers as to form a veritable rolling barrage of insect projectiles. No insects are more conspicuous in action, yet on close examination the observer finds that the individual hopper is dull and obscure in color. The point is worthy of attention because it proves that the formula that abundant and conspicuous insects tend to be warningly colored and inedible has numerous exceptions. None of our grasshoppers of the northeastern United States are warningly colored, unless the Oedipodinae with brightly and contrastingly colored hind-wings, and in many instances a loudly rattling flight, may be so considered. Whatever their status in adaptation theories such genera as *Arphia, Dissosteira,* and *Hippiscus* seem to supply their full quota to the food of birds and other predatory enemies. On the other hand some of the "sympathetically" colored species mentioned in the remarks on adaptations quoted from Morse are the very bread of avian diet. Grasshoppers of the genus *Melanoplus* for instance were identified 543 times among the records here considered, and were found in the stomachs of more than 85 species of birds. These and other Acridids are taken not only frequently but often in quantity, for instance, the remains of no fewer than 123 specimens were found at one time in the stomach of a common crow and 340 in that of a Franklin's gull. Judging from the records, the green grasshoppers or Locustidae and the crickets also bear their appropriate burden of predatory attack.

The imposing total of 17,641 identifications of Saltatoria, more than a tenth of all insect determinations, shows what an important staple for the birds these creatures are, and how poorly their prevailing elaborately cryptic coloration succeeds in foiling their enemies. They are preyed upon voraciously not only by birds but by a host of other animals, but the effect of the attacks of predators, parasites, and diseases together in no way suggests that the Saltatoria are a disappearing race. Despite persecution, these insects abound and the reasons are high fecundity and the great surplus of food available to them; these are substantial realities and outweigh immeasurably those airy intangibilities classed as protective adaptations.

PALEOPTERA (ROACHES)

Protective adaptations.—The comparatively few native species of roaches in the United States are secretive and nocturnal in habit but appear to have no other special protective adaptations. The introduced species live chiefly in structures of man hence have little relation to the indigenous fauna.

Bird enemies.—Thirty-six species of birds share the 117 identifications of roaches in the food of nearctic birds. The number of records was 10 or more in the case of four species of birds, and the number of specimens eaten was as high as 10 in two instances but usually was less.

Percentage of identifications among those of all insects, .0613; percentage of species in this group among the whole number of insect species known, .3123.

Other enemies.—Roaches seem to be more or less regularly eaten by toads, frogs, the armadillo, spiders, rats, scorpions, and wasps. They have specific parasites among the Evaniidae.

Discussion.—Owing to the poverty of the roach fauna of the United States, research here is not likely to throw much light on relations of these insects and their adaptations to predators. Tropical species are said to resemble various other organisms, including isopods, myriopods, longicorn, and coccinellid beetles, and hemiptera of the family Miridae. But since all of these models themselves are freely eaten by predators, the significance of the resemblances is hardly that usually attributed. In the United States natural enemies would seem to be proportional to the scanty population of native roaches.

DICTYOPTERA (MANTIDS)

Like the roaches, the mantids of the United States are few in number and do not exhibit the unusual modifications displayed by some of the tropical representatives of the group. The principal defenses of our species must be their comparatively large size among insects and their highly predatory nature. However, these characteristics are of little avail against still larger predators and we find these insects taken by birds in numbers probably bearing no distant relation to the frequency of mantids in the country. Number of identifications, 58; percentage of identifications among those of all insects, .0304; percentage of species in this group among all insect species, .2082 (for the world, of course). The number of species of birds concerned in the records here cited is 21. Mantids are eaten also by lizards.

CORRODENTIA (PSOCIDS)

The Psocidae, which include the booklice seen in houses, are delicate and minute insects. Many of the out-of-door species are winged and the wings bear color patterns which may assimilate the insects more or less to the bark surface upon which many of them dwell. These insects mostly below the size of food objects ordinarily taken by birds were identified 17 times in the stomachs of nine species of birds. In one case, that of a chimney swift the stomach contained hundreds of specimens, gleaned no doubt from a swarm on the wing.

Percentage of identifications among those of all insects, .0089; percentage of species in this group among the whole number of insect species, .0780.

MALLOPHAGA (BITING LICE)

The only opportunity birds have to get these usually minute insects is to capture those parasitic on their own bodies, or in the case of raptorial birds to engulf some with their prey. Apparently either of these occurrences is rare; six records for as many species of birds being all included in the present tabulation. Percentage of identifications among those of all insects, .0031; percentage of species in this group among all insect species, .3383.

SIPHONAPTERA (FLEAS)

Only a single instance of a flea being eaten by a bird has thus far come to light; the opportunities for getting these small agile insects must be very few since our native birds are parasitized by fleas to only a very slight extent. That fleas are in no way distasteful (as food) to some of their hosts is evident to anyone who has observed dogs, monkeys, and other animals in their persistent and often successful search for these pests.

Percentage of identifications among those of all insects, .0005; percentage of species in this group among all insect species, .0130.

THYSANOPTERA (THRIPS)

Protective adaptations.—Some are contrastingly black and white colored and the immature stages of many are red. It is doubtful however if these colors have any warning significance. The small size and secretive habits of these insects doubtless are the most effective factors in restricting predation upon them.

Bird enemies.—No identifications of thrips appear in the analyses of the stomach contents of nearctic birds here reported upon. Wetmore reports a thrips from the stomach of a hummingbird (*Anthracothorax viridis*) from Porto Rico. (Bull. 326. U. S. Dep. Agr., p. 73, 1916.)

Other enemies.—Thrips are eaten by small predacious hemiptera, especially Anthocoridae, and egg parasites are known. Hamilton

(Copeia, 1930, p. 45) says of 400 young toads examined, "Thrips formed 10.1 per cent of the food, but were found in all but a few stomachs. These small insects appear to be a staple article of diet for young *Bufo*."

Discussion.—Thrips are too small for most birds to notice, but considering our ignorance of the subject, the notes on enemies given indicate that they have foes, the character and number of which, probably as in other cases, are regulated largely by the factor of availability.

RHYNCHOTA (BUGS, CICADAS, LEAFHOPPERS, SCALE INSECTS)

For the reason that the term Hemiptera in a broad sense was used for about one-fourth of all the identifications of Rhynchota, it is not practicable entirely to separate Heteroptera and Homoptera. However the identifications of these groups are distributed as far as possible to families in the tables presented. In using these tables, it should be kept in mind that could the incomplete determinations have been distributed, the figures would average about a fourth higher throughout.

Protective adaptations.—The popular expression 'a nasty bug' undoubtedly has reference, in most instances, to insects of this order, many of which produce scents disagreeable to human senses. Theorists have assumed these must also be repulsive to animal predators, a doctrine briefly stated in the following quotation from E. B. Poulton: "The Heteroptera (Hemiptera) are obviously, as a whole, a specially protected group, commonly defended by taste or smell from large numbers of insect-eating animals."[1]

A great series of Heteroptera are more or less aquatic in habit and thus are screened from the attacks of purely terrestrial enemies. Some are very active, as the Saldidae and many Miridae; some are said to be "mimics," as for example immature Nabidae resembling ants and certain Reduviidae resembling wasps.

Mimicry, so-called, is exemplified among the Homoptera, also, as some Fulgoridae are considered to resemble Lepidoptera in appearance. The Membracidae with a host of bizarre forms, are thought to present cases of mimicry to ants, and of resemblance to thorns and seed pods of plants. One author further remarks: "Evidently the strong pronotal processes, which are often sharp and hard enough to pierce the skin if the insect is seized suddenly, are unpalatable and irritating."[2] Quoting Poulton again (op. cit., p. 4): "Allusion must

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[1] In Buckton, G. B., A monograph of the Membracidae, separate, p. 3, 1903.

[2] Funkhouser, W. D., Mem. 11, Cornell Univ. Agr. Exp. Sta., p. 417, June, 1917.

be made to the special and curious defence by a waxy secretion which is common in the Homoptera. The method may be compared to the defensive silken walls of the cocoon in other insects, while the long trailing filaments of wax borne by certain species of Homoptera may play the same part as the 'tails' on the hind wings of many Lepidoptera, or the 'tussocks' of hair on some of their larvae—all these probably acting as directive structures which divert the attention of an enemy from the vital parts."

Many plant lice have the waxy filaments alluded to by Poulton, while most of them exude special secretions from the cornicles, supposed to be protective. Leafhoppers of various groups have been thought to resemble color or structural details of plants they frequent, and as for scale insects, their small size, waxy secretions and great resemblance to the bark upon which they rest, have given them high rank among the theoretically protected insects. Indeed they have been thought well-nigh immune to attack and one author has intimated that birds never eat scale insects. (Smith, J. B., Proc. State Hort. Soc. N. J., vol. 29, p. 90, 1904.)

Bird enemies.—Below are tabulations of the identifications of Hemiptera in the stomach contents of nearctic birds followed by supplemental comment. Comparative percentages are not given for the plant lice, scale insects, and mealybugs as these have not been catalogued with the same degree of thoroughness as the other groups.

Total number of identifications of Hemiptera, 22,395; percentage of identifications among those of all insects, 11.7301; percentage of species in this order among those of all insect species known, 8.5899.

The Corixidae, although they spend practically all of their existence in water and usually on the bottom, do not thereby secure immunity from bird enemies.

Like other hemiptera, however, they are supposed to be specially protected, one author saying:

> As to the function of the stink-apparatus in the adult *Corixa,* there is no need to look beyond defence. The insect frequently leaves the water, and it is then exposed to all the dangers met with by the land Heteroptera. Also there is no reason to doubt that the odoriferous secretion is equally efficacious against enemies in water.[1]

Results indicate that this efficacy is nothing remarkable; indeed it is a fallacy to suppose that so abundant and accessible a group does not pay due toll to predators. The number of species of birds that

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[1] Brindley, Maud D. Haviland, On the repugnatorial glands of Corixa, Trans. Ent. Soc. London, vol. 77, p. 13, 1929.

Identifications of Rhynchota

Group	Number of identifications	Percentage of identifications among those of all Rhynchota	Percentage of species in this group among the whole number of nearctic Rhynchota [1]
Unidentified	5,650	27.5325	...
Heteroptera (further unidentified)	389	1.8956	...
Scutelleridae	187	.9112	.8673
Cydnidae	232	1.1305	1.5677
Pentatomidae	5,582	27.2011	5.5037
Coreidae	395	1.9248	4.1361
Aradidae	15	.0731	2.0014
Neididae	17	.0828	.2668
Lygaeidae	524	2.5334	2.8353
Pyrrhocoridae	18	.0877	.7338
Tingitidae	66	.3216	2.3349
Enicocephalidae	...	...	.0667
Phymatidae	19	1.0926	.4003
Reduviidae	633	3.4846	3.7692
Hebridae	2	.0097	.1334
Mesoveliidae	16	.0780	.0334
Nabidae	163	.7943	.7005
Cimicidae	2	.0097	.1334
Anthocoridae	3	.0146	1.1007
Termatophylidae	...	...	.0334
Miridae	518	2.5242	14.8101
Isometopidae	...	...	.1334
Dipsocoridae	...	...	.1001
Schizopteridae	...	...	.0334
Hydrometridae	22	.1072	.0667
Gerridae	228	1.1110	.6671
Veliidae	32	.1559	.6004
Saldidae	74	.3606	1.0674
Notonectidae	327	1.5935	.6004
Naucoridae	306	1.4911	.4336
Nepidae	40	.1949	.2668
Belostomidae	326	1.5886	.6671
Gelastocoridae	3	.0146	.2001
Ochteridae	...	...	.1001
Corixidae	1,391	6.7783	2.0347
Homoptera (further unidentified)	107	.5214	...
Cicadidae	556	2.7094	2.7685
Cercopidae	102	.4970	.8673
Membracidae	960	4.6781	6.2042
Cicadellidae	1,435	6.9927	25.0837
Fulgoridae	59	.2875	11.9414
Psyllidae	122	.5945	4.7365

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[1] Computed from Van Duzee, E. P., Catalogue of the Hemiptera of America north of Mexico, excepting the Aphididae, Coccidae and Aleurodidae. Univ. California Publ. Ent., vol. 2, 902 pp., 1917.

feed upon them shown by the present tabulation is 85 and the number of specimens taken at a meal ran over 200 in several cases, and up to 1,300 in one instance (eared grebe). The Belostomidae or giant water bugs, including the largest of North American Heteroptera, have strong, grasping forelegs and a stout beak which readily pierces the skin of man, making an aching, evidently envenomed wound. Notwithstanding these characteristics they do not escape the birds. Fifty-three species are on our list of captors, ducks, herons, and the like preponderating; in two cases, both herons, as many as 10 specimens were found in a stomach at one time. The Notonectidae again are sharply biting and exceedingly active under-water bugs; but the larger types are eaten by no fewer than 44 species of birds, sometimes in considerable number (30-57), while the little crawling and obscure *Plea* were identified in 60 stomachs of 12 species of birds, in numbers up to 40 in a single instance. The Gerridae, so very active on the water surface, fall a prey to at least 49 kinds of birds, sometimes being taken in considerable numbers (20-40). The Miridae or plant bugs are agile and rapid in their movements and of great variety in form and color, but corresponding with their abundance and wide distribution, we find them preyed upon by 108 species of birds. The Anthocoridae and Cimicidae, both odoriferous families, seem poorly represented in our tables, but from their habits we should hardly expect the latter to be found at all, while most Anthocoridae also live largely hidden lives. We have found Nabidae in the stomachs of 52 species of birds, Emesidae in 10, and Reduviidae in 115; these highly predatory forms therefore seem to have bird enemies about in proportion to their abundance.

There are only a few species of Pyrrhocoridae in the United States and none of them are abundant; hence the 18 captures by nine species of birds are perhaps not below proportion; while the relations of birds to the Lygaeidae shows again that an abundant and diversified group is sure to be frequently taken by a large variety of birds. In this family may be specially mentioned *Myodocha serripes*, a bug with an extraordinarily long neck, for what purpose is unknown; at any rate it is one of the most bizarre of the group in our area, but it is eaten by more than 20 species of birds and no fewer than 27 specimens have been found in a single stomach (purple martin). The large red and black *Lygaeus* species were taken by 14 species of birds, and the superabundant chinch bug (*Blissus leucopterus*), frequently observed in prodigious numbers, by 29. Three species of birds, the bobwhite, meadowlark, and brown thrasher, had records of a hundred or more chinch bugs at a meal. These facts contrast strongly with the statement that "Very few birds prey upon it because of its repulsive smell and taste. It is questionable whether any of them are fond of it." (Garman, H., Bull. 74, Ky. Agr. Exp. Sta., p. 56, May, 1898.) In the series of Heteroptera composing the Coreidae and the groups aggregated as the Pentatomidae or Pentatomoidea, we have the typically stinking bugs. Practically all of them have powerfully scented secretions usually of a character obnoxious to man, but it is not evident that they are equally so to birds. Some of our Coreids (*Thasus*) are too large for most of our birds to prey upon, but those of the next rank in size are more or less freely taken, as *Acanthocephala* by 12 species, in numbers as high as 14-22 by Franklin's gull; and the various species of *Leptoglossus* by 16, 10-15 individuals at a meal by the same gull; Alydinae, nearly as large and equally smelly, are preyed upon by 21 kinds of birds. All Pentatomids are eaten so freely that it is difficult to pick the most representative examples. However, to begin, let us consider *Podisus,* a predacious, but nevertheless highly scented genus; it has been found in the stomachs of 29 species of birds, the most remarkable record being for a bird not included in these tabulations, namely a black duck collected in Maine, which had in its gullet alone 525 specimens of *Podisus sereiventris.*

One of the largest and most highly scented stink bugs of our fauna (*Acrosternum hilaris*) was found in the stomachs of 37 species of birds, in number up to 26 in one instance (purple martin), while for our typical and most abundant genus (*Euschistus*) 62 avian predators are known. The number of specimens found in a stomach exceeded 10 in a number of cases, and in one, that of a Franklin's gull, reached 175. The little Thyreocoridae, polished black with touches of yellow on the costa, were found in the stomachs of 65 kinds of birds, and the Scutelleridae in 60.

E. A. D'Abreu in his report on "Some insect prey of birds in the Central Provinces" [of India] (Rep. Proc. Third Ent. Meeting, Pusa, 1919, Vol. iii, p. 866, 1920) says "Pentatomids seem a favorite diet with birds." He gives notes also on bird enemies of 16 other families of Rhynchota.

The only report on the food habits of birds in the American Tropics, namely, the "Birds of Porto Rico" (Bull. 326, U. S. Dep. Agr., 1916), by Alexander Wetmore, in the accounts of the species throughout shows Hemiptera to be taken in due proportion.

The Cicadidae are chiefly large insects, a factor which to some extent must limit the number of their bird enemies; however the list here drawn upon shows 87 species and there are four records for one of our smallest birds, the house wren. Some of the larger birds devour considerable numbers of the smaller cicadas, for example, 30 *Okanagana rimosa* were found in a nighthawk's stomach and from 19 to 41 *Tibicina septendecim* in each of several crow stomachs. It is of interest in this connection that adult as well as immature domestic fowls have been killed by crop-binding due to eating too many cicadas. (Weekly News Letter, U. S. Dep. Agr., vol. 6, no. 46, p. 14, June 18, 1919.) Wild birds, however, not only take large numbers of cicadas, but feed on them steadily day after day when the chance comes. The English sparrow and the crow blackbird are notable examples of this and it has been concluded by entomologists that broods of the periodical cicada issuing in parks and other places, where exposed to concentrated attacks of these species, are doomed to extinction. (Smith, J. B., Economic entomology, pp. 142-143, [1896]; Marlatt, C. L., Bull. 90, U. S. Dep. Agr., p. 10, 1894.)

Our records do not show whether any immature Cercopidae (spittle insects) are eaten by birds, but the adults are taken by 41 species. One chimney swift had eaten about 100 cercopids of the genus *Clastoptera*. Despite the numerous defenses they are said to have, Membracidae were eaten by no fewer than 136 species of birds represented in the present tabulation and in numbers up to 26 individuals in a single stomach. They have been found in 15 or more stomachs of each of the following species: Least, great-crested and ash-throated flycatchers, wood pewee, meadowlark, Brewer's blackbird, Bullock's oriole, English sparrow, cliff swallow, red-eyed, solitary, and warbling vireos, bush-tit, and ruby-crowned kinglet. The tree hoppers identified belong to 21 different genera, indicating that no partiality is shown. Membracids with the most prominent horns and spines of any in our fauna, such as those of the genera *Campylenchia, Platycotis, Thelia, Ceresa,* and *Platycentrus,* are taken with the rest. During stomach examinations 175 kinds of nearctic birds have yielded leafhoppers (Jassidae sens. lat.) and 10 or more stomachs of no fewer than 35 species have disclosed them. In a number of cases from 20 to 50 leafhoppers were found in single stomachs and in one case (barn swallow) a thousand.

The fulgorid fauna of the United States is scanty and our records of birds feeding on these insects correspond. Beyond the fact that they are well distributed through the various groups of the family and pertain to 18 species of birds, there is little of special interest concerning them. Some lesser yellow-legs had eaten from 50 to 400 each. The Psyllidae were found in the stomachs of 46 kinds of birds and the Aphididae in 86. Cases are known in which the former have been devoured very extensively by birds, an entire orchard having been cleared of the pear psylla by nuthatches. (Zool. Bull. Pennsylvania Dep. Agr., vol. 3, p. 79, July, 1907.) Plant lice were found in large numbers in the stomachs of some birds, up to 200 or more in each of five species of the finch family, 300 or more in three of them (pine siskin and two goldfinches), about 650 in the stomach of a nighthawk and 1,600 in that of a wood duck. On a 200-acre farm in North Carolina, birds were found to be destroying more than a million grain aphids daily. (McAtee, W. L., Yearbook, U. S. Dep. Agr. (1912), pp. 397-404, 1913.) Aleurodidae have not as yet been identified from stomachs of nearctic birds; possibly some may have been confused with scale-insects. The latter, notwithstanding deprecatory statements that have been made relative to birds as predators upon them, have been found in the stomachs of 88 species of nearctic birds. No fewer than 100 *Eulecanium cerasifex* were found in the stomach of a rose-breasted grosbeak, 300 *Margarodes* in one of a scaled quail, 304 *Saissetia oleae* in that of a black-headed grosbeak and 200, 700, and 800 of the same scale, respectively, in three stomachs of the pine siskin.

Other enemies.—Salamanders, toads, and frogs are recorded in the Pennsylvania reports as feeding upon both Heteroptera and Homoptera, as are also the common swift lizard (*Sceloporus undulatus*) and the copperhead (*Agkistrodon contortrix*) and the hog-nosed snake (*Heterodon platirhinos*). The same source credits five species of turtles with eating Heteroptera and one with devouring Homoptera. Munz found that all the common frogs feed on Hemiptera about as freely as upon any other insects, and Garman found bugs in 6 out of 20 stomachs of the common toad. Winton reports the Texas horned lizard (*Phrynosoma cornutum*) as eating stink bugs.

Aquatic hemiptera, particularly Corixidae, are eaten by most freshwater fishes, while scattering representatives of the terrestrial families are taken now and then as opportunities occur. Forbes records from fish stomachs representatives of 14 families of Heteroptera and three of Homoptera. Among mammals, the common mole is known to take leafhoppers, chinch bugs, and other species; shrews do not entirely neglect Hemiptera; the nine-banded armadillo devours Cydnidae and Pentatomidae.

Insect enemies of Hemiptera include both nymphal and adult dragonflies, the former getting considerable numbers of Corixidae and the latter representatives of various families. Robber flies feed freely upon Hemiptera, ground beetles and ladybirds devour them, and the

Nyssonidae, Mimesidae, and Crabronidae, among predacious hymenoptera, prey more or less selectively upon Homoptera; in the eastern States a large Sphegid wasp is a special foe of cicadas. Other enemies of cicadas include dragonflies, wasps, predatory beetles and bugs, mantids, spiders, mites, hymenopterous and dipterous parasites, fishes, snakes, turtles, squirrels, badgers, armadillos, skunks, moles, and fungi. Spiders consume many Hemiptera of a wide variety and are credited with being among the most important natural enemies of leafhoppers. The latter insects are heavily parasitized by the *Dryinidae,* and by at least five other families of Hymenoptera, by *Pipunculidae,* and Strepsiptera; and are preyed upon by larvae of Chrysopidae, and by Coccinellidae, Reduviidae, and certain other insects.

The Pyrrhocoridae said to be specially protected are preyed upon by spiders, pseudoscorpions, thrips (the eggs), tachinid flies, reduviid bugs, and lizards. The Coreidae have special parasitic foes among the Tachinidae; while the order of Rhynchota in general is subject to hymenopterous parasites, the abundance of plant lice and scale insects in particular depending to a large degree in many cases upon the relative numbers of these destructive foes. Lycaenid caterpillars feed upon aphids, coccids, jassids, and membracids. A page would scarcely suffice to list the numerous enemies of plant lice which include, besides parasites, coccinellid, lampyrid, syrphid, hemerobiid, and chrysopid larvae, in addition to adult ladybird beetles, assassin bugs, and other insects, mites, and spiders. Fungi are known to destroy, at times, large numbers of hemiptera, among which may be mentioned plant lice, scale insects, mealybugs, and the chinch bug.

Discussion.—Despite their malodorous secretions and other "protective devices" there can be no doubt that Rhynchota are taken fully in proportion to their abundance by nearctic birds, and the evidence is that their other enemies are numerous and effective. If we consider the most pronouncedly repugnant species found in the United States, such as the harlequin bug (*Murgantia histrionica*) and the squash bug (*Anasa tristis*),[1] we find that severe infestations of the former have been kept in check by English sparrows (Sherman, F., Bull. North Carolina Dep. Agr., vol. 32, no. 7, p. 21, July, 1911) and that the squash bug has a number of deadly enemies. It has been shown that the volatilized secretions of squash bugs if confined in a glass container are capable of killing toads (Weed and Conradi, Bull. 89, New

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[1] It is worth noting that of these two common and exceedingly malodorous bugs, one is warningly, one obscurely colored. Where is the correlation that theories as to warning colors demand?

Hampshire Agr. Exp. Sta., pp. 21-23, Feb., 1902), and the conclusion was drawn that "toads do not ordinarily devour many of these pests." Perhaps they do not "devour many" of them, nor, with the whole insect world available for them to prey upon, should they be expected to specialize upon squash bugs, but they do eat them, as found by Kirkland (Bull. 46, Hatch Exp. Sta., p. 26, 1897) and also by Biological Survey investigators. Bird enemies also are not lacking, present records showing six species of birds known to feed upon *Anasa tristis* and four upon other species of the genus. The harlequin bug is sometimes heavily parasitized also, while the squash bug has both tachinid and hymenopterous parasites and is subject to a bacterial disease.

Disregarding the "protective adaptations" and reasoning alone from the prevalence of hemiptera, there would be no presumption that these insects would constitute a tenth of the food of any species of birds, yet they actually do contribute 10 per cent or more of the subsistence of the following 12 species in the United States: Nuttall woodpecker (number of stomachs examined 53), percentage of Rhynchota in the food, 14.76 per cent; Scissor-tailed flycatcher (129), 10.17 per cent; eastern phoebe (370), 10.38 per cent; black phoebe (344), 10.56 per cent; crested flycatcher (265), 14.26 per cent; least flycatcher (177), 11.12 per cent; Bullock's oriole (162), 10 per cent; sharp-tailed sparrow (51), 12 per cent; spotted towhee (139), 14 per cent; purple martin (205), 14.58 per cent; barn swallow (467), 15.1 per cent; and rough-winged swallow (136), 14.9 per cent; more than 20 per cent of the food of two birds, namely the black-headed grosbeak (225), 21 per cent, and cliff swallow (375), 26.32 per cent, and more than 30 per cent of the total diet of the violet-green swallow (110), 35.96 per cent.

If the glandular secretions of hemiptera had the repugnatorial, not to say dangerous, qualities attributed to them, there would be no such wholesale preying upon them as is shown in the foregoing data. Descending to milder forms of "protection" as afforded by pointed protuberances and secretions of wax, we find that the "hardihood" of birds (from the selectionist point of view), or in other words their tendency not to be bound by human criteria, is so great that such devices simply do not count.

NEUROPTEROIDEA (DOBSONFLIES, SNAKEFLIES, SCORPIONFLIES, ANT-LIONS, CADDISFLIES)

In the period during which the records of bird food here discussed were obtained, the conception of the group of insects broadly termed Neuroptera has gradually evolved from that of a catch-all for net-veined insects to a restricted group of very few families. Hence many of the determinations (in want of re-examination) cannot be definitely correlated with modern classification. With little doubt, therefore, there has been confusion of records between Neuropteroidea (in the present sense) and some of the orders elsewhere discussed as Agnatha, Mecaptera, and especially Plecoptera. Hence the tabulation figures given are only approximations, and a better conception of the relations of birds to the insects would be obtained by lumping all of the so-called net-veined insects together.

Protective adaptations.—The Neuropteroidea have not been given so much attention by adaptationists as some other groups of insects, but certain supposedly protective features have been pointed out or are suggested by analogy with other described cases. Dobsonflies are large, the larvae and females have powerful biting-jaws, while in some cases the males have enormously developed mandibles of less sturdy construction, and the coloration of the wings of some presents strong contrasts. The latter characteristic is possessed by the Myrmeleonidae also, while their larvae, the ant-lions, have large, strong jaws and an antlike odor. Some Ascalaphidae are said to resemble dragonflies both in appearance and habits; Chrysopidae have vile smells earning them the name of stink flies; and Mantispidae not only have predatory forelegs but are said to be protected by their resemblance to Hymenoptera. (Poulton, E. B., Trans. Ent. Soc. London, 1902, p. 536.) "The well-known cases of Caddice-worms (Trichoptera) are partly for concealment and partly for defence." (Poulton, Colours of Animals, p. 77, 1890.) Some of them resemble snail-shells.

Bird enemies.—While Neuroptera (sens. lat.) have been identified from the stomachs of 56 species of birds there is little object in discussing further this heterogenous assemblage. Sialidae (dobsonflies etc.), despite their average large size and biting powers, were taken by 38 kinds of birds; 58 specimens were found in the stomach of a Bonaparte's gull and from 55 to 93 larvae in three stomachs of lesser scaups and 192 in one of a canvas-back. Snakeflies, of bizarre appearance, and of limited distribution in the United States were identified in the food of 22 species of birds; and Mantispidae, "protected by their resemblance to Hymenoptera," and also by considerable rarity in our fauna, were found in the stomach of 11 species. Stink flies (Chrysopidae) were eaten by 18 kinds of birds, and Myrmeleonidae by 20. *Ascalaphus* was identified but once, quite in keeping with its extreme rarity, and Hemerobiidae 11 times. The figures for identifications are low for scarce or locally distributed groups, but when we come to one of common and general occurrence, the corresponding rise in frequency of capture by birds is apparent at once. The caddisflies, more numerous in species and individuals than all our other Neuropteroidea together, appropriately contribute nearly two-thirds of the total number of records for the group. The number of species of birds feeding upon them is 113, and of these 45 or more had taken the "specially protected" larvae. The number of records of caddisflies determined was 10 or more for 23 species of birds, and more than 20, 30, and 40 in the case of four, three, and three species respectively. The number of specimens taken by single birds exceeded 30 of larvae in a number of instances and ran as high as 207 (in a scaup duck), and of adults reached such figures as 280 and 400 in the case of the nighthawk.

Identifications of Neuropteroidea

Group	Number of identifications	Percentage of identifications among those of all Neuropteroidea	Percentage of species in this group among the whole number of nearctic Neuropteroidea [1]
Neuroptera (sens. lat.)	119	9.0564	...
Megaloptera	167	12.7094	3.5648
Rhapidioidea	54	4.1096	1.6886
Neuroptera (sens. str.)	108	8.2192	32.2706
Phryganoidea	866	65.9061	62.4774
All Neuropteroidea	1,314		

Other enemies.—Forbes reports that neuropteroid larvae compose about 10 per cent of the food of the sucker and catfish families in Illinois; he found caddis larvae in the stomachs of 17 species of fishes. According to various authors, these larvae are an important element in the food of most kinds of trout. Salamanders, frogs, larvae of stoneflies, and parasitic hymenoptera also are enumerated among the enemies of caddis larvae. Forbes found larvae of Sialidae in seven species of fishes, and these are known to be eaten also by frogs and turtles. Chrysopidae have been seen to be eaten by frogs, salamanders, and ants, and they have numerous hymenopterous parasites sometimes destroying inmates of about half of the cocoons. (McGregor, E. A., Can. Ent., vol. 46, pp. 306-308, 1914.) Frogs are recorded also as capturing Mecaptera, as are also lizards and larvae of ant-lions. Robber flies and dragonflies apparently devour any Neuroptera chance throws their way.

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[1] Computed from Banks, Nathan, Catalogue of neuropteroid insects (except Odonata) of the United States, 53 pp., 1907.

Discussion.—It is obvious from the available data on enemies of Neuropteroidea that the small or rare groups have few, the large and abundant families many foes, the result that would be predicted with "protective adaptations" discounted. The group most numerous in species and individuals, namely the caddisflies, has the most enemies, and their larvae, said to be well defended from enemies, form one of the staple elements of the food of fresh-water fishes all over the globe, as well as a favorite prey of aquatic birds.

LEPIDOPTERA (MOTHS, BUTTERFLIES)

Protective adaptations.—In the space that can be devoted in this paper to protective adaptations of Lepidoptera it is impossible to do more than call attention to general aspects of theoretical considerations, since what has been written on the subject would fill many volumes. This flood of literature is due principally to the fact that Lepidoptera have been regarded as the chief examples of the phenomena of warning colors and of mimicry, subjects that have been expounded and discussed at great length.

Warning coloration, it need hardly be stated, designates the conspicuous, often highly contrasted, patterns, which it is held may be assumed with relative impunity by tough, distasteful, or dangerous species. Batesian mimicry is the more or less pronounced resemblance to these species by others supposedly less qualified to cope with the struggle for existence, while Mullerian mimicry is mutual approach in appearance by species all of which belong to "specially protected" groups. As remarked in my 1912 paper, these theories were chiefly built up at a time when there was almost complete ignorance of the actual feeding habits of predacious animals, and attempts to secure evidence on the subject by experiment were in most cases characterized by a singular lack of appreciation of the vital factors involved and of realities in nature.

The following statement by Alfred Russell Wallace gives the gist of the principal nearctic instances of mimicry among Lepidoptera: "In North America, the large and handsome *Danais archippus* with rich reddish-brown wings is very common, and it is closely imitated by *Limenitis misippus,* a butterfly . . . . which has acquired a color quite distinct from that of the great bulk of its allies. In the same country there is a more interesting case. The beautiful dark bronzy-green butterfly, *Papilio philenor,* is inedible both in larva and perfect insect, and it is mimicked by the equally dark *Limenitis ursula.* There is also in the Southern and Western States a dark female form of the yellow *Papilio turnus*, which in all probability obtains protection from its general resemblance to *P. philenor*." (Darwinism, p. 248, 1896.)

Mimicry of another order of insects, the Hymenoptera, is shown by many of the clear-winged moths (Syntomidae and Sesiidae) as adults; and of black-and-yellow ringed larvae, it is said they gain great advantages from resemblance to the justly respected appearance of hornets and wasps.

The majority of adults of Lepidoptera, especially the moths, exhibit in greater or less perfection what is called cryptic coloration, that is resemblance to details of the environment, exemplified by the species that are inconspicuous on bark, old leaves and the like. This style of protective adaptation also is attributed to many larvae and pupae. On this topic Poulton says: "There is no better instance of special protective resemblance than that afforded by the larvae of Geometrae, 'stick caterpillars' or loopers as they are often called. These caterpillars are extremely common and between two and three hundred species are found in this country [Great Britain]; but the great majority are rarely seen because of their perfect resemblance to the twigs of the plants upon which they feed." (Poulton, E. B., The colours of animals, p. 26, 1890.)

This idea is pushed to an extreme by another author as shown by the following quotation relating to the caterpillar of "a geometrid moth. In the larval state the insect bears a very close resemblance to a twig. Its habit of clinging to a real twig with its posterior 'legs' and allowing the body to swing out, adds to the illusion. The head of the caterpillar resembles a leaf bud, while in color the entire creature is an exact counterpart of a rough apple twig, the plant upon which it naturally feeds. Thus complete immunity is secured from the attacks of birds and all enemies which depend chiefly upon sight."[1] (Howes. Paul Griswold, Insect behavior, pp. 164-165, 1919.)

Adaptations of caterpillars supposed to repel enemies, which have received the most attention from writers on the subject, include: armatures of hairs or spines, repugnant odors, warning colors, and terrifying attitudes, in addition to various special resemblances. Among the latter, Howes considers especially remarkable those that "rely for their protection upon their mimicry of the excreta of birds. I have been completely fooled by these larvae on more than one occasion. They frequently rest in the center of a green leaf and while conspicuous, never suggest a living insect to the uninitiated. In color, the upper and lower portions of the body are dark chocolate brown.

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[1] See pages 56 and 85 for the facts as to immunity of loopers.

banded through the center with pure white, which suggests the lime so often seen in the excreta of birds. The entire creature is highly glossed, which gives a fresh and moist appearance to the object, which makes no attempt to conceal itself, depending entirely upon its strangely camouflaged body for protection." (Insect behavior, p. 165, 1919.)[1]

Poulton summarizes the purpose of caterpillar adaptations as follows: "In the remarkable abundance and variety of methods by which concealment is effected in Lepidopterous larvae, we probably see a result of their peculiarly defenceless condition. . . . . Hence larvae are so colored as to avoid detection or to warn of some unpleasant attribute, the object in both cases being the same—to leave the larva untouched, a touch being practically fatal." (The colours of animals, p. 51, 1890.)

On the concealment of lepidopterous pupae, the same author says: "Protective Resemblance, either Special or General, is seen in nearly all exposed pupae, but most chrysalides are buried in the earth or protected by cocoons. The cocoons are often sufficient defense, because the silk is very unpleasant in the mouth; but such protection only applies in the warmer weather when there is an abundance of insect food. In the winter, insectivorous animals are pinched by hunger, and would devour the pupa in spite of the cocoon. We therefore find that all cocoons which contain pupae during the winter are well concealed, either spun between leaves which fall off and become brown, or hidden under bark or moss, or constructed on the surface of bark with a color and texture which renders them extremely difficult to detect." (Op. cit., pp. 51-52.)

Pausing only long enough to note the incorrectness of the statement "all cocoons which contain pupae during the winter are well concealed" (witness those of Saturniidae, not to speak of the cases of many Tineidae), we may pass to Howes' more imaginative account.

> We find, for instance, the chrysalis of a butterfly, a species of Vanessa. It hangs by a tiny silk-fastened stem under a protecting fence rail. Within the shell of the chrysalis, there is nothing but a mass of disintegrating tissues, a thick fluid, studded with globules of fat. It is neither caterpillar nor butterfly. It cannot thrash about from side to side or make a demonstration, there are no spines to pierce a would-be enemy, no wings by which the creature might take flight. It is as helpless now as so much custard, for the insect is in the process of change from one form to another.

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[1] This comment ignores the fact that a great many birds habitually devour the excreta of their young, even returning to it when accidentally dropped, and this nestling excreta is exactly of the luscious appearance described by Howes.

> Such is the actual condition of the pupal butterfly, but let us examine its outer covering. It is a frightful-looking object, armored, and covered with sharp spikes between which beady false eyes peer out. It is absolutely harmless but appears otherwise. To birds it is doubtless a thing to beware of, yet one tiny puncture of its brittle covering would reveal a delicious feast within.
>
> Many insects are thus protected, ones that could not compete in any form of battle. They are given immunity from attack because they could not ward it off themselves. In the case of the transforming pupa, some such form of protection becomes a necessity. A butterfly in the making is as helpless as the egg from which it sprung, so Nature resorts to camouflage to terrorize the destroyers of her children. (Insect behavior, p. 168, 1919.)

Aside from the fact that *Vanessa* pupae do not enjoy immunity (see p. 62), we may well inquire whether birds are not Nature's children just as much as the butterflies, and just as fully entitled to be her beneficiaries?

Bird enemies.—Identification to species especially has lagged more in the case of lepidopterous items of food, than in those of any of the other larger orders of insects, due chiefly to poor condition of the remains of adults, and to lack of knowledge of larvae. Unidentified Lepidoptera exceed 2.85 times those in some degree identified, and in considering the relation of the percentages of identifications to those of the number of species of various groups, the former figures should be multiplied by 2.85.

In view of the very unsatisfactory distribution of identifications of Lepidoptera to families (over 70 per cent of the whole number being merely as Lepidoptera), it would be of little avail to discuss the relative importance of family groups as bird food. Rather it will be better to treat the subject along lines of general interest already developed, as the preference between larval and adult Lepidoptera, the extent to which hairy caterpillars are eaten, and the relation of birds to butterflies, the chief illustrations of mimicry theories.

The question as to which is eaten most extensively, adult or larval Lepidoptera, is easily answered in favor of the latter. As the table shows 68 per cent of all records of Lepidoptera are for larvae, further unidentified; moreover, it is certain that the great bulk of specimens identified to families also were larvae. Thus the Noctuidae determined were chiefly cutworms, the Geometridae were mostly loopers, the Tineidae principally case-bearers, and so on. Caterpillars, not further identified, were found from 50 to 100 times in the stomachs of 23 species of birds; from 100 to 200 times in 21 species; from 200 to 300 times in eight species (downy woodpecker, blue jay, red-winged and Brewer's blackbirds, warbling vireo, black-capped chickadee, hermit thrush, and bluebird); from 300 to 400 times in two species

Identifications of Lepidoptera

Family	Number of identifications	Percentage of identifications among all Lepidoptera	Percentage of species in this family among described nearctic species of Lepidoptera[1]
Tineidae	499	.2098	6.3575
Elachistidae	5	.0021	2.9296
Gelechiidae	5	.0021	4.4548
Tortricidae	149	.0626	7.2183
Crambidae	17	.0071	...
Pyralidae	38	.0160	10.0573
Sesiidae	2	.0008	1.5252
Cossidae	5	.0021	.3171
Cochlidiidae	2	.0008	.4983
Psychidae	2	.0008	.1963
Geometridae	87	.0366	12.2318
Bombycidae	6	.0025	.0151
Lasicampidae	174	.0731	.3624
Liparidae	7	.0029	.2265
Notodontidae	118	.0496	1.2533
Noctuidae	1,128	.4742	32.1049
Agaristidae	4	.0017	.2265
Arctiidae	68	.0286	1.7668
Ceratocampidae	66	.0277	.1812
Saturniidae	29	.0122	.4681
Sphingidae	156	.0656	1.2533
Moths (further unidentified)	2,116	.8896	...
All moths	*4,683*	*1.9685*	*90.1541*
Hesperiidae	9	.0038	2.9447
Lymnadidae	1	.0004	.0453
Nymphalidae	59	.0248	2.5218
Pieridae	1	.0004	.9664
Papilionidae	2	.0008	.3171
Butterflies (further unidentified)	41	.0172	...
All butterflies	*113*	*.0474*	*9.8459*
Lepidopterous eggs	134	.4233	...
Lepidopterous larvae	12,676	5.3291	...
Lepidopterous cocoons and chrysalides	227	.0954	...
Lepidopterous adults	654	.2749	...

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[1] Computed from Dyar, H. G., A list of North American Lepidoptera, etc., U. S. Nat. Mus. Bull. 52, 723 pp., 1902.

(red-eyed vireo and robin); and more than 400 times in the following five species: crow (438), starling (727), meadowlark (474), crow blackbird (600), and English sparrow (466). One hundred or more caterpillars further unidentified were found in single stomach contents of each of the following birds: sparrow hawk, downy woodpecker, hairy woodpecker, black-billed cuckoo, yellow-billed cuckoo, crow, starling, crow blackbird, hermit thrush, wood thrush, and robin. A very characteristic phase of the destruction of caterpillars by birds is their use as a special food for the young; numerous species of birds make a practice of feeding the young a very much higher proportion of caterpillars than is taken by the adults.

It has often been asserted that hairs and spines are very effective in protecting certain caterpillars from birds.[1] Bastin for instance, states that "stinging hairs defend their possessors from almost all birds except the cuckoos." (Insects, their life-histories and habits, p. 168, 1913.) These claims ignore the fact that birds are very well equipped with relatively insensitive bills and feet for removing spines and hairs from larvae if they choose. Some birds do this, others actually dissect caterpillars, eating parts they want from the inside, piecemeal. Hairy and spiny armature is no bar to birds with such feeding habits, and, furthermore, do not seem to be of any great service in relation to numerous birds which swallow entire larvae thus defended. A characteristic statement about hairy caterpillars is: "Tent caterpillars have few enemies. . . . . Our two species of Cuckoos make it a regular business to feed upon these worms which no other birds will eat." (Lugger, Otto, Fourth Ann. Rep. Ent. Minn. (1898), p. 142, 1899.)

Seventeen of the species of birds included in the tabulations on which this paper is based had eaten tent caterpillars or the eggs from which they hatch; numbers of larvae taken at a meal ran up as high as 200 in case of the black-billed cuckoo, and of eggs as high as 1,047 in that of a blue jay. Compiling records from the reports of entomologists and others who have found birds feeding upon tent caterpillars, we get a list of 43 species of bird predators upon the so-called "Orchard" species (*Malacosoma americana*) and 32 upon the "Forest" species (*M. disstria*). Caterpillars even more offensively

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[1] In the case of this as in other similar claims, we may well ask why such theoretically effective defenses have not been developed by a larger proportion or in fact by all larvae? The most cursory consideration of the subject shows that hairiness of caterpillars is in the main a phyletic character. A few related families include the great bulk of the hairy larvae.

hairy than these are those of the gipsy and the brown-tailed moths; the hairs of the latter species especially cause a troublesome and painful rash upon the skin of man. Nevertheless 46 kinds of birds are known to eat caterpillars of the former species and 31 those of the latter. (For a valuable article on bird enemies of these and other hairy caterpillars, see Forbush, E. H., Bull. 20, n. s., U. S. Div. Ent., pp. 85-93, 1899.)

The larvae of the tussock moth (*Orgyia leucostigma*) are supposed to be especially distasteful to birds, but Forbush records (Mass. Crop Rep., July, 1900, p. 36) nine species of birds as feeding upon them. The writer has observed English sparrows and robins eating them; in the spring of 1921 in Washington, D. C., the larvae were quite common and robins were feeding freely upon them, carrying them to their young, I believe, as it was a common sight to see the birds flying with the white tufts showing at the tips of their bills.

Again records of birds feeding on fall webworms (*Hyphantria textor*) are relatively scanty, only six species being named, yet careful observation in the field has proved one of them to be a very effective foe. Dr. C. Gordon Hewitt informs us that of the various factors operating in the reduction of this insect in Nova Scotia in 1916, the red-eyed vireo was most important and "it was estimated that about 40 per cent of the larvae had been destroyed in the webs by this bird." (Rep. Dominion Ent. 1917, p. 8.) A later report shows an average destruction of 68 per cent.

It would not be necessary to refer to the preying of birds upon smooth caterpillars, a thing universally done, except for theoretical disquisitions as to the "protected nature" of certain groups. The Geometridae, loopers or measuring worms, are said to be protected by resemblance to twigs, etc., a statement made without giving due weight to the fact that such a defense depends upon immobility whereas these caterpillars must be in motion the greater part of the time while searching for and devouring food. Forty-four species of birds are recorded as feeding upon Geometridae in our tabulation and numbers of specimens as high as 20 were taken at one meal by the starling and 90 by the robin.

Larvae of the Sphingidae are said to be protected by their "horns" and by "terrifying attitudes," but 44 species of birds covered by the present investigation do not seem to agree with the theorists on these points. Ten species are known to prey upon *Dielephila lineata* alone, and in field observation the crow has been known to clear tomato patches of the hornworm (*Phlegethontius sexta*).

Many printed pages have been devoted to discussion of the question: "Do birds eat butterflies?" but the natural answer: "Certainly, but probably not out of proportion to their abundance," seems not to have occurred to the disputants.

At this point it will be well to say a word about the alleged difficulty of identifying adult Lepidoptera, especially butterflies in the stomach contents of birds. But for this, some argue, the number of records of butterflies eaten would be much larger. The assumption is made that the scales are necessary to identification, and since they are so easily rubbed off, determination will usually be impossible. This objection serves mainly to exhibit the ignorance of its proposers relative to the analysis of the contents of bird stomachs. In the first place when adult Lepidoptera have been eaten at all recently, that fact is evident to the practiced eye, even unaided, on first glance at the stomach contents. A characteristic fuzzy, felted appearance, due to the distribution of the hundreds of scales throughout the mass, tells the tale at once. Even after digestion is far advanced the scales do not disappear because they are so numerous and stick to everything, and they are evident under magnifications used in the analysis of practically every stomach contents. Moreover were all scales absent, it would be possible to unroll the wing membrane, if swallowed, and examine the venation; the antennae also would usually be present; and the form of the head, thorax, and body, which are characteristic, could be made out.

In addition we would remind the reader that all things found in birds' stomachs are not ground to a powder. Just the reverse in fact is true; birds feed more or less constantly, and whenever shot they will as a rule just have swallowed some article of food which, of course, will be in good condition for study. In the long run all constituents of the food will be found nearly or quite intact in the stomachs in proportion to the frequency in which they are taken.

However it is unnecessary to discuss the matter further. One need only consider the extent to which we have identified certain insects far more fragile than butterflies, as mayflies (Ephemeridae) 484 records, midges (Chironomidae) 1,003 records, and crane flies (Tipulidae) 1,565 records, to be assured that there is no likelihood whatever of a butterfly being overlooked during careful stomach analysis.

Of the 113 records of birds eating Rhopalocera included in the present tabulations, 24 refer to larvae and two to chrysalides. It is worth noting that one of the larval records was for *Anosia plexippus*, two for *Papilio* species, and six for *Vanessa* species, supposedly the best protected forms. Nymphalidae and Hesperiidae are most numerously represented among the adults taken.

The 87 records of imago butterflies are distributed among 15 species of birds, but all save 18 of them pertain to a single bird, the pigeon hawk. The specimens of this hawk examined were taken on their southward migration at a point that is in the migration path of butterflies also, so that opportunities for catching these insects were at the best. (It is worth noting here that dragonflies, swallows, swifts, and bats also using this same migration track were preyed upon by the pigeon hawk.) In this case as in many others the abundance and availability of prey is shown to have great influence upon the choice of food by birds. Amid the butterflies, this hawk preyed upon them; elsewhere we have no record of its doing so. Clearly the other birds (14 species) in whose stomachs butterflies have been found (18 records) are only occasional predators upon them. This is only what would be expected, for ordinarily butterflies, numerically, are no considerable part of the insect fauna; when under extraordinary circumstances they do become over-abundant they are more frequently devoured by birds. Thus Bryant found Brewer's blackbird eating large numbers, and three other species of birds smaller numbers, of *Eugonia californica* during an unusual outbreak of the species. (Condor, vol. 13, pp. 195-208, Nov. 1911.)

Summary of identifications of Lepidoptera: Total number 18,487; percentage of identifications among those of all insects, 9.6831; percentage of species in this group among the whole number of insect species, 15.6180.

Other enemies.—For the most part fishes are only casual devourers of Lepidoptera, getting chiefly larvae which fall into the water, most of which would perish anyway. However, gamy fishes such as trout snap up adults that incautiously fly near the surface of the water.

Bullfrogs have been observed feeding freely on *Papilio turnus* adults (Mallonee, Science, 1916, pp. 386-387) and half a dozen leopard frogs have been noted as eating 500 *Argynnis aphrodite* in a week (Shiras, Nat. Geogr. Mag., 1921, p. 174). Kirkland found cutworms, tent and other caterpillars to compose 28 per cent of the total food of 149 toad stomachs examined by him, and Munz found lepidopterous larvae in stomachs of four species of frogs. In 209 leopard frogs, Drake found one imago, one chrysalid, and 121 larvae of Lepidoptera. Surface reports remains of Lepidoptera in stomachs of eight species of salamanders, one toad, and nine frogs. In the Tropics lizards are said to be important enemies of adults of this order and our lizards are known to eat both larvae and imagos. Surface records Lepidoptera from the stomachs of five species each of snakes and turtles.

Cutworms are commonly taken and other caterpillars and chrysalides are devoured to a smaller extent by moles. A number of small mammals, such as opossums, spermophiles, ground squirrels, tree squirrels, prairiedogs, grasshopper mice, skunks, raccoons, shrews, armadillos, the mongoose, and *Nasua* feed more or less regularly on caterpillars, and take an occasional pupa or imago. Bird has observed that field mice and skunks are effective enemies of the gall-making larvae of *Papaipema*. (Can. Ent., vol. 41, no. 2, pp. 67-68, Feb., 1909.) Haskin has reported squirrels devouring large numbers of *Melitaea chalcedon* adults (Ent. News, vol. 27, no. 8, p. 370, Oct., 1916), and Attwater found wings of several hundred *Danais archippus* that had been eaten by the Texas grasshopper mouse (Bull. Amer. Mus. Nat. Hist., vol. 6, p. 181, 1894). Bats catch moths, and monkeys also have been reported as eating butterflies commonly. (Trans. Ent. Soc. London, 1912, p. iv, xvii-xviii.)

The insect enemies of Lepidoptera also are numerous and some of them are exceedingly destructive. Robber flies and dragonflies are frequently observed devouring adult Lepidoptera, and a Natal collector considers Mantidae the chief enemies of butterflies. (Proc. Ent. Soc. London, 1906, p. lii.) Spiders catch them directly or trap them in their webs, Phymatidae lie in wait for them, and predacious beetles sometimes capture them. However, the latter predators are more serious foes of caterpillars, in the pursuit of which they have as fellows numerous wasps. Ants, chrysopid larvae, and other insects and mites feed upon the eggs; and parasites often destroy large proportions of the eggs laid. Parasites of lepidopterous larvae also are legion, including numerous species of Hymenoptera and Diptera, and they take a large toll from every generation of the insects. Exceedingly high percentages of parasitism have frequently been observed, reaching locally in a few cases even to 75 and 100 per cent. It has been found in one case at least that no fewer than 63 species of hymenopterous parasites attack a single species of moth. (Cambridge Nat. Hist., vol. 5, p. 521, 1910.)

Bacterial diseases frequently kill large numbers of caterpillars and sometimes locally extirpate certain species.

Discussion.—It is one thing to record a proved fact, but quite another to assert that a certain thing does not occur in nature. Our stock of verified data stands as an imperishable record and addition to it, not subtraction, is the rule. Let none be tempted therefore to add to the vast body of speculation that has proceeded from slight premises by data in a preceding paragraph apparently indicating that birds do not eat many chrysalides of butterflies. For in that case we must refer him to Bryant's statement that about 15 per cent of the pupae of *Eugonia californica* at a time when they were very abundant showed evidences of attack by birds (Condor, vol. 13, p. 200, Nov., 1911), and to Chittenden's that " in one case it was found that during the winter the number of pupae of the cabbage butterflies was reduced more than 90 per cent by birds feeding upon them." (Farmers' Bull. 766, U. S. Dep. Agr., p. 9, 1916.)

In this paper we cannot possibly discuss all of the data relating to predators upon insects and other animals, but the evidence we present in our tabulations surely goes far to prove that no groups are neglected by predators (except as availability or sheer size dictates) and that the various groups are preyed upon more or less in proportion to their numbers. As applied to Lepidoptera this rule is apparent in the greater number of records for such large families as the Noctuidae, Tineidae, and Tortricidae for instance as contrasted to such smaller ones as the Sphingidae, Arctiidae, and Bombycidae or of the more numerous Nymphalidae to the less numerous Papilionidae. Due to the high proportion of unidentified Lepidoptera, our tables are not as complete and informing as could be desired, but where there are apparent exceptions to the rule of proportional loss to predators, data from other sources usually indicates unreliability of the apparently negative evidence. For instance the records of Geometridae in our table seem too low for this rather important family which is undoubtedly numerous in individuals. But that this is due solely to the make-up of our material is proved at once by reference to the literature; no fewer than 73 species of nearctic birds have been observed feeding on cankerworms (*Paleacrita* and *Alsophila*) for instance. Wellhouse, who reports finding cankerworms in 98 of 100 stomachs of birds (36 species) collected near Lawrence, Kans., in 34 of which they composed the total food, says: " Probably no insect is a favorite food of more species of birds than the cankerworm larva." (Bull. Univ. Kansas, vol. 18, no. 1, p. 301, Oct. 1917.) In a study of birds in relation to cankerworms in Illinois, Forbes found these larvae to compose 45 per cent of the food of a collection of 55 birds (15 species) and that one species, the cedarbird, was destroying them at the rate of at least 90,000 per month. (Forbes, S. A., Trans. Illinois State Hort. Soc. (1881), pp. 123-130, 1882.)

The snow-white linden moth (*Ennomos subsignarius*) has a typical twiglike caterpillar, but several entomologists have testified that it was practically exterminated in cities by the English sparrow. (See Herrick, G. W., Bull. 286, Cornell Univ. Agr. Exp. Sta., p. 62, Nov., 1910.)

The only other important family of moths which our tabulations might indicate to be neglected by birds is the Pyralidae. With little doubt this condition is due either to the larvae not being recognized or to our stomach material not being fully representative. Certainly birds are known to be enemies of our pyralid larvae, a little search revealing records of avian predators upon *Loxostege similalis, L. sticticalis, Pilocrocis tripunctata, Pinipestis zimmermanni, Diatraea saccharalis, Acrobasis nebulella*, and *Pyrausta nubilalis.* Five species are known to feed on the last-named, the corn rootborer, while of *Loxostege sticticalis*, the beet webworm, it is recorded that: "Insect-eating birds devour the worms in large quantities. Where the worms were abundant [in Colorado] . . . . blackbirds were attracted in flocks of thousands and in several instances . . . . the worms were all cleaned out of fields by them in the course of two or three days." (Gillette, C. P., Bull. 98, Colorado Agr. Exp. Sta., p. 10, Mar., 1905.)

These instances emphasize the universal scope of the predatory activities of birds; in general the enemies of economic species of insects are better known, and fully discounting the fact that they are most studied, this is only another way of saying that the most abundant species have the most numerous enemies.

COLEOPTERA (BEETLES)

Protective adaptations.—While more pages have been written about warning colors, mimicry and the like in Lepidoptera, which insects furnished the inspiration for this line of speculation, the important and extensive order of Coleoptera has been far from neglected and perhaps the most positive statements of all have been made regarding the "protected" status of some of its members. In conclusions derived from G. A. K. Marshall's data on "The Bionomics of South African Insects" (Trans. Ent. Soc. London, 1902, pp. 393-584), Prof. E. B. Poulton in discussing the chief specially defended Coleoptera mentions: "The groups about which there seems to be no doubt at all—conspicuous, constantly refused by insect-eaters, and liable to be mimicked by other Coleoptera are the following: Erotylidae, Coccinellidae, Malacodermidae, including the Lycinae, Lampyrinae and Telephorinae, Melyridae, Cantharidae, Chrysomelidae, Endomychidae, and Pyrochroidae." The Cleridae are cited as a family that while undoubtedly distasteful, in forming color associations take the colors and patterns of other insects "rather than impress the stamp of their own likeness on the assemblage." The following four families are said to be "at any rate partially distasteful": Scarabaeidae, Cetoniidae, Tenebrionidae, and Lagriidae. The longicorns are thought to include a few distasteful species in addition to many that mimic aculeate Hymenoptera and other specially defended insects. Cicindelidae are said by Wallace to be protected by cryptic coloration, the refuge of the weak, while Poulton and Shelford have recorded them as models mimicked by species less prepared for the struggle for existence—a tribute to the strong.

"The Carabidae are a powerful specially defended group," writes Poulton (op. cit., pp. 513-514) "and it is of advantage to be recognized as belonging to the group, even though it is no doubt of still greater advantage to be mistaken, as may happen at a distance, or on a superficial view, or during rapid movement, for the still more formidable Mutillidae and ants" . . . . . "Dr. A. R. Wallace has always thought that the extreme hardness of the mimicked Curculionidae and Anthribidae is the character which protects them." (Poulton, op. cit., pp. 522-523.)

Comment of this kind could be cited indefinitely, for something or other has been claimed to be "special protection" for practically every group of beetles. It is undesirable and unnecessary to cite this matter in detail, but some attention should be given to the subject of repugnatorial secretions which has figured considerably in accounts of protective adaptations of beetles. For convenience, a summary of the occurrence of such secretions is quoted from a recent article on the topic:

"It has been well understood that the presence of defensive or repugnatorial scent glands in certain insects exists in direct adaptation to the needs and habits of their owners and in close response to their environment; also that such glands are of very frequent occurrence and with much variation as to position, form, and function; and that their presence is of value to the insect for repellent, defensive and warning purposes. . . . . Biologically speaking, the principle involved in such cases, though often modified, is practically identical with that of the mephitic, sulphuretted, oil-like fluid ejected by the skunks. Thus far anal glands are known to be present in the following families of Coleoptera: Cicindelidae, Carabidae, Dytiscidae, Gyrinidae, Staphylinidae, Silphidae, and Tenebrionidae. The blood itself serves as a repellent fluid in the Meloidae, and in the Coccinellidae and Lampyridae, and it issues from a pore at the end of the femur as a yellowish fluid. The cantharidin in the blood of some species of Meloidae, commonly known as 'Spanish Fly,' forms an especially caustic protection against birds, predacious insects and reptiles." (Wade, J. S., Notes on defensive scent glands of certain Coleoptera, Psyche, vol. 28, nos. 5-6, p. 146, Oct.-Dec., 1921.)

Bird enemies.—It is worth pointing out that about 15 per cent of all the determinations of beetles were not carried to the family, and consequently that the percentages for the various families should be, on the average, about a seventh larger than shown in the tabulation

Identifications of Coleoptera

Family	Number of identifications [1]	Percentage of identifications among all Coleoptera	Percentage of species in this family among described nearctic species of Coleoptera [2]
Cicindelidae	649	.7606	.6146
Carabidae	15,887	18.6200	11.6730
Amphizoidae	...	...	.0107 (2)[3]
Omophronidae	16	.0187	.0808 (15)
Haliplidae	363	.4254	.2210
Dytiscidae	1,729	2.0264	1.7954
Gyrinidae	64	.0750	.0808
Hydrophilidae	2,418	2.8340	1.0244
Platypsyllidae	...	...	.0053 (1)
Brathinidae	...	...	.0161 (3)
Leptinidae	...	...	.0161 (3)
Silphidae	409	.4794	.7386
Clambidae	...	...	.0323 (6)
Scydmaenidae	...	...	.9381 (174)
Orthoperidae	4	.0047	.3073 (57)
Staphylinidae	1,605	1.8811	14.8163
Pselaphidae	3	.0035	1.9140
Clavigeridae	...	...	.0161 (3)
Ptiliidae	...	...	.4690 (87)
Sphaeritidae	...	...	.0053 (1)
Colydiidae	5	.0059	.4520
Murmidiidae	...	...	.0269 (5)
Monoedidae	...	...	.0053 (1)

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[1] There is an omission of 737 records of Carabidae and 574 of Chrysomelidae, enough to make more than 1.5 per cent of the total of beetle records.

[2] Computed from Leng, C. W., Catalogue of the Coleoptera of America north of Mexico, 470 pp., 1920.

[3] The number of nearctic species in the family.

Identifications of Coleoptera—Continued

Family	Number of identifications	Percentage of identifications among all Coleoptera	Percentage of species in this family among described nearctic species of Coleoptera
Lathridiidae	16	.0187	.5607
Mycetaeidae Endomychidae	1	.0012	.2048
Phalacridae	27	.0316	.6308
Coccinellidae	1,455	1.7053	1.9517
Alleculidae	34	.0398	.6685
Tenebrionidae	2,197	2.5749	6.1411
Lagriidae	8	.0094	.0916
Monomidae	...	...	.0323 (6)
Melandryidae	39	.0457	.4367
Ptinidae Anobiidae	51	.0598	1.4556
Bostrichidae	24	.0281	.3288
Lyctidae	...	...	.0862 (16)
Sphindidae	...	...	.0323 (6)
Cisidae	4	.0047	.4582
Scarabaeidae	13,252	15.5317	5.3701
Lucanidae Passalidae	121	.1418	.1724
Cerambycidae	1,585	1.8577	6.0548
Chrysomelidae	5,666	6.6407	5.2515
Mylabridae	47	.0551	.5014
Scaphidiidae	8	.0094	...
Histeridae	1,063	1.2459	2.0704
Lycidae Lampyridae Phengodidae Telephoridae	879	1.0302	1.5095
Melyridae	38	.0445	1.7307
Cleridae Corynetidae	35	.0410	1.1806
Othniidae	...	...	.0269 (5)
Lymexylidae	...	...	.0107 (2)
Telegeusidae	...	...	.0053 (1)
Micromalthidae	...	...	.0053 (1)
Cupedidae	1	.0012	.0215
Cephaloidae	2	.0023	.0431
Oedemeridae	9	.0105	.2641
Mordellidae	34	.0398	.7656
Rhiphiphoridae	2	.0023	.1347
Meloidae	279	.3270	1.2239
Aegialitidae	10	.0117	.0161
Pythidae	6	.0070	.0916
Pyrochroidae	4	.0047	.0593

Identifications of Coleoptera—Continued

Family	Number of identifications	Percentage of identifications among all Coleoptera	Percentage of species in this family among described nearctic species of Coleoptera
Pedilidae Anthicidae Euglenidae	573	.6716	1.5311
Cerophytidae Cebrionidae Plastoceridae Rhipiceridae	7	.0082	.1939
Elateridae	4,489	5.2612	3.1056
Melasidae	4	.0047	.3073
Throscidae	6	.0070	.1347
Buprestidae	662	.7759	2.0434
Psephenidae Dryopidae Helmidae	33	.0387	.3072
Heteroceridae	143	.1676	.0593
Georyssidae	...	...	.0107 (2)
Dascillidae Helodidae	17	.0199	.3288
Chelonariidae	...	...	.0053 (1)
Dermestidae	190	.2227	.6955
Byrrhidae	312	.3657	.5229
Rhyssodidae	...	...	.0215 (4)
Ostomidae	28	.0328	.3450
Nitidulidae	327	.3832	.7117
Rhizophagidae	...	...	.0754 (14)
Monotomidae	3	.0035	.1941
Cucujidae	28	.0328	.4582
Erotylidae	14	.0164	.3828
Derodontidae	...	...	.0269 (5)
Cryptophagidae	18	.0211	.7278
Mycetophagidae	24	.0281	.1725
Brentidae	16	.0187	.0323
Platystomidae	29	.0340	.3342
Belidae	11	.0129	.0053
Curculionidae	11,740	13.7596	9.9153
Platypodidae	25	.0293	.0215
Scolytidae	494	.5790	2.0488
Water beetles (further unidentified)	369	.4325	...
Rhynchophora (further unidentified)	7,557	8.8570	...
Beetles (further unidentified)	7,192	8.4292	...
Beetle larvae (further unidentified)	862	1.0103	...

The tiger beetles "are avoided on account of their ferocity" (Bastin, Insects, their life-histories and habits, p. 151, 1913), and have been referred to as "dreaded insects" (Poulton, Colours of animals, p. 252, 1890), but what creatures capable of feeling dread so regard these beetles is unexplained; certainly the facts indicate they are not birds. The 649 records included in the present tabulation are distributed among 99 species of birds. Eight species have 10 or more records each, two others, the eastern meadowlark and eastern kingbird, over 20, the crow more than 60, and the crow blackbird 94. No fewer than 25 larvae of tiger beetles were found in a single stomach of an eastern bluebird, and 156 adults in that of a sparrow hawk and 164 in that of a long-billed curlew. If tiger beetles ever evade attacks by birds it is by celerity of motion rather than by any special defenses.

With respect to Carabidae or ground beetles, Forbes in his report on the food of thrushes may have given some comfort to protective adaptation theorists when he said: "We note, however, a remarkable deficiency of the highly colored genera—such as *Galerita, Brachynus, Lebia, Platynus, Chlaenius,* etc., which are either absent, or found but rarely in these birds' (thrushes, bluebird) food. Evidently these more showy beetles are protected by some more effective means than obscurity of color." (Forbes, S. A., Bull. Illinois State Lab. Nat. Hist., vol. 1, no. 6, p. 57, May, 1883.)

However, this statement is but another instance of the danger of generalizing from insufficient data. In the study of the food of birds and other animals we are always adding to the list of species eaten and to the number of times they are taken; the movement is never in the contrary direction. We are constantly finding enemies of forms previously held to be more or less exempt, and usually to an extent which more than compensates for previous lack of knowledge on the subject.

In the present instance such progress in knowledge since Forbes' study is indicated by 535 records of the capture of *Chlaenius* by 41 species of birds, 254 for *Platynus* by 55 species, 44 records for *Galerita* by 13 species, 39 for *Lebia* by 21 species, and eight for *Brachynus* by seven species; figures more or less in harmony with the relative abundance in individuals of these groups. In this connection it may be well to note also F. H. Chittenden's remark that *Lebia grandis* "is protected by its warning color from rapacious birds." (Farmers' Bull. 1020, U. S. Dep. Agr., p. 16, 1919.) Six of the 39 *Lebia* records here cited are for *grandis,* and the writer submits that six records for this single species out of a total of 85,322 for all beetles (18,548 nearctic species) fully satisfies expectations based on the relative availability of the species to birds.

Species of *Agonoderus*, much more common than *Lebia* but just as contrastingly colored, contribute 188 records to our tabulations and were eaten by no fewer than 57 species of birds. From 10 to as many as 50 specimens had in several instances been taken at a meal. There are 57 records for *Casnonia*, a small genus of " long-necked " distinctly " warningly-colored " beetles in stomachs of 14 species of birds.

Even black, alone, the predominant color among Carabidae has been held to have a warning value, but *Amara*, *Anisodactylus*, *Harpalus*, and *Pterostichus*, chiefly typically black species, are eaten by the hundreds. There are 445 records for the powerful *Pasimachus* (80 individuals in one crow stomach), and 497 for the species of *Calosoma* which are not only large, but some of which have contrasting blue margins, others fiery spots, and all powerful, ill-scented excretions. In fact, it is everywhere evident that the special defenses alleged for the Carabidae are more in the nature of pleasing fictions for theorists to speculate upon than practical reliances for the beetles concerned. Eloquent is the fact that between a sixth and a fifth of all determinations of beetles in the stomachs of nearctic birds are of Carabidae.

The Haliplidae, all of which have " warning colors," and the Dytiscidae and Gyrinidae, said to be protected by anal glands, all seem to be preyed upon in proportion to their abundance. The Silphidae quite generally have nauseous excretions and include numerous species with distinct warning colors, but it is the latter forms such as *Necrophorus* with 102 records and *Silpha* with 213 that most evidently are eaten in due proportion. The apparent falling of records of this family below the index of frequency must be attributed to the smaller and rarer species with more concealed habits being overlooked, rather than to the larger familiar ones enjoying immunity on account of alleged special defenses which they possess in the highest degree.

That the Staphylinidae is the family most numerous in species, and probably therefore of individuals, among all Coleoptera is a fact not realized by the average collector. It has been brought out only by the accumulated research of generations of coleopterists, and its lack of obviousness must be attributed to the secretive habits of so many of these small or even minute beetles. Most of them spend their lives chiefly under cover of various kinds, for example, in fungi, in leaf-mold, under bark, in old logs, and in ant nests, and it must be on this account that the records of birds capturing them are not very much more numerous, rather than that they are disliked. In fact the 1,605 determinations for them proves they are not disliked, and these records are shared by more than 160 species of birds. Fifteen of these kinds of birds had more than 10 records each, nine others more than 20, six others from 30 to 60 records, one other, the chimney swift, 76, the crow 190, and another, the starling, more than 200. In several instances the number of specimens found in a stomach was as many as from 20 to 50 and larger numbers were 85 for the baldpate and 150 for the dowitcher. Such data certainly do not indicate distaste for Staphylinidae, hence the failure of the total number of captures to come up to theoretical expectations must be due to some other factor, presumably the small size and concealed habit of living characteristic of so large a proportion of the beetles of this family.

The same causes also serve to explain why a number of the minor families of beetles have not yet been identified in bird stomachs; the Platypsyllidae, and Leptinidae are parasitic upon mammals, the Scydmaenidae, and Clavigeridae mostly live in ant nests, the Ptiliidae are minute, while the others most of which have five or fewer species in our region owe their degree of immunity to their very rarity.

Passing now to one of the larger groups of beetles about whose protected status " there seems to be no doubt," namely the malacoderms, variously regarded as forming from one to four families, we find that they are devoured in no mincing way by nearctic birds. While various authors refer to these beetles (generally known as Lampyridae in the United States) in terms varying from distasteful to inedible or immune, our records show 879 determinations of them from bird stomachs. All of the groups were preyed upon, the Lycinae and Phengodinae least, however, because they are scantily represented in our fauna. The adult lampyrids identified were eaten by no fewer than 108 species of birds and the larvae by 25. Larvae in number up to 50 were found in a bluebird's stomach, and in three instances as many as 100 were taken from a single stomach of the robin. Our most common lampyrids are *Chauliognathus* and *Telephorus*. The former genus was identified 179 times in the stomachs of 34 species of birds. Three of these had from 30 to 38 records each and the number of individual beetles eaten ran as high as 30 in a single instance. *Telephorus* (*Cantharis*) were determined 274 times in the stomachs of 35 species of birds; the number of imagines in a stomach ran as high as 16 and of larvae, 100. If the Lampyridae fail in any degree to attain proportional representation among the food items taken by nearctic birds it is due to the nocturnal habits of a large number of the species. The diurnal species seem to be captured as frequently as would be expected.

The Melyridae (Malachiidae) are poorly represented compared to the Lampyridae, yet upon inspection of the records it does not seem that they are really avoided. Six genera and at least 10 species of these beetles were identified; 21 species of birds had eaten them, and for one of these birds, Say's phoebe, there were eight records of feeding on *Collops*. Identifications of the Cleridae again include numerous (21) species distributed among an equal number of species of birds. One of these birds, the red-eyed vireo, had eight of the records. In our experience Cleridae occur chiefly scattered and in small numbers, a type of distribution with which the records of birds preying upon them seem to harmonize.

Of the Histeridae, Donisthorpe says: "All the species of this family are protected by their oval shape and hardness. They also 'feign death.'" . . . . the "species which are spotted with red, are probably protected by their resemblance to Coccinellidae." (Trans. Ent. Soc. London, 1901, p. 354.) The prevailing color in this family, *i. e.* black, has also been said to have a warning significance. Our records show 1,063 identifications of Histeridae representing 116 species of birds; they are very freely eaten by some of these birds, the number of records per species exceeding 20 in the case of at least 12 kinds, and the number of specimens eaten at a meal running up to as high as 200 as a maximum.

The family of blister beetles (Mylabridae, Cantharidae, or Meloidae as it is variously known) is especially noted for the presence in the bodies of its members of a vesicant poison, cantharidin, of which as small a quantity as one grain has proved a fatal dose for a human being. Bastin says of them "the blood contains cantharidin, an extremely caustic substance, which is an almost perfect protection against birds, reptiles, and predacious insects." (Insects, their life-histories and habits, p. 167, 1913.) While these beetles are supposed to enjoy a very high degree of protection from natural enemies, 47 species of birds included in the tabulations here discussed had fed upon them. Seven of the species had 10 or more records apiece of preying upon blister beetles, the eastern kingbird having no fewer than 77. In some cases from 12 to 16 specimens of cantharids were found in single stomachs and a maximum of 31 in the case of a magpie; more than 30 species in all of these beetles were identified.

Pyrochroidae are said to be another specially defended group of the first order, but in view of the fact that there are only 11 nearctic species of the family and they usually rare, we believe that the four records of our birds capturing them are as many as could be expected. One of the birds eating Pyrochroidae, namely a hairy woodpecker, must have had unusual luck in order to obtain the 12 specimens it contained.

Donisthorpe says "The Elaters 'feign death' and their ability to 'skip' . . . . is no doubt of great use to them. Mr. Holland points out that many of them possess a colour and shape suggesting the appearance of bits of dry brown stick." (Trans. Ent. Soc. London, 1901, p. 360.) Over four thousand (4,489) records of these beetles being eaten by nearctic birds show that the protective devices mentioned are of no particular account. There would appear to be no doubt whatever that birds feed upon Elateridae whenever available to them.

The larvae of Buprestidae live in wood, and the adults have hard chitin and metallic or other brilliant coloration, but since there are more than 650 records of their occurrence in the stomach contents of nearctic birds, it is certain that concealment of the larvae rather than color protection is their main defense. Heteroceridae or mud beetles certainly seem well concealed to the human eye but the records indicate they are taken fully in proportion to their abundance. Dermestidae, said to be protected because they are carrion-feeders, are taken freely considering their availability in nature. Byrrhidae are thought to be excellent examples of cryptically defended insects. "The legs and antennae are packed close to the body, fitting into cavities for their reception and the beetles then represent rabbits' dung, or little lumps of earth; they in no way suggest the appearance of living beetles." (Donisthorpe, Trans. Ent. Soc. London, 1901, p. 357.) However 312 records for them show American birds are not especially deceived by the alleged protective devices.

It is unnecessary to comment on every family, but coming to the Erotylidae we have a group which though small in numbers is said to be one of the most highly protected groups. However, in the United States, insects of this family in general do not have the bold habits supposed to be associated with warning colors; in fact most of them feed concealed in fleshy fungi. Correspondingly most of the determinations of beetles of this family are for the species which live exposed as *Languria,* for which there are 10 records, probably all that should be expected for a single small genus. Similarly the Endomychidae are protected by feeding inside of fungi or on fungi growing on the under side of logs rather than by their "warning colors." It should puzzle selectionists to explain why these and other brightly colored, supposedly distasteful insects have such retiring habits that their "warning coloration" is seldom displayed.

Contrasting these elusive beetles with another brightly colored but decidedly not secretive group they are supposed to mimic, the Coccinellidae, it is easy to see what factor makes for greater depredations by birds; it is none other than the frequently mentioned "availability." Endomychids and Erotylids are red and black or yellow and black beetles, less abundant and much more retiring in habits; while coccinellids with the same colors are more common and live unconcealed. The former are relatively seldom captured, the latter are freely eaten. No better example of the influence of availability in guiding choice of food by birds could be desired. This despite universal acclaim of coccinellids as specially defended insects. "All the lady-birds are very gaily colored" says Donisthorpe. "They boldly walk about without any attempt at concealment, as do also their larvae. Both their larvae and pupae are very brightly spotted. The distastefulness of the perfect insects was proved[1] by Jenner Weir, and has since been confirmed by both Poulton and Wallace." (Trans. Ent. Soc. London, 1901, p. 354.)

Packard states that "The Coccinellidae are . . . . protected by a yellow mucilaginous disagreeable fluid oozing out of the sides of the thorax," (Journ. N. Y. Ent. Soc., vol. 3, p. 116, 1895), and Wallace says: "The Coccinellidae or lady-birds are another uneatable group." (Darwinism, p. 234, 1896.) Let us see. The total number of records of coccinellids in the food of nearctic birds is 1,455 and these are shared by 127 species. Twenty-seven kinds of birds had 10 or more records each, nine of which ran over 50, and three over 100. Not only is the effect of availability noted in birds eating more coccinellids than other similar but less abundant and conspicuous beetles, but its influence is evident in at least two other ways, namely that leaf-feeding birds, as warblers and vireos, get the most ladybird beetles, and that in California where coccinellids are notably more abundant than they are in the eastern States, a larger number of birds feed upon them and they get a great many more of the beetles. The largest numbers of coccinellids found in individual stomachs were 12 and 18 taken by English sparrows, 13 by the summer warbler, 14 by the warbling vireo. and 15 by the valley quail.

We now come to the consideration of three families (the Scarabaeidae and Cetoniidae being reckoned as one) which Poulton says are "at any rate partially distasteful." Regarding one of these families, the Lagriidae, which has only 17 species in the nearctic fauna, it

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[1] The "proof" was experimental, of course; for the value of this proof see my 1912 paper. Also note that Meisner's results on the poisonous effect of Coccinellid juices (Ent. Bl. Nurnberg, vol. 5, no. 9, pp. 180-182, Sept. 20, 1909) are controverted by a repetition of his experiments by Heikertinger (Wien. Ent. Zeit., vol. 38, Heft 4-8, pp. 109-113, June 15, 1921).

may be said that almost any small number of captures by our birds would satisfy expectations. There are eight records distributed among six species of birds, about all that probabilities demand. As to the Tenebrionidae so many species of which have secretions nauseous to man, the nearly 2,200 records are eloquent of the fact that these beetles are not disliked by birds. If they do enjoy any degree of immunity from bird attacks, it is probably on account of their characteristic nocturnal or otherwise seclusive habits. The number of species of birds known to prey upon Tenebrionids is in excess of 175; nine birds had over 20 records each, five others more than 40, one additional over 50, and two others more than 100. The number of specimens taken at a meal ran up to 44 in two cases and to 46 in another and 53 in still another. The number of species of Tenebrionidae identified was over 100, including 12 of Eleodes, the largest and most potently odoriferous of the family.

Of these a recent article says: "It was interesting to note that the quantity of the secretion voided varies noticeably with the different species under observation, both under field and under laboratory conditions, and some of the species, notably *Eleodes tricostata* Say, undoubtedly have the habit of erecting the abdomen in a threatening manner when approached, though no secretion may be voided. Such species undoubtedly find protection through imitation of the threatening movements of their more formidable associates. Two of the characteristics of the Eleodes are their slowness of movement, and their habit of coming out of their hiding places about sunset for feeding purposes, and their presence is readily noticed on the bare sandy plains by birds, skunks, and other enemies, hence their protective secretion, or, in the absence of this, their threatening maneuvers are no doubt of highest value to them." (Wade, J. S., Notes on defensive scent glands of certain Coleoptera, Psyche, vol. 28, nos. 5-6, p. 148, Oct.-Dec., 1921.)

In this connection it may be said that our tabulations show 51 records of birds feeding on *Eleodes tricostata* and 109 for the other species. Other large Tenebrionids as *Asida* and *Nyctobates* are well represented in the table of determinations as are also the metallic forms such as *Helops*, *Meracantha*, and *Epitragus*. *Blapstinus* with 286 records for 11 species is the favorite genus, and the reason is what?—simply that it is the most widely distributed and the most numerous in individuals.

With respect to the other "partially distasteful" family of beetles, the Scarabaeidae (sens. lat.), the more than 13,000 records in our tabulations speak for themselves. The selectionist protectionists have simply made a very bad guess. Consider for instance the Cetoniini, the best "protected" tribe, some of which are said to mimic bees in flight. Our most numerously represented genus, *Euphoria*, has 445 records, of which 148 are for the most beelike species of all, *E. inda*. *Cotinis*, very poorly represented in our fauna, has 156 records, and *Cremastochilus*, noted for their association with ants, 77.

Species of *Onthophagus* "live in and about dung and are of a colour which conceals them well in those surroundings." (Donisthorpe, Trans. Ent. Soc. London, 1901, p. 358.) However, they were preyed upon 642 times by the birds included in the present tabulations. The species of *Aphodius* also are dung-feeders and said to be protected The number of determinations of this genus is approximately 3,565; in numerous cases 100 of these beetles were found in single stomachs and in one instance no fewer than 900. A warningly colored species, *A. fimetarius* (with the thorax black and elytra red), was identified in 913 stomachs. Consider the entirely different case of a beetle, the rose chafer (*Macrodactylus*), known to be actually poisonous (see Science, n. s., vol. 43, pp. 138-139, Jan. 28, 1916) besides having protective (cryptic) coloration and long spiny legs: although there are but two species in the country, we have 52 records in our tabulations representing 15 species of birds. The larger numbers of specimens taken were: nine by a crow, 12 by a road-runner, and from 15 to 40 in five instances by the eastern kingbird. These records show that the most potent protective adaptations possible do not necessarily protect. The highly significant fact about the case is that predators do not seem to recognize the dangerous qualities of the rose chafer; every generation of young chicks and pheasants will pay a heavy death toll if permitted to stuff themselves with these beetles. Even trout kill themselves in the same way. But what advantage is all this to the beetle? Those that cause the death of some predators, themselves lose their lives, that is, all of those actually proved "fit" in this respect are eliminated; the only effective poisonous action is upon young (among birds)—adults can and do eat them freely. No considerable body of predators has ever been killed, and "warning color" has not been acquired (the rose chafer is a uniform and inconspicuous brownish-yellow). Theories as to protective adaptations seem to suffer from every angle of this case. (For fuller discussion of the subject see Lamson, Geo. H., Journ. Econ. Ent., vol. 8, no. 6, pp. 547-548, Dec., 1915; Bates, J. M., Science, n. s., vol. 43, pp. 209-210, Feb. 11, 1916; and McAtee, W. L., The Auk, vol. 33, no. 2, pp. 205-206, Apr., 1916.)

Some curiosity may be felt as to the relations of birds to the large Scarabaeidae and Lucanidae with thoracic horns and especially strong or greatly enlarged mandibles. In nearctic America we have few species in any of these groups; another limiting factor important in relation to bird predators is the large size of these beetles. Nevertheless all of the genera are represented in the food of birds, *Passalus* by 32 records, *Platycercus* by 19, *Lucanus* by 25, *Ceruchus* by three, *Dorcus* by six, *Sinodendron* by seven, and lucanids further unidentified by 28 determinations; our largest scarabaeid, *Dynastes* is represented by five identifications, *Strategus* by 27, *Xyloryctes* by seven, *Copris* by 62, and *Phanaeus* by 252. The latter genus, besides being "horned," has brilliant metallic colors.

The long-horned beetles or Cerambycidae include many species with showy colors, but selectionists as a rule have not attributed distasteful qualities to the group; rather they have considered these beetles mimics of various more strongly "protected" insects such as wasps and other Hymenoptera and weevils. Numerous longicorns have cryptic coloration also, but their chief defense must be residence of the long larval stages in wood where they can be reached only by a small proportion of insect predators. The imago state, only in which the colors theorized about are displayed, is of relatively short duration. Bearing these facts in mind we believe the records show that longicorns are fed upon to such an extent as to indicate that in proportion to availability they contribute their due share to the subsistence of birds.

The total number of determinations in the present tabulations is 1,585, shared by 162 species of birds. Twenty-one kinds of birds have from 10 to 19 records each; six additional species from 20 to 29; six others from 30 to 39; one other 42; still another 53; and two as many as 169 and 173 respectively. The woodpeckers, on account of their peculiar qualifications for obtaining the larvae, naturally are the chief enemies of Cerambycidae. Several of the species prey upon these beetles to the extent of from 10 to 50 per cent of their total food. The number of adult beetles taken at a meal by these or other birds exceeded 30 in a number of cases and in four ran as high as 83, 100, 102, and 168. The last named figure is for one of our most wasplike species, *Xylotrechus colonus*, in the stomach of a raven. There are 10 identifications of *Xylotrechus;* of the other wasp-colored longhorns, we have the following numbers of determinations: *Cyllene*, 10 (28 specimens of *C. robiniae* in the stomach of a magpie); *Calloides nobilis* 1, *Neoclytus* 11, *Clytanthus* 12, *Clytes* 5, *Strangalia* 6, *Typocerus* 16, and *Leptura* 39. It is noticeable that the numbers appended correspond very closely to the relative abundance in individuals of these genera. Of the ant-suggesting genera, we have for *Euderces* five records and for *Cyrtophorus* one; and for the ichneumonid-mimic *Neolorchus* three identifications.

The figures for the distinctly warningly colored genera are *Acmaeops* seven, *Desmocerus* two, *Gaurotes* two, *Tetraopes* nine, and *Oberea* five. Such a catalogue shows that all the forms, whatever their alleged " protection " are eaten more or less, and there is no other explanation of the comparative extents to which they are taken so reasonable and satisfying as that it probably depends almost entirely on their relative abundance and availability to birds.

The Chrysomelidae or leaf beetles are classed by Professor Poulton as undoubtedly specially protected, and Donisthorpe writing of them under another name says: " The Phytophaga are considered to be all more or less distasteful, and no doubt justly so. Many species have been proved to be so, and the group is mimicked by various orders of beetles throughout the world." (Trans. Ent. Soc. London, 1901, p. 367.) Selectionists should have been somewhat restrained in their theorizing by the very name Phytophaga, for the leaf beetles and their allies being groups that subsist directly upon vegetation, must according to inevitable law in the organic world form the base of a column of predacious life more or less exclusively dependent upon them. Like the grazing mammals, all plant-feeding insects, no doubt, have their lions, wolves, and eagles, their hyaenas, jackals, and vultures.

No reason appears from the records of bird food here discussed to warrant doubt that the leaf beetles do in fact contribute their full quota toward the subsistence of predatory animals. The total number of identifications of Chrysomelidae is 5,666, and these are shared by well over 200 species of birds, so it is certain that practically all of our birds feed more or less upon these beetles. More than 230 species of Chrysomelidae are represented in the determinations, this in turn indicating that all tribes of the family are preyed upon. The Cassidini, on account of their bright colors and specialized larvae, receive frequent mention as a specially protected group but our scant representation of this tribe seems to bear its share of bird predation; *Cassida* 3 records, *Physonota* 2, *Coptocycla* 48, and *Chelymorpha* 48. Again correspondence of the number of identifications with observed frequency of the insects is quite evident.

Resemblance to caterpillar droppings always is spoken of by selectionists as a prime defense, and one tribe of our leaf beetles, the Chlamydini, exhibits this to a high degree. When feigning death, as they do when disturbed, they "resemble the excrement of certain caterpillars so closely as to render their detection difficult . . . . and it is said that birds will not pick them up." (Blatchley, Coleoptera of Indiana, p. 1,114, 1910.) Two genera represent this tribe in our fauna and of these, *Chlamys* has been found 56 times in bird stomachs and *Exema* 17 times; 10 of the latter beetles were contained in a single stomach of a Bewick's wren. The number of determinations cited, in view of the few species we have of this tribe, fully satisfies the probabilities.

The genus *Diabrotica*, chiefly yellow and black species, has received special attention from the standpoint of protective adaptations. "I believe," says C. J. Gahan, "that the species of *Diabrotica* are protected, and that the species of *Lema* derive advantage by mimicking them." (Trans. Ent. Soc. London, 1891, p. 369.) The tabulations of bird food here discussed show 41 records of *Diabrotica vittata* distributed among 17 species of birds; 107 of *D. 12-punctata* for 42 species of birds (18 specimens being found in a stomach of a cliff swallow); and 194 records of *D. soror* for 22 kinds of birds (a black-headed grosbeak had eaten 21 of these beetles). There are also 34 other records for scattering and unidentified species of the genus. Thus there is no evidence of special protection for *Diabrotica;* as for *Lema* the species are much less numerous in individuals, and that is the real reason they are captured less frequently by birds; we have 22 identifications shared by 14 species of birds.

One other Chrysomelid, the Colorado potato beetle (*Leptinotarsa 10-lineata*), has had its protective adaptations pointed out on numerous occasions, and like the rose chafer, among the Scarabaeidae, seems to be actually poisonous. (See Riley, Seventh Missouri Rep., 1875, pp. 6-7.) However, our records show that 23 species of birds devour the insect and 11 others are added by the literature of the subject. One hundred and eighteen identifications of this pest are included in our tabulations; the larger number of specimens found in single stomachs are 8 in that of a starling, 10 in a sharp-tailed grouse, 12 in a black-headed grosbeak, and 14 in a rose-breasted grosbeak. Birds such as the bob-white, crow, and rose-breasted grosbeak are recorded as having cleared fields of these pests.

Before leaving the Phytophaga or Chrysomelidae it may be well to cite certain records of large numbers of individuals being taken at a meal by birds, since they show not only that there is no restriction of bird attack to certain tribes of the family but also that there is no restriction of the more important avian predators to certain groups of birds. Some of the larger records are: 36 specimens of *Micro-*

rhopala vittata taken by a starling; 47 *Donacia* by a red-winged blackbird; 50 of *Systena* sp. by a Baird's sparrow; 50 of *Disonycha caroliniana* by a horned lark; 58 of *Myochrous denticollis* by a house wren; 212 *Donacia subtilis* by a Franklin's gull; 250 *Colaspis brunnea* by a nighthawk; and about 300 *Epitrix cucumeris* by each of five individual tree swallows.

Bruchidae spend so much of their lives within seeds that they are little exposed to attack by birds; an advantage which probably is compensated for by their being devoured with the seeds by some birds and other seed-eating animals. However, this is a subject that has scarcely been investigated. Our 47 records represent nine or more species of bruchids and were distributed among 29 species of birds. Expectations based on availability of free bruchids probably are satisfied.

The great series or suborder of beetles known as the weevils or Rhynchophora, for the most part, are said to be cryptically colored, resembling seeds, buds, bark, bits of earth, bird droppings, etc. Wallace adds: "One of the characters by which some beetles are protected is excessive hardness of the elytra and integuments. Several genera of weevils (Curculionidae) are thus saved from attack and these are often mimicked by species of softer and more eatable groups." (Darwinism, p. 260, 1896.) However, it should be pointed out at once that those who predicate hardness as a defense against predators do so without due reflection upon the digestive powers of animals.

Recall the fragmentation and gulping down of bones by dogs; the swallowing of snails, shells and all, by squirrels; while reptiles, amphibians, birds of prey, and predatory mammals either swallow their vertebrate prey whole or in large pieces, the bones included; waterfowl and shorebirds habitually take shellfish entire, including such hard-shelled forms as clams and oysters; gallinaceous birds are provided with gizzards which grind up the hardest seeds; and finches and numerous other birds are just as effectively equipped if on a smaller scale. Not only do birds with gizzards grind up their food materials, but the grit and pebbles they swallow are in most cases gradually ground down and pass out through the intestines in the form of fine sand. Most predators, in fact, have either a powerful mechanical or a resistless chemical digestion that as a rule is fully competent to dispose of anything entrusted to it. With such digestive powers at the service of predators, it is extremely unlikely that hardness in the degree possessed by weevils is any bar to their being eaten; moreover being jointed, weevils are thoroughly susceptible to chemical digestion.

In illustration of the factor of hardness as related to bird food the three genera *Lixus, Thecesternus,* and *Sphenophorus,* representing as many families of weevils, may be discussed. *Lixus* is so hard that the entomologist usually finds drilling a necessary preliminary to pinning; moreover the species are full of vitality, sometimes living through 24 to 36 hours in the cyanide bottle. Records of this genus in our tabulations total 102, distributed among 27 species of birds. No fewer than 18 specimens were found in a single stomach of a nighthawk. *Thecesternus,* a weevil with unusually thick and hard integument, was identified 151 times in the stomachs of 22 species of birds. Twelve specimens were taken by a meadowlark at a meal and 15 by a robin. The billbugs of the genus *Sphenophorus* not only are hard, but like *Lixus* have much ability to resist the fumes of cyanide and prolonged submersion in water. However 1,397 determinations were made representing 34 species of these weevils. They were found in the stomachs of no fewer than 110 species of birds. Some of the larger numbers taken from single stomachs were: 10 in the cases of the upland plover, clapper rail, and yellow-headed blackbird; 11 in a robin; 12 in an avocet; 17 in a crow blackbird; 20 in a killdeer; 33 in a crow; and 34 in a magpie.

Hardness thus appears to be of no consequence as a defense. Brief attention may be paid to a few other of the so-called protective devices of weevils. One of the obscurely colored genera, with the habit of dropping to the ground and feigning death, is *Rhinoncus;* such weevils are said to resemble seeds, but what good this would do, since most birds eat seeds, theorists have left unexplained. *Rhinoncus* has been identified 73 times from the stomachs of 30 species of birds, of one of which, the olive-backed thrush, an individual had eaten 20 of these weevils. *Rhodobaenus,* our only conspicuous red and black weevil, was identified 14 times in the stomachs of 10 species of birds, and *Tyloderma,* black weevils with whitish or yellowish markings, 133 times in 48 species of birds. Fifteen specimens of *Tyloderma* were taken from the stomach of a meadowlark.

To mention the relations of birds to a few representative genera of weevils, we may record that the rare *Otidocephalus* were identified six times in the stomachs of an equal number of species of birds; that the minute *Apion* were taken 91 times by 36 species; the nut weevils (*Balaninus*) 380 times by 85; the cotton-boll weevil (*Anthonomus grandis*) 348 times by 43 species of birds (23 other species are recorded as enemies in the literature); the alfalfa weevil (*Hypera murinus*) 2,222 times by 50; the clover root weevils (*Sitona*) 1,611 times by 94; the engraver beetles (*Ips* [*Tomicus*]) 120 times by 24; and the Anthribidae 29 times by 21 species.

A few of the larger numbers of weevils found in single stomachs also may be cited; thus 109 *Dorytomus mucidus* were found in one stomach of a downy woodpecker; 153 *Calandra oryzae* in a barn swallow; 167 *Barypithes pellucidalis* in a starling; 282 *Hyperodes* sp. in an eared grebe; and 281 larval and adult alfalfa weevils in a Brewer's blackbird, 300 in a killdeer, and 317 in a valley quail.

The nearly 20,000 identifications of weevils in birds' stomachs attest to the frequency of their capture, and records such as those just cited to the relish with which they are eaten.

Though to all weevils are attributed various protective adaptations, weevils of all sorts are preyed upon; the secret of the whole relationship between prey and predator in this as in other cases is distribution of the attack. All available food supplies are sought by predators and the amount of attention they receive is in direct proportion to their availability.

Total number of identifications, of Coleoptera 85,322; percentage of identifications among those of all insects, 44.6899; percentage of species in this order among those of all insect species known, 46.2032.

Other enemies.—It is difficult to summarize what is known regarding the predatory foes of so extensive an order as the Coleoptera. Fresh-water fishes prey systematically upon both larvae and adults of the aquatic beetles but secure other forms only incidentally. However it appears that falling into the water or otherwise becoming available as prey for fishes is a more or less frequent happening to terrestrial beetles, since most of the families are represented in the food of these animals. (See especially Forbes, papers, bibliography p. 188.)

Kirkland reports Coleoptera as making up the following percentages of the food of 149 common toads: ground beetles and their allies, 8 per cent; May beetles and allies, 6 per cent; wireworms and allies, 5 per cent; weevils, 5 per cent; potato beetles and allies, 1 per cent; carrion beetles, 1 per cent; and miscellaneous beetles, 1 per cent. Drake found Coleoptera to constitute 33 per cent of the whole number of animals consumed by 209 leopard frogs and 54 per cent of the insects. The number of specimens of various families identified was: Carabidae 176, Cicindelidae 44, Hydrophilidae 1, Staphylinidae 12, Coccinellidae 13, Erotylidae 1, Elateridae 1, Spondylidae 2, Cerambycidae 4, Chrysomelidae 2, Tenebrionidae 1, and Rhynchophora 146. It is worth noting that this author says of weevils: "The habit of these insects of dropping to the ground when disturbed gives the frog a chance to capture them." This is just the habit the selectionists have declared protective. Klugh reports finding 35 Colorado potato beetles and five other Coleoptera in 25 stomachs of the leopard frog. Surface's report shows that other frogs and toads feed extensively upon beetles, the larger families contributing most heavily; the salamanders also eat a great many beetles, especially aquatic forms. Lizards, snakes, and turtles also feed upon beetles, some of the smaller terrestrial snakes taking a great many of them. Pack reports lizards feeding on beetles of such "protected" groups as Coccinellidae, Erotylidae, Meloidae, and Chrysomelidae.

Among mammals, moles and shrews prey freely upon beetles, taking Scarabaeidae and their larvae more and wireworms and ground beetles less often. Spermophiles, prairiedogs, chipmunks, squirrels, grasshopper mice, and other rodents as well as raccoons, foxes, and coyotes prey upon beetles occasionally, and such animals as bats, skunks, and armadillos depend upon them to a much larger extent. There is no reason to believe that the "protected" groups of beetles fare any better with mammalian than with avian predators. However citation of a few instances of the capture of such beetles may be advisable. A series of three armadillo (*Tatu novemcinctum*) stomachs from Texas contained Carabidae and Scarabaeidae in profusion, also weevils, Histeridae, Lampyridae, Staphylinidae and Tenebrionidae (including *Eleodes*). The stomach of a skunk (*Mephitis occidentalis*) collected at Nelson, Calif., held 60 per cent of pupae of the Colorado potato beetle; two shrews (*Sorex vagrans amoenus*) from Crater Lake, Ore., had fed on Silphidae, one to the extent of 50 per cent, the other to 100 per cent of the total food. A prairiedog (*Cynomys gunnisoni*) from Magdalena, N. Mex., had nothing but remains of *Calosoma triste* in its stomach, and a badger (*Taxidea taxus*) from Ash Meadows, Nev., had eaten no fewer than 150 *Calosoma prominens*.

Passing to the enemies of beetles in the insect kingdom, it is well known that the various predatory tribes make no exception of beetles even though their generally hard integuments would seem to be a bar. Mantids, chrysopids, robber flies, predacious bugs and beetles, wasps, ants, dragonflies, and spiders all feed upon beetles, and every tabulation of the species eaten by them shows "protected" forms liberally represented. Beetles are subject to numerous parasites which attack them in all stages from egg to imago, and like most insects, they at times are decimated by fungal or bacterial intruders.

While it has been impossible in the limits of this paper to discuss fully the enemies of beetles other than birds, a few cases may be cited in more detail as showing how the activities of such foes supplement the predatory activities of birds. Take for example the wood-boring beetles, which although they are eaten by birds to an extent that indicates that no special protective adaptation operates in their favor, yet are shielded from most birds during the greater part of their lives by living under bark or even within solid wood. However this habit does not put them out of the reach of predatory and parasitic insects. Thus Kleine records 159 hymenopterous parasites of Cerambycidae, and 136 beetle predators and 157 hymenopterous parasites of Scolytidae in Europe. (Ent. Bl. Nurnberg, vols. 4-5, 1908-1909.) The cotton-boll weevil (*Anthonomus grandis*) again passes the larval and pupal stages apparently well hidden from most enemies, yet some of the 66 kinds of birds known to prey upon it remove the immature stages from the cotton bolls, and in addition the weevil has 54 insect enemies, about half of which attack the concealed stages. (Bull. 100, U. S. Bur. Ent. 1912.)

So it is with the mechanically protected species; all have in the chains of their life histories weak links, of which hungry predators and assiduous parasites are not slow to take advantage. For contrast, consider the case of the Colorado potato beetle, an insect exposed almost throughout its life history, and with all of the attributes—color, reflex bleeding, nastiness, even poisonous qualities—of a most highly "protected" insect. Besides the 27 species of wild birds known to feed upon this insect, ducks, chickens, guinea fowls, skunks, snakes, frogs, toads, at least eight species of Pentatomidae, two of Reduviidae among bugs, and eight of Coccinellidae and seven of Carabidae among beetles, besides robber flies, wasps, spiders, phalangids, and mites prey upon the various stages. Despite all of its protective adaptations, the Colorado potato beetle undoubtedly has its full quota of foes; its rapid increase and spread over the United States was due to enormous increase by cultivation of a favored food plant and not to lack of enemies. Dr. F. H. Chittenden remarks: "Few, if any, noxious insects have so many recorded natural enemies as the Colorado potato beetle." (Bull. 82, pt. 7, U. S. Bur. Ent., p. 85, Feb., 1911.) In other words, the potato beetle, being an important economic insect, has been much studied, and among other things we have learned that it has numerous enemies. If less were known about the species it would be hailed as a marvelous instance of protective adaptation; facts are a terrible handicap to theorizing.

Discussion.—In general we have seen that whatever the beetle, something in the way of protective adaptation has been claimed for it, yet practically all are eaten. On the other hand we have also seen that the large families of Coleoptera, those abundant in individuals, are most freely eaten by birds, while the small families with few species escape with small losses. It is the old story over again of food supplies (beetles in the present consideration) being drawn upon in proportion to their abundance and availability.

MECAPTERA (SCORPIONFLIES)

Protective adaptations.—The scorpionflies are predacious; those of the genus *Panorpa* commonly have yellow bodies and black markings in the wings; and the males have enlarged genitalia carried aloft somewhat like the stings of scorpions. The species of *Bittacus* resemble crane flies.

Bird enemies.—We have only five records of scorpionflies being eaten by nearctic birds, these being distributed among four species.

Number of identifications, 5; percentage of identifications among those of all insects, .0026; percentage of species in this group among the whole number of insect species, .0260.

Other enemies.—There seem to be no records of such.

Discussion.—Poverty of data is the chief characteristic of the record for scorpionflies. These insects are not an obtrusive part of the insect fauna and have been little studied. The question of the efficiency of their protective adaptations in relation to predators can hardly be intelligently discussed at present.

DIPTERA (FLIES)

Protective adaptations.—Not much has been written about the protective adaptations of diptera, the suggestion most often made being that a considerable number of them " closely resemble wasps, and bees, and no doubt derive much benefit from the wholesome dread which those insects excite." (Wallace, Natural selection, p. 69, 1891.) The families that have the most numerous species supposed to resemble Hymenoptera are the Stratiomyidae, Bombyliidae, Asilidae, Conopidae, and Syrphidae. Many flies have metallic colors, which are alleged to be warning; such insects are common among the Stratiomyidae, Dolichopodidae, Tachinidae, and Muscidae. A large number of Diptera pass the greater part of their lives in the larval stage and many of these larvae are more or less protected from birds by their habitat, as the Cecidomyidae in galls, the Mycetophilidae and others in fungi, the Culicidae, Chironomidae, many Tipulidae, the Simuliidae, Stratiomyidae, Tabanidae, and Ephydridae in mud or water; and various others in excrement and other decaying organic matter. Of course this sort of protection is of no avail in the case respectively of birds which eat galls or fungi or which obtain their food chiefly in or about water, or which feed directly upon or by tearing up carrion and the like.

Bird enemies.—Until comparatively recently it was very difficult to get identifications of flies found in bird stomachs, and even more so of their larvae, hence nearly half of the identifications of Diptera were not carried further than to the order.

The large proportion of the unidentified to the total number of records of Diptera has one advantage, namely that it is distributed probably among nearly as great a number of species of birds as are the records for all flies. Since that number exceeds 250, we may be sure that there is no group of birds that habitually avoids Diptera. Among these records are numerous instances of from 50 to 500 specimens of flies or their larvae being taken at a single meal, good evidence that the flies concerned were not at all distasteful. These data are sufficient commentary also on the state of determinations of Diptera, scores of specimens being present and not being named even to the family. The material will be re-examined in the future to obtain more satisfactory results, but there has been no time for that in connection with the present paper, which is wholly a by-product.

A satisfactory discussion of the relations of birds to Diptera is hardly possible therefore, and the best that can be done is to present the fragmentary data available and to make allowances for deficiencies.

Identifications of Diptera

Family	Number of identifications	Percentage of identifications among those of all Diptera	Percentage of species in this family among the whole number of nearctic Diptera [1]
Tipulidae	1,565	14.4426	5.7309
Dixidae	3	.0277	.0922
Psychodidae	5	.0461	.3920
Chironomidae	1,003	9.2562	3.0903
Culicidae	112	1.0336	1.9257
Mycetophilidae	53	.4891	2.9058
Cecidomyidae	15	.1384	1.6835
Bibionidae	140	1.2920	.8648
Simuliidae	8	.0738	.3173
Blepharoceridae	1	.0092	.1384
Rhyphidae	1	.0092	.0807
Orphnephilidae	...	...	.0115
Stratiomyidae	732	6.7553	3.4362
Tabanidae	336	3.1008	3.5285
Acanthomeridae	...	...	.1153

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[1] Computed from Aldrich, J. M., A catalogue of North American Diptera, etc., Smithsonian Misc. Coll., vol. 46, pp. 1-680, 1905.

Identifications of Diptera—Continued

Family	Number of identifications	Percentage of identifications among those of all Diptera	Percentage of species in this family among the whole number of nearctic Diptera
Leptidae	42	.3876	1.4644
Nemestrinidae	...	...	.0692
Cyrtidae	1	.0092	.4843
Bombyliidae	8	.0738	5.2581
Therevidae	5	.0461	.8187
Scenopinidae	1	.0092	.1268
Mydaidae	...	...	.5074
Apioceridae	...	...	.0807
Asilidae	170	1.5688	6.3536
Dolichopodidae	86	.7936	6.2959
Empididae	48	.4430	5.4196
Lonchopteridae	...	...	.0346
Phoridae	9	.0830	.7380
Platypezidae	...	...	.2998
Pipunculidae	...	...	.3229
Syrphidae	259	2.3902	9.3401
Conopidae	...	...	1.0378
Oestridae	4	.0369	.3459
Tachinidae	54	.4983	12.6841
Dexiidae	...	...	1.9833
Sarcophagidae	102	.9413	1.4183
Muscidae (sens. lat.)	512	4.7250	...
Anthomyiidae	109	1.0059	3.4478
Scatophagidae	79	.7290	.9917
Heteroneuridae	7	.0646	.1614
Helomyzidae	11	.1015	.4728
Borboridae	29	.2676	.2767
Phycodromidae	20	.1846	.0231
Sciomyzidae	13	.1200	.7380
Sapromyzidae	24	.2215	1.2338
Ortalidae	18	.1661	1.7181
Rhopalomeridae	...	...	.0346
Trypetidae	10	.0923	2.3984
Micropezidae	...	...	.7380
Sepsidae	8	.0738	.3344
Psilidae	...	...	.2883
Diopsidae	...	...	1.0115
Ephydridae	305	2.8147	1.6720
Oscinidae	20	.1846	1.5451
Drosophilidae	2	.0184	.8763
Geomyzidae	1	.0092	.1730
Agromyzidae	2	.0184	1.0954
Hippoboscidae	1	.0092	.5304
Nycteribiidae	...	...	.0576
Unidentified	4,904	45.2566	

From the foregoing table it is evident that crane flies (*Tipulidae*), midges (*Chironomidae*) and mosquitos (*Culicidae*) are adequately represented, and it is fair to say that an important reason for this showing is that the groups of birds eating most of these flies and their larvae have been examined rather recently and that in consequence closer identification of their food items has been made. This would indicate that records for the other families will be similarly increased by future studies. It is worth noting that most of the larvae of Chironomidae which are so commonly eaten by birds are red (a warning color) so much so as to be popularly called "bloodworms." There are numerous instances of hundreds of these larvae being taken at a single meal.

The more than 10,000 records of Diptera mark these insects as a valuable bird food; as in other cases certain birds prey to a greater extent upon the group than others; of these may be cited seven species of swallows which make 13 per cent to 40 per cent of their total food of flies and an equal number of flycatchers consuming them to the extent of from 11 per cent to 44 per cent of their entire subsistence.

Total number of identifications, 10,836; percentage of identifications among those of all insects, 5.6757; percentage of species in this order among the whole number of insect species known, 11.4432.

Other enemies.—Fishes are among the most important enemies of flies having aquatic immature stages. Pearse, writing of the food of 33 species of fishes in Wisconsin lakes, reports 20 per cent of their food to consist of flies and their larvae, chiefly the latter. Marine Chironomidae are eaten by shrimps and sea-anemones. A variety of fishes, the top minnows and killifish in particular, are such efficient enemies of mosquito larvae that they have been widely used in mosquito-control campaigns. Diptera are eaten quite freely by frogs and toads and to a lesser extent by lizards, snakes, and turtles. Among mammals, shrews, moles, and bats feed regularly and extensively upon Diptera; other mammals that get at least some Diptera are mice, squirrels, foxes, and armadillos.

Among their own kind, *i. e.,* insects, about all the predacious kinds feed freely on flies. The latter are soft-bodied insects easily pierced by the sucking predators or chewed up by the biting kinds. Tiger beetles, assassin bugs, mantids, ants, panorpids, dragonflies, and robber flies and other predacious members of their own order habitually feed upon flies. A number of families of wasps, such as the Nyssonidae, Bembecidae, Crabronidae, and Vespidae, prey freely upon Diptera, and spiders gain from their ranks a considerable share of their subsistence. Flies appear to be subject to parasitism only to a comparatively slight extent but some of them are decimated by fungal diseases.

Discussion.—While flies in the adult stage appear to have a degree of freedom from predators, it is evident that the immature stages of many groups of them pay a heavy toll; the chief food of predacious fly and beetle larvae that live under bark, in decaying fungi or carrion are the fly larvae they find there; the chief food especially of the young of a great many fresh-water fishes again are fly larvae and pupae; and a very important element of the food of the mold- and earth-traversing shrews and moles are the larvae of flies. Fly larvae perish in large numbers also because of the drying up or exhaustion of their breeding nidus. Possibly some relative good fortune for the adults may be only compensatory, but so little is known about the subject that discussion is not on a very firm basis. Regarding the fate of adults it is worth while recalling the all but universal destruction at times wrought among the ranks of its hosts by the fungus *Empusa muscae.*

Evidence showing the importance of availability as regulating the consumption of dipterous food is presented in testimony of an Alaskan correspondent about birds feeding on mosquitos. These insects, so much more prominent an element of the insect fauna of that territory than they are in the United States, apparently are fed upon much more freely by birds. This correspondent, A. H. Twitchell, a reindeer breeder, reports all small birds frequenting the vicinity of his camp, as myrtle, blackpoll, and Wilson's warblers, Gambel's sparrow, and Alice's thrushes preying regularly on mosquitos and feeding them extensively to their young.

HYMENOPTERA (ANTS, BEES, WASPS)

Protective adaptations.—In selectionist writings, Hymenoptera usually are classed as the very acme of protected insects, and protective qualifications are broadly assigned to the whole group. Poulton says: "Ants and wasps are known to be aggressive dominant insects avoided by the majority of insect-eating animals." (Essays on evolution, p. 281, 1908.) Drummond, in similar vein, declares that "well-armed or stinging insects are always conspicuously ornamented with warning colours. The expense of eating a wasp, for instance, is too great to lead to a second investment in the same insect, and wasps therefore have been rendered as showy as possible so that they may be at once seen and as carefully avoided. The same law applies to bees, dragonflies, and other gaudy forms; and it may be taken as a rule that all gaily-coloured insects belong to one or other of these two classes; that is, that they are either bad eating or bad stingers." (Tropical Africa, p. 163.)

Mimicry of a group is supposed to be a tribute to its specially defended character and it is said that: " The hymenoptera including the formidable hornets, wasps, bees and ants are more frequently mimicked than any other order." (Poulton, The colours of animals, p. 245, 1890.) " Stinging hymenoptera . . . . are sedulously avoided by insectivorous creatures in general." (Bastin, Insects, their life-histories and habits, p. 247, 1913.) Numerous Hymenoptera which do not possess stings are said to mimic those that do have them and species of one non-stinging group, the sawflies, are alleged to be protected in the larval stage by distasteful or disagreeable internal or external secretions.

Bird enemies.—For many years difficulty was experienced in obtaining identifications of hymenoptera and the following table plainly shows the effect of this situation, more than a third of the determinations being to the order only.

Identifications of Hymenoptera

Family	Number of identifications	Percentage of identifications among those of all Hymenoptera	Percentage of species of this family among the whole number of species of these groups in New York State[1]
Xyelidae	2	.0074	.4640
Pamphiliidae	5	.0185	1.2529
Tenthredinidae	263	.9732	17.5407
Xiphydriidae	5	.0185	.3248
Siricidae	16	.0592	.3719
Cephidae	2	.0074	.2320
Oryssidae	1	.0037	.1392
Tenthredinoidea (further unidentified)	85	.3145	...
Vipionidae	72	.2664	.9745
Alysiidae	13	.0481	.2320
Capitoniidae	1	.0037	...
Braconidae	28	.1036	9.0488
Evaniidae	5	.0185	.3719
Trigonalidae	1	.0037	.6496
Ichneumonidae	1,113	4.1184	25.6614
Ichneumonoidea (further unidentified)	13	.0481	...

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[1] Computed from Bradley, J. Chester, Hymenoptera, in A list of the insects of New York, etc., Mem. 101, Cornell Univ. Agric. Exp. Sta., pp. 870-1,033, 1926, the most comprehensive checklist of nearctic forms available.

Identifications of Hymenoptera—Continued

Family	Number of identifications	Percentage of identifications among those of all Hymenoptera	Percentage of species of this family among the whole number of species of these groups in New York State
Figitidae	14	.0518	.0464
Cynipidae	38	.1406	6.7286
Pteromalidae	22	.0814	.9280
Eupelmidae	3	.0111	.1392
Callimomidae	12	.0444	.6032
Eurytomidae	5	.0185	1.5313
Perilampidae	3	.0111	.0464
Chalcididae	73	.2701	3.1091
Leucospidae	1	.0037	.0464
Chalcidoidea (further unidentified)	14	.0518	...
Platygastridae	7	.0259	.7889
Scelionidae	4	.0148	1.1137
Ceraphronidae	2	.0074	...
Diapriidae	12	.0444	.4640
Belytidae	7	.0259	.5568
Serphidae	8	.0296	.4176
Pelecinidae	9	.0333	.0464
Serphoidea (further unidentified)	18	.0666	...
Formicidae	2,092	7.7410	1.1137
Myrmicidae	1,200	4.4404	1.2529
Formicoidea (further unidentified)	9,451	34.9715	...
Chrysididae	61	.2257	1.0673
Bethylidae	9	.0333	.1392
Dryinidae	4	.0148	.3248
Scoliidae	285	1.0546	.9281
Myrmosidae	3	.0111	.0928
Mutillidae	23	.0851	.9745
Psammocharidae	36	.1332	3.6195
Eumenidae	35	.1295	1.8562
Vespidae	144	.5328	.5104
Vespoidea (further unidentified)	222	.8215	...
Sphecidae	76	.2812	3.2019
Bembecidae	4	.0148	2.5986
Sphecoidea (further unidentified)	23	.0851	...
Halictidae	134	.4958	.9745
Andrenidae	92	.3404	2.4594

Identifications of Hymenoptera—Continued

Family	Number of identifications	Percentage of identifications among those of all Hymenoptera	Percentage of species of this family among the whole number of species of these groups in New York State
Panurgidae	2	.0074	.3248
Nomadidae	12	.0444	.8817
Euceridae	10	.0370	...
Anthophoridae	4	.0148	.5568
Hylaeidae	1	.0037	.3248
Colletidae	8	.0296	.3248
Megachilidae	18	.0666	1.6241
Ceratinidae	2	.0074	.0464
Stelidae	1	.0037	.0928
Xylocopidae	2	.0074	.0464
Apidae	139	.5143	.8353
Apoidea (further unidentified)	372	1.3765	...
Unidentified	10,682	39.5266	...

Examination of the preceding tabulation shows again the influence of availability upon choice of food. It is at once evident that the groups more numerous in species and individuals are taken most often by birds. Whether all are taken in sufficient number to satisfy expectations is subject to discussion but the relativity of capture to abundance is unmistakable. Superfamilies such as the Cynipoidea and Chalcidoidea, owing to the minute size of most of their species, could not be expected to figure largely in the diet of birds, and the same is true for most Serphoidea. These are just the groups and the only ones in the table except the Sphecoidea that seem obviously to be inadequately represented. The Sphecoidea perhaps verge toward the opposite limit of size for bird food.

Since so many Hymenoptera were determined no further than to the order, the number of species (over 300) of birds eating these unidentified forms may be taken as an approximation to the entire number of bird species consuming Hymenoptera. It is enough at any rate to indicate that Hymenoptera are eaten by birds of all groups studied, just as the total number of records (over 27,000) of Hymenoptera clearly shows that these insects are one of the most important elements of bird food.

Beginning our consideration of the Hymenoptera with the sawflies, it may be said that some of these insects are alleged to obtain protection from their resemblance to stinging members of the order. As to the larvae, Poulton says: "Numerous experiments have convinced me that the latter are almost invariably distasteful." (Essays on evolution, p. 238, 1908.) However, the present tabulations reveal more than 30 species of birds as predators upon sawfly larvae and no fewer than 50 to 100 specimens of these larvae have been found in single stomachs of the mockingbird and from 10 to 25 in those of other species. Hewitt records seven species of British birds as feeding upon larvae of the large larch sawfly (*Nematus erichsonii*) (Bull. 10, Div. Ent. Dom. Can. Dep. Agr., p. 22, 1912), and attributes to them great destruction of the larvae. The 380 records of Tenthredinoidea in our table are distributed among 99 species of birds and such wasp-suggesting forms as *Cimbex,* and the horntails of various kinds, with 24 records, seem to be proportionally represented.

Most of the Ichneumonoidea are not credited with any special defenses besides their resemblance to stinging hymenoptera, and the more than 1,200 records of their being eaten would seem to indicate that this means of protection is more imaginary than real. Some of the more interesting records may be cited as indicating the extent to which birds eat these insects: *Protapanteles:* 50 specimens in the stomach of an English sparrow (one of a series of 12 containing 10 or more each), and 120 in one stomach each of a Brewer's blackbird and an Aleutian sandpiper; Ichneumonidae, further unidentified: 68 specimens in a sanderling's stomach (19 birds have from 10 to 42 records each); *Ichneumon* sp.: 37 specimens in the stomach of a burrowing owl; *Glypta tuberculifrons:* 44 individuals taken at a meal by a yellow-throated vireo; *Ophion* spp.: 54 records for these large ichneumons which can sting.

Most ants, their size considered, can bite severely; their body fluids contain formic acid and other pungent substances; and many of them also can sting. As further tribute to their prowess the reference of Poulton may be quoted to the "numerous mimetic resemblances to the aggressive, abundant, and well-defended ants." (Essays on evolution, p. 252, 1908.) Badenoch says that ant-models "as a rule are exempt from persecution." (Romance of the insect world, p. 300, 1893). The confidence of selectionists in the protective nature of ant mimicry is further shown in the following statement by Donisthorpe on *Nabis lativentris:* "I consider this insect to be an ant mimic in its earlier stages, when it is usually found in the company of ants. From this mimicry it obtains protection from outside enemies, both as much when away from ants as when with them." (Ent. Monthly Mag. 3rd ser., vol. 7, pp. 137-138, 1921.)

But why this conclusion? The more than 12,000 records of ant-eating by the birds represented in our tabulations certainly indicate no sort of immunity on the part of ants from the attacks of birds. These records are shared by well over 300 species of birds which, practically speaking, means that all birds eat ants. Ninety-three of the species of birds represented in our tabulations have from 10 to 49 records of ant-eating each, 18 others from 50 to 99, 17 others from 100 to 199, four additional over 300, and one additional species, the eastern flicker, in excess of 500. All these records are among the Formicoidea further unidentified, three-fourths of the total for all ants. From 200 to 300 ants at a meal is a common number; the swallows often get 800 or more; the nighthawk 1,000; and woodpeckers 2,000 or more. In two cases stomachs of flickers yielded more than 3,000 ants each, and in one case more than 5,000. Out of 684 stomachs of this last named species, 524 contained ants.

In this connection the extent to which ants enter into the diet of certain birds is of considerable interest; our five species of thrushes of the genus *Hylocichla* consume ants to an average of 12.65 per cent of their total food, while 16 species of woodpeckers, the food of which was tabulated by Prof. F. E. L. Beal, ate ants to extents varying from 5 to 85 per cent of their entire subsistence, the average for the 16 species being 28.49 per cent.

The stinging ants, of course, are the most highly "protected" of all and it is unfortunate for our discussion that the group is so poorly represented in the United States. Myrmicidae, including Ponerinae and Dorylinae, are more or less generally provided with stings, which however in the most of our species are too small to inflict damage on a human subject. Our tabulations show 1,200 records for Myrmicidae, and they are eaten in just as large numbers as are other ants. The harvester ants of the genus *Pogonomyrmex* are larger and equipped with stings which can painfully wound a human being. We have 66 records of these ants being taken by 25 species of birds; no fewer than 200 and 400 individuals were taken from the stomachs of two Texan nighthawks. Mitchell and Pierce write of birds feeding freely on *Pogonomyrmex* and note a case of a group of nesting jackdaws (*Megaquiscalus*) cleaning up a colony in a short time. (Proc. Ent. Soc. Washington, vol. 14, no. 2, p. 72, June, 1912.)

Among the remaining, mostly stinging, Hymenoptera are the Chrysididae, supposed to be protected by their hardness, abililty to roll into a ball, and by metallic colors. We have 61 records of these being eaten, shared by 37 species of birds. The Vespoidea or wasps as a whole have 822 records representing 140 species of birds. Some of the larger numbers of wasps consumed at a meal were 10 *Vespula germanica* by a wild turkey, 10 *Polistes* sp. by a yellow-billed magpie, and the following numbers of unidentified wasps by the birds mentioned: purple martin 17, olive-sided flycatcher 24, and kingbird 30.

The 103 records of Sphecoidea are distributed among 43 species of birds, none of which took any notable number of these large insects. Bees all sting, and the 797 records of their being eaten by the birds examined by us would seem to indicate considerable disregard for the stings on the part of birds. The number of species of birds represented in these bee-eating records is 144. Thirty-two species of birds took honey bees (*Apis mellifera*) on a total of 118 occasions and nine species of birds ate bumble bees a total of 18 times. These numbers of determinations seem in fair proportion to the availability of the bees concerned. The largest numbers of bees taken at a meal were 26 Andrenidae by a rose-breasted grosbeak, 34 honey bees by a cactus wren, and 106 of the domestic species by a road-runner.

It is of interest to note that besides the thrushes and woodpeckers previously mentioned, two other groups of birds are very notable consumers of Hymenoptera. Thus the seven species of swallows make an average of 24.9 per cent of their diet of these insects, and 14 species of flycatchers average 33 per cent.

Summary.—Number of identifications of Hymenoptera 27,025; percentage of identifications among those of all insects, 14.1551; percentage of species in this group among all insect species, 17.1798.

Other enemies.—Hymenoptera, having so few aquatic representatives, do not figure in the diet of fishes as anything but an incidental item, consisting of specimens, a considerable proportion of them ants, that have approached too near or have fallen upon the surface of the water.

Passing to batrachian enemies of Hymenoptera we may note that Kirkland found ants to compose 19 per cent of the contents of 149 toad stomachs, and that he had evidence also of their feeding extensively upon honey bees. Garman also found not only the common toad (*Bufo lentiginosus*) but also the pigmy toad (*Bufo quercicus*) to be very fond of ants. Toads have been observed to feed freely upon the larger stinging insects also, such as yellowjackets and wasps. Drake found 25 ants and 21 other Hymenoptera in 209 stomachs of the leopard frog. Insects of this order, especially ants, are eaten by all frogs and toads and to a considerable extent by salamanders also. Most lizards feed freely on ants, bees, and wasps. Winton found agricultural ants (*Pogonomyrmex*) in 80 per cent of the horned-toad stomachs (485) examined by him, and Mitchell and Pierce record the extermination of a colony of these ants by horned-toads. Several species of snakes and a few turtles feed to a slight extent upon Hymenoptera.

Among mammals, moles prey extensively upon ants, and shrews and bats by no means avoid them. In our country armadillos are destructive ant eaters and in other continents various mammals specialize upon ants. Spermophiles and other slightly insectivorous rodents include ants and other Hymenoptera in their bill-of-fare. Skunks are assiduous in digging out the nests of yellowjackets (*Vespula*), the comb, its contents and active inhabitants of the nest all being devoured. Mice, weasels, foxes, and especially badgers similarly ravage the nests of bumble bees, while bears plunder not only these insects but also honey bees and hornets. Meadow mice and shrews have been found to be among the most effective enemies of sawflies, extracting the larvae from the cocoons, and these and deer mice take a heavy toll of the Hessian fly, nibbling the stem-galls and devouring their inmates. Squirrels feed freely upon galls produced by Hymenoptera.

The insect enemies of Hymenoptera are numerous and effective and strangely enough many of them are within the ranks of the order. Philanthidae use Aculeates for food, many bees, cuckoo wasps, and the like live parasitically in the nests of other Hymenoptera; the surprising phenomena of hyper-parasitism reveal numerous serious enemies of Hymenoptera among their own kin; and a number of dipterous parasites of sawflies, bees, and wasps are known. The so-called guests in the nests of bees and ants destroy many of the larvae of their hosts. Predacious insects such as assassin bugs, Phymatidae, dragonflies, and robber flies feed freely upon Hymenoptera, the last-named foes almost appearing to have a preference for the larger and better armed sorts of stinging Hymenoptera. Spiders of certain species entrap and devour large numbers of Hymenoptera. Nematode and protozoan parasites exist and some Hymenoptera have important fungal and bacterial diseases.

Discussion.—According to selectionists, Hymenoptera are the most highly protected insects and the so-called mimicry of examples of this order, such as the ants, by numerous spiders, long-horned beetles and rove beetles, plant-bugs, and other insects is regarded as strong evidence for the truth of the claim. Let the case be presented in the words of an advocate (Poulton, Essays on evolution, p. 260-261, 1908): "The means by which the resemblance to ants is brought about are diverse, the end—the resemblance itself—is uniform. Furthermore the likeness is almost always detailed and remarkable, however it is attained, while the methods made use of differ absolutely. . . . . We are compelled to believe that there is something advantageous in the resemblance to an ant, and that Natural Selection has been at work. The phenomena do not merely disprove all other suggested causes of change; they constitute the most powerful indirect proof of the operation of Natural Selection."

If the above reasoning has any application so far as the attacks of predators upon ants are concerned, we should expect some evidence that ants are relatively free from such attacks. Let us see what is the case. Beginning in the very homes of the ants we find, among creatures habitually living in ant colonies, that numerous Staphylinid beetles devour the brood, besides crippled and even normal ants; the larvae of Clythrinae (Chrysomelidae) feed on the eggs; lycaenid caterpillars and paussid beetles eat the eggs and larvae. Numerous ectoparasitic mites and some chalcidids also attack the ants in their domiciles, as well as entoparasites among the Strepsiptera, Phoridae, Conopidae, Braconidae, Chalcididae, Proctrotrupidae, and Nematoda. Ants have very important predatory enemies in their own ranks, namely the doryline and slave-making ants. Ant-lions of the family Myrmeleonidae, Diptera with similar habits, predacious wasps, especially the Crabronidae, assassin bugs, ground and tiger beetles, and spiders are serious invertebrate enemies of ants. Most toads, frogs, and lizards, the amphisbaenids, and certain snakes feed upon ants; fishes take them when opportunity affords; practically all birds eat ants, several groups as the song thrushes, ant-thrushes (Formicariidae), and woodpeckers depending upon them for a large part of their food; in the same way most of the insectivorous mammals are fond of ants and several groups of this phylum are specialized ant eaters, namely Echidnidae (spiny anteaters) among the Monotremata, the banded anteater (*Myrmecobius*) among the Marsupialia. and nearly the whole order of Edentata (antbears, pangolins, and armadillos).[1]

In fact it would be difficult to name a group of insects that is so thoroughly preyed upon as the ants, and impossible to name one that has so many specialized foes scattered through the various animal phyla. So far as predatory attack is concerned, it would seem that ant-mimics court rather than avoid danger. To recapitulate: if there is any virtue in the protective adaptations of the " aggressive, abun-

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[1] For a comprehensive account of "The predacious enemies of ants," see Bequaert, Bull. Amer. Mus. Nat. Hist., vol. 45, pp. 271-331, 1922.

dant, and well-defended ants," it should be apparent in some lessening of predatory attacks upon them. However the very opposite is true and the case affords the best sort of proof of the thesis of this paper, namely that the number of enemies, or perhaps better stated, the total losses to enemies, is in direct proportion to abundance of the group concerned.

Selectionists regard bees as very highly protected insects, but taking the honey bee as type of the group because more is known about the species than any other, we find that bee-keepers complain bitterly of the numerous enemies of the inmates of their hives. Wasps, velvet-ants, robber flies, Phymatid bugs, mantids, and dragonflies are serious insect enemies of honey bees; spiders, toads, lizards, rats, mice, and skunks prey upon them; numerous wild birds join in the attack (32 nearctic species according to our tabulations), and domestic ducks are said to be insatiable in devouring bees. A mite is the primary cause of the so-called Isle-of-Wight disease among hive-bees; ants and wax moths destroy the comb; and there are at least two serious infectious diseases. At times bees rob other colonies, the rifling being accomplished however only after great slaughter. In the case of the honey bee, much study has been devoted to the insect and we know considerable about its enemies, but the ruling principle is as clear in this case as in that of the ants, namely, that common species have numerous enemies.

Since ants and the honey bee fairly exemplify two of the main phases of protective adaptation in Hymenoptera, despite which these species clearly have their full quota of enemies, we cannot doubt that other species of the order, when they are as well known, will prove to have predatory foes fully in proportion to their relative abundance.

In fact the 27,000 records of Hymenoptera now available are sufficient indication that the order contributes its due toll to the subsistence of one of the chief groups of its enemies—the birds.

Arachnida (Scorpions, Spiders, Ticks, Etc.)

Protective adaptations.—Most arachnids possess venom of sufficient strength, and means of injecting it into other creatures, to enable them to overcome the animals upon which they prey. Numbers of them have chelicerae, which in a few cases are rather powerful. The poisonous nature of many of the species has been greatly exaggerated especially by primitive races of man so that they are held in extreme dread.

Besides these direct means of defense, ticks and spiders exhibit in a high state of development that class of protective adaptations known as cryptic coloration (both defensive and aggressive). Certain groups, however, are brilliantly colored; some spiders also have the body integuments hardened and produced in the form of angles or spines, and numerous spiders resemble ants. Among the forms of this class ordinarily coming to the attention of man, spiders are by far the most numerous, but the small often minute mites prove, when the care necessary to their study is bestowed, to be exceedingly abundant. However, these small forms are beneath the notice of most birds.

The following table shows the relation of the records of the various orders to their approximate representation by species in the nearctic region.

Identifications of Arachnida

Order	Number of identifications	Percentage of identifications among those of all Arachnida	Percentage of species in this order among all nearctic Arachnida[1]
Unidentified	26	.2386	...
Xiphosura	20	.1836	.0513
Microthelyphonida	...	...	.0513
Scorpionida	18	.1652	1.1801
Pseudoscorpionida	80	.7343	2.4115
Pedipalpida	4	.0367	.3078
Solpugida	24	.2203	.6157
Phalangida	478	4.3873	3.4376
Araneida	9,966	91.4729	66.7044
Acarina	258	2.3681	23.0886
Pycnogonida	11	.1010	2.1549

Bird enemies.—Birds certainly specialize upon the group of arachnids—spiders—that to man seems most abundant and easily available, over 91 per cent of their arachnid captures coming from this order. We have records of more than 300 species of nearctic birds feeding on spiders. The freedom with which they take these creatures is illustrated by the following citations of records; of those identified to the order alone or about 92 per cent of the total, 81 birds have from 10 to 49 captures each; 28 birds from 50 to 99; 15 from 100

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[1] Computed from Comstock, J. H., The spider book, etc., 721 pp., 1912, with numbers of Araneida and Acarina approximated from the following works, respectively: Banks, N., Catalogue of nearctic spiders, U. S. Nat. Mus. Bull. 72, 80 pp., 1910, and Banks, N., A catalogue of the Acarina, or mites, of the United States, Proc. U. S. Nat. Mus., vol. 32, pp. 595-625, 1907.

to 199; two additional above 200; one more above 300; besides the following with greater numbers of records; English sparrow, 420; Eastern meadowlark, 425; crow blackbird, 621; starling, 631; and crow, 722. Some of the larger counts of spiders taken at a meal were 25 by a Say's phoebe, 33 by a greater yellow-legs, 46 by a wood duck, 58 by a Louisiana heron, 187 by a starling, and 300 by a hairy woodpecker.

A rather small proportion (less than 8 per cent) of spiders found in bird stomachs were identified, but results obtained along this line show the determinations are distributed to cryptically colored groups as the Epeiridae (30 records) and Thomisidae (28); more brilliant forms as the Attidae (158) and to the formidable Lycosidae (370), in a way that would indicate availability to be the principal factor in choice. There are two records of *Synemosina formica*, the most antlike of our spiders, a small and rather uncommon form that one would expect no more frequently regardless of its "protected" status. As noted in the last section, however, resemblance to an ant is no protection whatever against predators. There are 134 records of the cocoons or egg-cases of spiders being eaten showing that even these quiescent stages do not escape the birds. In bulk spiders do not ordinarily form any considerable percentage of the total food of birds, but the proportion runs as high as 6 per cent and 8 per cent of the annual diet in the case of certain song thrushes and petty flycatchers.

There are 34 records in our tabulations of ticks being eaten, and 224 of mites. Of interest in connection with the latter are the finding of 100 Parasitidae in the stomach of a red-eyed vireo; 320 mites further unidentified in the stomach of a pipit; 535 water mites in the gizzard of a green-winged teal, and 594 of the same group in the stomach of a pied-billed grebe.

Such geographically restricted and relatively uncommon forms as the scorpions, pedipalps, and solpugids, even though having only a small number of records each, would seem, nevertheless, to be amply represented, considering their availability. Pseudoscorpions are present throughout our area but lead chiefly concealed lives; the 80 records are distributed among 22 species of birds.

The daddy-long-legs, or Phalangida, with 478 determinations certainly have not been slighted; 10 of the birds taking them have 10 to 19 records each; two others over 20 records; and one each additional, the yellow-billed cuckoo, 34; and crow blackbird, 60. Large numbers of the arachnids captured for one meal were 20 by a yellow-billed cuckoo and 77 by an ovenbird.

Number of identifications, 10,885; percentage of identifications among those of all arthropods, 5.1648; percentage of species in this class among those of all arthropods, 3.8254.

Other enemies.—Spiders are frequently snapped up by fresh-water fishes, and mites often, especially the water mites. Pycnogonids, or sea-spiders, have occasionally been found in the stomachs of marine fishes and are consumed also by sea-anemones. Kirkland found spiders to compose 2 per cent of the food of 149 common toads examined by him, and Drake found them to constitute about 27 per cent of the entire number of animals found by him in the stomachs of 209 leopard frogs. However, practically all frogs, toads, and salamanders that have been studied have been found to feed upon spiders, often extensively, and mites, pseudoscorpions, and phalangids are not neglected. Lizards commonly prey upon spiders, while snakes and turtles so far have rarely been observed to do so.

Spiders appear to constitute an important element of the food of our shrews, and a lesser, though frequently taken, item in the diet of the moles. We have records of the wood rat and armadillo preying upon spiders, and evidence that the badger at times is a destructive enemy of scorpions. Monkeys and marmosets are said to be very fond of spiders, and anteaters also are listed among their foes.

Of invertebrate enemies various wasps (Pompilidae, Sphegidae, and Trypoxylonidae) are among the most effective destroyers of spiders, some species preying exclusively upon them, temporarily at least, even upon single species. The writer has found the cells of *Pelopaeus cementarius* filled entirely with flower spiders, *Misumena americana*, supposedly one of the most perfectly protected (cryptically colored) species. Dragonflies prey upon spiders. Tiger beetles and ants eat spiders and mites, ground beetles and ladybirds also figure as enemies of mites and spiders. Water mites are preyed upon by dragonfly nymphs and aquatic Hemiptera. There are a number of kinds of spiders that habitually prey upon their fellows when adult, and cannibalism among young spiders is the rule. Mantispidae and other spiders eat the eggs and young of spiders, and there are many proctotrupid and ichneumonid parasites of the eggs. Parasitic nematodes also afflict the adults. Scorpions are notoriously cannibalistic, so much so in fact that it is said in some cases that whenever two of them are found together, one is eating the other.

Discussion.—All spiders have venom and some of them are large and venomous enough to be able to kill birds. The case would seem to be crucial for the usefulness of this direct means of defense, but we may well say, in the light of the evidence, that the defense is entirely disregarded by birds. Not only do our records show more than 10,000 records of spiders having been eaten by more than 300 species of birds, but the birds emphasize their disregard for the dangerous qualities of spiders by making them in many cases the staple food for their callow young. Such minor protective adaptations as those of color and form necessarily fall with the greater, and there is no evidence whatever but that birds eat spiders under any and all conditions as freely as they choose. The nearly 1,000 records of arachnids other than spiders seem to be distributed among the orders in very just proportion to the extent these creatures are available to birds. No evidence of "special protectedness" obtrudes itself.

MOLLUSCA (SNAILS, SLUGS, MUSSELS, LIMPETS)

Protective adaptations.—The great majority of mollusks are equipped with calcareous shells into which they can entirely withdraw. Besides this protection more than half of the species are aquatic and hence are more or less out of reach of many birds. Many land snails have the apertures of their shells furnished with processes or teeth which partly bar these openings and operculi to close them. Snails and especially slugs secrete mucus freely; a habit thought by some to be protective. Numerous mollusks are colored more or less in harmony with their environments, this being especially noted of marine forms living on seaweeds, gorgonians, etc. The nudibranch mollusks are characteristically brightly colored and have been said to be distasteful. Of shelled mollusks, Wallace remarks: "The brilliant colors of the scallops (*Pecten*) and some other bivalve shells are perhaps an indication of their hardness and consequent inedibility." (Darwinism, p. 266-267, 1896.)

Bird enemies.—The tabulation of identifications herewith presented is the best that could be made so far as comparative records is concerned; these had to be gleaned from two sources as noted, which between them do not include all of the families, nor, because of disparity of data, do they give even the grand divisions comparable treatment.

Identifications of Mollusca

Aquatic shells

Group	Number of identifications	Percentage of identifications among those of all Mollusca	Percentage of species in this group among marine mollusks of the Southeast Coast [1]
Unidentified	1,032	8.7673	...
Pelecypoda (further unidentified)	513	4.3582	...
Ostreidae	552	4.6895	.2516
Anomiidae	...	...	.1887
Dimyidae	...	...	.0629
Spondylidae	...	...	.1887
Pectinidae	193	1.6396	1.8868
Limidae	...	...	.6918
Aviculidae	...	...	.5031
Mytilidae	674	5.7260	1.6353
Unionidae	8	.0679	...
Arcidae	73	.6201	2.0755
Nuculidae	45	.3823	.6289
Ledidae	1	.0085	1.9497
Solenomyidae	1	.0085	.1887
Carditidae	...	...	.4402
Astartidae	20	.1699	.6918
Crassatellidae	...	...	.1887
Erycinidae	2	.0170	.5031
Ungulinidae	...	...	.6289
Cyrenellidae	...	...	.0629
Lucinidae	...	...	1.4465
Diplodontidae	...	...	.2516
Chamidae	...	...	.3145
Cardiidae	20	.1699	.8176
Veniliidae	2	.0170	.0629
Isocardiidae	...	...	.1887
Veneridae	131	1.1129	1.9497
Corbiculidae	...	...	.1258
Petricolidae	28	.2378	.4402
Donacidae	122	1.0364	.3773
Psammobiidae	...	...	.3773
Tellinidae	324	2.7525	2.3270
Semelidae	...	...	.6289
Gnathodontidae	4	.0340	.1258
Mactridae	21	.1784	.3145
Anatinidae	...	...	.8176

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[1] Compiled from Dall, W. H., A preliminary catalogue of the shell-bearing marine mollusks and brachiopods of the southeastern coast of the United States, with illustrations of many of the species, U. S. Nat. Mus. Bull. 37, 221 pp., 74 pls., 1889.

Identifications of Mollusca—Continued

Aquatic shells

Group	Number of identifications	Percentage of identifications among those of all Mollusca	Percentage of species in this group among marine mollusks of the Southeast Coast
Lyonsiidae	...	...	.4402
Verticordiidae	...	...	.6289
Cuspidariidae	...	...	1.1321
Poromyidae	...	...	.5031
Pandoridae	...	...	.3145
Corbulidae	92	.7716	.6918
Myidae	10	.0849	.0629
Saxicavidae	25	.2124	.1887
Paphiidae	400	3.3982	...
Solenidae	4	.0340	.3145
Gastrochaenidae	...	...	.2516
Pholadidae	...	...	.7547
Teredidae	5	.0425	.5031
Gastropoda (further unidentified)	3,421	29.0631	...
Dentaliidae	1	.0085	2.7673
Limacinidae	...	...	.6289
Cavoliniidae	...	...	1.1950
Cymluliidae	...	...	.0629
Clionidae	...	...	.0629
Cliopsidae	...	...	.1258
Pneumodermatidae	...	...	.0629
Actaeonidae	...	...	.6289
Ringiculidae	...	...	.1258
Tornatinidae	77	.6541	1.2207
Scaphandridae	...	...	.5660
Aplustridae	...	...	.1258
Bullidae	...	...	.6918
Philinidae	...	...	.3373
Gastropteridae	...	...	.0629
Umbraculidae	...	...	.1258
Aplysiidae	...	...	.1258
Pleurobranchidae	...	...	.1887
Onchidiidae	...	...	.0629
Veronicellidae	...	...	.0629
Auriculidae	158	1.3423	1.0063
Siphonariidae	...	...	.1887
Gadiniidae	...	...	.0629
Terebridae	1	.0085	.6289
Conidae	...	...	.6918
Pleurotomidae	43	.3653	8.3019
Cancellariidae	...	...	.5031
Olividae	11	.0934	.5031

Identifications of Mollusca—Continued

Aquatic shells

Group	Number of identifications	Percentage of identifications among those of all Mollusca	Percentage of species in this group among marine mollusks of the Southeast Coast
Marginellidae	7	.0595	2.9560
Volutidae	...	...	.3145
Turbinellidae	...	...	.1258
Mitridae	...	...	1.0692
Fasciolariidae	18	.1529	1.6981
Buccinidae	7	.0525	1.9497
Nassidae	424	3.6021	.5031
Columbellidae	346	2.9394	1.6352
Muricidae	111	.9430	2.6415
Scolidae	...	...	3.3962
Janthinidae	...	...	.2516
Eulimidae	2	.0169	1.0692
Pyramidellidae	176	1.4952	3.3333
Tritoniidae	...	...	1.0063
Oocoritidae	...	...	.1887
Cassidae	...	...	.5031
Doliidae	...	...	.3145
Amphiperasidae	...	...	.3773
Cypraeidae	...	...	.6918
Carinariidae	...	...	.5031
Strombidae	...	...	.3145
Triforidae	17	.1444	1.0063
Cerithiopsidae	4	.0340	.6918
Cerithiidae	218	1.8520	1.0063
Planaxidae	...	...	.1258
Modulidae	2	.0169	.0629
Trichotropidae	13	.1104	.1887
Caecidae	7	.0595	.8176
Seguenziidae	...	...	.3145
Vermetidae	...	...	.5031
Turritellidae	2	.0169	.3145
Mathildiidae	...	...	.3145
Litorinidae	564	4.7915	.6918
Fascaridae	...	...	.2516
Litiopidae	...	...	.1887
Solariidae	...	...	.8176
Rissoidae	67	.5692	1.5094
Adeorbidae	...	...	.3145
Limacidae	2	.0169	...
Philomycidae	1	.0085	...
Ampullariidae	4	.0340	.1258
Assimineidae	11	.0934	.1887
Cymatidae	1	.0085	...

Identifications of Mollusca—Continued

Aquatic shells

Group	Number of identifications	Percentage of identifications among those of all Mollusca	Percentage of species in this group among marine mollusks of the Southeast Coast
Truncatellidae	...	...	.2516
Choristidae	...	...	.0629
Calyptraeidae	135	1.1469	.5031
Capulidae	...	...	.1887
Amaltheidae	...	...	.1887
Xenophoridae	...	...	.1258
Naticidae	47	.3993	1.5094
Lamellariidae	...	...	.1887
Acmaeidae	43	.3653	.3145
Lepetidae	...	...	.2516
Scutellinidae	...	...	.0629
Addisoniidae	...	...	.0629
Cocculinidae	...	...	.3773
Phasianellidae	...	...	.1887
Turbinidae	...	...	.8176
Trochidae	18	.1529	3.9622
Delphinulidae	...	...	.6289
Cyclostrematidae	...	...	.8805
Neritidae	374	3.1773	.5031
Stomatiidae	...	...	.0629
Haliotidae	...	...	.0629
Scissurellidae	...	...	.1887
Pleurotomariidae	...	...	.1258
Tissurellidae	...	...	2.2012
Chitonidae	26	.2209	1.4465
Cephalopoda (further unidentified)	86	.7306	...
Loliginidae	3	.0254	.1258

Land shells

Family	Number of identifications	Percentage of identifications in this group among those of all land Mollusca (except the unidentified)	Percentage of species in this group among all nearctic land Mollusca [1]
Cyclostomatidae	...	...	.5277
Truncatellidae	...	...	1.0554
Helicinidae	14	7.9096	1.0554
Helicidae	70	39.5479	37.7305

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[1] Compiled from Pilsbry, H. A., and Johnson, C. W., A classified catalogue with localities of the land shells of America north of Mexico. Reprinted from The Nautilus, 1897-1898, Philadelphia, 35 pp., 1898.

Identifications of Mollusca—Continued

Land shells

Family	Number of identifications	Percentage of identifications in this group among those of all land Mollusca (except the unidentified)	Percentage of species in this group among all nearctic land Mollusca
Bulimulidae	...	...	2.9023
Urocoptidae	...	...	4.2216
Pupidae	42	23.7287	13.1925
Achanitidae	1	.5649	1.5831
Glandinidae	...	...	1.0554
Testacellidae	...	...	.2638
Circinariidae	...	...	1.8469
Zonitidae	27	15.2542	17.6779
Limacidae	2	1.1299	1.5831
Arionidae	...	...	3.6939
Philomycidae	1	.5649	1.3192
Endodontidae	6	3.2898	4.2216
Succineidae	14	7.9096	5.8047
Vaginulidae	...	...	.2638

The outstanding impression given by the foregoing table is that notwithstanding their relatively low availability to birds, mollusks of practically all kinds are eaten. In general it is also true that the large groups more numerous in species and individuals contribute most heavily to avian subsistence, while the small groups of less abundance get off with a light toll.

Let us see what are the relations of birds to some of the protected mollusks. In a paper " On the Adaptive Coloration of Mollusca " (Proc. Boston Soc. Nat. Hist., vol. 14, pp. 141-145 (1871) 1872), Edward S. Morse alludes to protective coloration of several species. His remarks with comment deduced from our tabulations are herewith presented. "Among the marine forms we notice the adaptive coloration of certain species very well marked. The common *Littorina* of the coast swarms on the bladder weed, the bulbous portions of which are olive brown in color or yellowish according to age. The shells of the *Littorina* found upon it, present in their varieties these two colors and are limited to these colors " (p. 143). Our tabulations show 503 records of capture of *Littorina,* 11 species of which were identified from the stomachs of 46 kinds of birds. These shells are freely eaten as the following instances of large numbers taken by single birds testify: Pacific eider 110, surf scoter 120, black duck 150, purple sandpiper 205, and greater scaup duck 350.

"The few species common to the mud flats exposed by the retreating tide are colored black or dark olive." Examples: *Ilyanassa obsoleta, Nassa trivittata, Rissoa minuta* (p. 143). There are 78 records of *Ilyanassa obsoleta* distributed among 18 species of birds. Thirty-two of these shells were taken at a meal by a greater scaup duck, and from 42 to 62 by each of six knots. There are 98 records of *Nassa trivittata*, two of them being 275 and 285 specimens in the stomachs of greater scaups; and there are three determinations of *Rissoa minuta*.

Lacuna vincta: The colors "quite match the Laminarian upon which they are found" (p. 143). This species was identified 39 times in nine species of birds in which numbers from 32 to 75 were found, and in one case, that of a golden-eye, no fewer than 116.

"*Margarites helicina* I have found in numbers on the large Laminarian and on seaweed at low water mark and its color is decidedly protective" (p. 144). Our tabulation shows 10 records of this species of shell, distributed among five kinds of birds.

"A very evident case of protective coloring is seen in the three species of *Crepidula* found on our coast. *Crepidula fornicata* is drab, variously rayed and mottled with brown, and it lives attached to stones near the roots of the large Laminarian or upon stones clothed with algae of similar colors, or attached to the large *Mytilus*. *Crepidula convexa*, a much smaller species, lives on the roots of seaweed. Professor Perkins records its occurrence on the black shell of *Ilyanassa obsoleta*. This *Crepidula* has a very dark brown shell, according well with the dark color of its various places of lodgement. *Crepidula plana* or *unguiformis* lives within the apertures of the shells of larger species of Gasteropods, as *Buccinum, Natica, Busycon* and others. The shell of this *Crepidula* is absolutely white" (pp. 144-145).

All of the limpets named in the foregoing quotation have been identified from the stomachs of nearctic birds, and the total number of records for species of *Crepidula* is 135. Fifty specimens of *C. glauca* were found in one gizzard of a greater scaup duck and 60 in another. The "protection" of *C. plana* is very undependable since all of the mollusks named as its hosts are swallowed whole by birds and other predatory enemies of shellfish. With reference to a special enemy of limpets "it has been calculated that a single flock of oyster-catchers, frequenting a small Scotch Loch, must consume hundreds of thousands of limpets in the course of a single year." (Cooke, Cambridge Nat. Hist., vol. 3, pp. 56-57, 1895.)

As an example of the land snails thought to be defended from some enemies by the toothed apertures of their shells, the genus *Polygyra* may be mentioned. Twelve species have been identified from the birds represented in our tabulations, the total number of determinations being 42. Slugs were identified three times, but our findings in this respect probably are not representative since in Great Britain it is said that: "Every kind of slug and snail is eaten greedily by blackbirds, thrushes, chaffinches, and in fact by many species of birds." (Cooke, Cambridge Nat. Hist., vol. 3, p. 58, 1895.) With regard to highly colored shells, such as *Pecten*, conjectured by Wallace to be protected, it may be said that our table shows 193 records for *Pecten* and the Biological Survey has been called upon to make a special study of damage to the scallop industry by wild fowl in the vicinity of Marthas Vineyard, Mass. Teredos were identified from the stomachs of four Bachman oyster-catchers and of one egret.

It should be remarked that the very large number of records of Ostreidae in the tabulations is due also to a special investigation of the bird enemies of *Ostrea lurida*. The high records for Tellinidae (*Macoma*, especially) and Paphiidae (*Paphia staminea*) are chiefly by-products of this same study. The large numbers of identifications for such dominant families as the Mytilidae, Nassidae, Columbellidae, and Litorinidae among marine shells and Amnicolidae and Lymnaeidae among fresh-water ones, need no explanation.

Number of identifications, 11,771; percentage of identifications among those of all animals, 4.9583; percentage of species in this phylum among the whole number of animal species known, 10.8828.

Other enemies.—Mollusks are preyed upon to an important extent by very many marine fishes, as well as by most of the rays and sharks; among these being numerous forms specialized (as by possession of the pavement-like pharyngeal dentition) to feed upon shell fish. For such fishes as the haddock, cod, wolffish, and flounders they are a staple food. Field found razor-clams in 4 per cent of 388 stomachs of the smooth dogfish (*Mustelus canis*); and in 3.68 per cent of 516 stomachs of the summer skate (*Raja erinacea*). The same author found mollusks of various kinds in 17.64 per cent of the stomachs of 306 cunners (*Tautogolabris adspersus*), and in 27.2 per cent of those of 33 toadfish (*Opsanus tau*). Some of the marine fishes are known to be enemies of certain specially defended mollusks; as predators on *Crepidula*, the scup, tautog, swellfish and toadfish may be mentioned; upon chitons, the haddock and flounders (*Pleuronectes*); and upon *Eolis* and other nudibranchs, the cods, gurnards and flounders. Cephalopods, especially squids, are a favorite food of many of the highly predacious fishes as the sharks, rays, bonito, swordfish, bluefish, mackerels, pollock, and haddock. It would be easy to compile a very long list of squid-eaters. As to the extent to which these cephalopods are taken, Field reports squid from the following percentages of the stomachs examined by him: Summer skate 6.39 per cent, smooth dogfish nearly 10 per cent, and goosefish 17.39 per cent. Cuttlefishes are known to be eaten by the bonito, cod, whiting, and gurnard, and octopods by the ling, haddock, and conger eel.

Turning to the fresh-water mollusks, we find that they are equally beset by enemies. Pearse reports 2 per cent of the total food of 32 species of fishes in Wisconsin lakes consists of these animals, and from Forbes we learn that mollusks make up about one-fourth of the food of the dogfish (*Amia*) and a sheepshead (*Aplodinotus*), about half that of the suckers (*Catostomus*), rising to 60 per cent in the case of the red-horse (*Neoxostoma*), and a considerable proportion (14 to 16 per cent) of the food of the perch (*Perca flavescens*), catfishes, sunfishes, top minnows, and shiner (*Abramis*). Almost all fishes eat mollusks to some extent and practically all groups of mollusks suffer from these predatory attentions.

Taking up the relations of amphibians to mollusks, it may be noted that Kirkland found 1 per cent of the food of 149 toads to consist of snails and slugs, and Drake found 29 of these mollusks in 209 stomachs of the leopard frog. In general it may be said that most frogs consume aquatic snails when in the larval state and land snails when adult. With reference to European conditions, Cooke adds: "Frogs and toads are very partial to land mollusca. A garden attached to the Laboratory of Agricultural Chemistry at Rouen had been abandoned for three years to weeds and slugs. The director introduced 100 toads and 90 frogs, and in less than a month all the slugs were destroyed." (Cambridge Nat. Hist., vol. 3, p. 58, 1895.) Snails are eaten by most salamanders, the kind, whether water or land, depending on the habits of the salamanders concerned; small mussels even are consumed by some of the thoroughly aquatic forms.

Reptiles do not prey very extensively upon mollusks, yet snails are frequently eaten by lizards; slugs and snails are eaten by several species of snakes and by most turtles, the aquatic forms of the latter group consuming some bivalves.

Among mammals we find that some of the land forms consume mollusks to a slight extent; shrews, rats, white-footed mice, squirrels, and chipmunks may be mentioned as examples; a specimen of the eastern chipmunk (*Eutamias striatus*) taken near Fairfax, Va., had packed in its cheek-pouches or swallowed more than 47 *Pomatiopsis lapidana*. It is well known that the muskrat preys extensively upon fresh-water mussels, and the mink and otter must be listed as foes of fresh-water mollusks. The food of the walrus consists mainly of shellfish. Dyche reports that the California sea-lion feeds very largely upon squids and octopods and it is known that squids form a considerable proportion of the diet of sperm and other whales.

The enemies of marine mollusks include also sea-anemones, starfishes, and boring univalves of the genera *Purpura, Polynices, Thais, Lunatia, Natica, Cycotypus, Fulgur,* and *Urosalpinx.* Fresh-water mollusks form an important element of the food of dragonfly nymphs, and a lesser one of horse fly larvae, water beetle larvae, water bugs, leeches, and crayfishes. Land snails are attacked by predacious beetles and fly larvae. Mollusks also have enemies among such parasitic groups as mites, nematodes, and trematodes.

Discussion.—From the abundance of their enemies and from the extent to which these predators feed upon mollusks (more than 8,000 records for birds in our tabulations), it is evident that the possession of a shell as a means of defense has been entirely discounted so far as predators of any size are concerned. The relations of birds to the protectively colored forms show that some of these (Litorinidae) are freely eaten; the brightly colored shells (Pectenidae) also are freely taken, as well as the very hard and thick-shelled ones (Ostreidae). Slugs, snails, limpets, teredos, chitons, and cephalopods pay their toll also, testimony to the all-pervading search for food by birds. In fact the evidence is that birds feed more or less indiscriminately upon all mollusks of suitable size that are available to them. Other enemies follow mollusks, especially the marine forms, where most birds can not, and it would seem that the whole molluskan world is exploited as a source of food to as large an extent as could be expected.

CHORDATA (LANCELETS, TUNICATES, VERTEBRATES)

While the Chordata with 13,326 identifications contribute only 5.6133 per cent of the total determinations of the animal food of birds, yet the phylum comprises so many familiar animals that it probably will be best to treat it more in detail as was done in the case of insects.

Number of identifications, 13,326; percentage of identifications among those of all animals, 5.6133; percentage of species in this phylum among the whole number of animal species known, 8.8427.

A tabulation of the records of Chordata with frequency indices derived from estimates for the world fauna gives the following results:

Identifications of Chordata

Class	Number of identifications	Percentage of identifications among those of all Chordates	Percentage of species in this class among those of the whole number of Chordate species known
Urochorda	5	.0375	2.6228
Pisces	4,923	36.9427	26.2281
Amphibia	997	7.4816	4.4386
Reptilia	695	5.2153	12.1053
Aves	3,555	26.6771	40.3510
Mammalia	3,151	23.6454	14.1228

The urochordates listed are ascidians, in three cases being identified as *Boltenia ovifera.* While the identifications of urochords is far from proportional to the frequency of these animals, the result is only what would be expected in view of their strictly marine and chiefly submerged habitat in which they are exposed to the attacks of only a very small proportion of our birds. It may be noted here that tunicates have numerous enemies, however, among fishes which take the pelagic and both simple and colonial fixed ascidians. It is on record that these animals are not uncommon in the stomachs of cod and haddock, and they have been found also in herring, flatfishes, tilefish, cunner, scup, the great sunfish (*Mola*), and a number of other fishes. They are taken also by sea-anemones and sea-urchins.

Omitting the Urochorda and figuring frequency indices from the fairly well known numbers[1] of North American species in the various classes we obtain the following table:

Identifications of Vertebrata

Class	Number of identifications	Percentage of identifications among those of all Vertebrata	Number of nearctic species in this class	Percentage of species in this class among those of all nearctic Vertebrata
Pisces	4,923	36,9565	3,054	61.3253
Amphibia	997	7.4844	141	2.8313
Reptilia	695	5.2173	308	6.1847
Aves	3,555	26.6870	801	16.0843
Mammalia	3,151	23.6542	676	13.5743

In this as in other cases we clearly observe the tendency for losses to predators to correspond to the extent and abundance of a group. In fishes the largest class are preyed upon the most, but less than their

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[1] Counts derived from standard works on the various classes, as noted later in connection with the tabulations by classes.

relative abundance would seem to warrant, for the reason that, as a group, they are relatively inaccessible to birds, many of the deeper-water forms being entirely so.

Pisces (Fishes)

Protective adaptations.—It has been held that the great group of spiny-rayed fishes is protected from enemies to a greater degree than the soft-finned families, and in general harsh scales and spines are deemed protective. Some fishes have poison glands connected with certain specialized spines. Some of the species with disagreeable qualities have colors that are said to be warning, while the great majority of fishes exhibit varying degrees of cryptic coloration, many of them having more or less ability to change in color in response to that of their environment. Such in brief are some of the more or less theoretical defenses of fishes; as to actual physical protection, it may be said that fishes are shielded from most birds by their aquatic habits and many of them even from water birds by their living at considerable depths.

Bird enemies.—It is well known that whole families of the so-called lower orders of birds are specialized to prey upon fishes, for example the loons, terns, cormorants, anhingas, pelicans, mergansers, herons, and kingfishers. There are special fish eaters in other groups, and many birds not at all specialized to prey upon fishes nevertheless consume them to some extent more or less habitually. Nearctic birds which subsist almost exclusively upon fishes include: the western grebe, Caspian, royal and Cabot terns, black skimmer, anhinga, double-crested cormorant, brown and white pelicans, man-o'-war bird, and osprey. Others making fishes from 50 to 90 per cent of their diet are: the common loon, Holboell's grebe, black, Mandt's and pigeon guillemots, common and Brunnich's murre, kittiwake, glaucous-winged, herring, and ring-billed gulls, gannet, violet-green cormorant, American and red-breasted mergansers, bald eagle, and belted kingfisher.

Nearly 5,000 records of fishes being eaten are contained in our tabulations of the food of nearctic birds, and of these nearly half were identified no further than the class. The remaining determinations grouped by families are listed herewith:

Identifications of Pisces

Group	Number of identifications	Percentage of identifications among those of all fishes	Percentage of species of this group among North American fishes [1]
Unidentified	2,253	45.7652	...
Branchiostomidae	...	...	.1310
Heptatremidae	...	...	.0327
Myxinidae	...	...	.0327
Petromyzonidae	...	...	.3274
Chlamydoselachidae	...	...	.0327
Hexanchidae	...	...	.0982
Heterodontidae	...	...	.0655
Scylliorhinidae	...	...	.1965
Ginglymostomidae	...	...	.0327
Pseudotriakidae	...	...	.0327
Galeidae	...	...	.9823
Sphyrnidae	...	...	.0982
Alopiidae	...	...	.0327
Carchariidae	...	...	.0327
Lamnidae	...	...	.1637
Cetorhinidae	...	...	.0327
Rhinodontidae	...	...	.0327
Squalidae	...	...	.1637
Dalatiidae	...	...	.0327
Echinorhinidae	...	...	.0327
Squatinidae	...	...	.0327
Pristidae	...	...	.0655
Rhinobatidae	...	...	.2947
Rajidae	...	...	.6221
Narcobatidae	...	...	.1310
Dasyatidae	...	...	.5239
Myliobatidae	...	...	.2619
Mantidae	...	...	.0655
Chimaeridae	...	...	.1310
Polyodontidae	...	...	.0327
Acipenseridae	...	...	.1965
Lepisosteidae	5	.1016	.1310
Amiidae	1	.0203	.0327
Siluridae	100	2.0313	3.1107
Loricariidae	...	...	.3274
Catostomidae	62	1.2594	2.1284
Cyprinidae	482	9.7909	7.3346
Erythrinidae	...	...	.0327
Characinidae	...	...	.6221
Apodes	2	.0406	...

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[1] Computed from Jordan, D. S., and Evermann, B. E., The fishes of North and Middle America, etc., U. S. Nat. Mus. Bull. 47, 4 vols., 1896-1900.

Identifications of Pisces—Continued

Group	Number of identifications	Percentage of identifications among those of all fishes	Percentage of species of this group among North American fishes
Gymnotidae	...	...	.0655
Symbranchidae	...	...	.0327
Derichtyidae	...	...	.0327
Anguillidae	16	.3250	.0327
Simenchelyidae	...	...	.0327
Ilyophidae	...	...	.0327
Synaphobranchidae	...	...	.0982
Leptocephalidae	...	...	.2619
Muraenesocidae	...	...	.4584
Nettastomidae	...	...	.0655
Nemichthyidae	...	...	.2292
Myridae	2	.0406	.1310
Ophichthyidae	1	.0203	.9496
Muraenidae	...	...	.9496
Saccopharyngidae	...	...	.0327
Eurypharyngidae	...	...	.0327
Elopidae	...	...	.0655
Albulidae	...	...	.0327
Hiodontidae	...	...	.0982
Chanidae	...	...	.0327
Dorosomidae Clupeidae	249	5.0579	1.3097
Engraulididae	51	1.0360	.8841
Alepocephalidae	...	...	.3602
Salmonidae	198	4.0220	1.0478
Thymallidae	...	...	.0655
Argentinidae	30	.6094	.3929
Microstomidae	...	...	.1310
Synodontidae	2	.0406	.4257
Aulopidae	...	...	.1310
Benthosauridae	...	...	.0655
Bathypteroidae	...	...	.0655
Ipnopidae	...	...	.0327
Rondeletiidae	...	...	.0327
Cetomimidae	...	...	.0655
Myctophidae	...	...	1.4080
Maurolicidae	...	...	.0655
Chauliodontidae	...	...	.2947
Astronesthidae	...	...	.0982
Stomiatidae	...	...	.1965
Malacosteidae	...	...	.0327
Alepisauridae	...	...	.1637
Odontostomidae	...	...	.0327
Paralepididae	...	...	.1965

Identifications of Pisces—Continued

Group	Number of identifications	Percentage of identifications among those of all fishes	Percentage of species of this group among North American fishes
Sternoptychidae	...	...	.0982
Idiacanthidae	...	...	.0655
Halosauridae	...	...	.2292
Notacanthidae	...	...	.1965
Lipogenyidae	...	...	.0327
Dalliidae	...	...	.0327
Umbridae	9	.1828	.0655
Luciidae	22	.4469	.1965
Poeciliidae	530	10.7659	3.8638
Amblyopsidae	...	...	.1310
Esocidae	8	.1625	.6221
Hemiramphidae	4	.0812	.2292
Scombresocidae	...	...	.0655
Exocoetidae	1	.0203	.6221
Gasterosteidae	111	2.2547	.2292
Aulorhynchidae	...	...	.0327
Aulostomidae	...	...	.0327
Fistulariidae	...	...	.0982
Macrorhamphosidae	...	...	.0327
Syngnathidae	6	.1219	1.1460
Percopsidae	...	...	.0655
Aphredoderidae	1	.0203	.0327
Atherinidae	38	.7719	1.1133
Mugilidae	18	.3656	.5566
Sphyraenidae	...	...	.1637
Polynemidae	...	...	.1637
Ammodytidae	25	.5078	.1310
Bathyclupeidae	...	...	.0327
Stephanoberycidae	...	...	.0655
Trachichthyidae	...	...	.0327
Berycidae	...	...	.3274
Holocentridae	...	...	.4584
Polymixiidae	...	...	.0327
Mullidae	...	...	.2619
Scombridae	1	.0203	.4912
Gempylidae	...	...	.2292
Lepidopidae	...	...	.1310
Trichiuridae	...	...	.0327
Istiophoridae	...	...	.0982
Xiphiidae	...	...	.0327
Nematistiidae	...	...	.0327
Carangidae	7	.1422	1.0974
Pomatomidae	4	.0812	.0327
Rachycentridae	1	.0203	.0327

Identifications of Pisces—Continued

Group	Number of identifications	Percentage of identifications among those of all fishes	Percentage of species of this group among North American fishes
Nomeidae	...	...	.1637
Coryphaenidae	1	.0203	.0655
Lampridae	...	...	.0327
Pteraclidae	...	...	.0327
Bramidae	...	...	.1310
Steinegeriidae	...	...	.0327
Centrolophidae	...	...	.0655
Stromateidae	...	...	.1965
Icosteidae	...	...	.1310
Grammicolepididae	...	...	.0327
Tetragonuridae	...	...	.0327
Pempheridae	...	...	.1310
Elassomidae	...	...	.0655
Centrarchidae	164	3.3313	1.0478
Kuhliidae	...	...	.0655
Percidae	171	3.4735	2.8160
Cheilodipteridae	...	...	.4912
Centropomidae	...	...	.4257
Serranidae	5	.1016	3.0779
Lobotidae	...	...	.0327
Priacanthidae	...	...	.1310
Lutianidae	...	...	1.1133
Haemulidae	2	.0406	1.8009
Sparidae	5	.1016	.7858
Maenidae	...	...	.0655
Gerridae	3	.0609	.5566
Kyphosidae	...	...	.3929
Sciaenidae	14	.2844	3.5036
Cirrhitidae	...	...	.0655
Embiotocidae	7	.1422	.5894
Cichlidae	...	...	1.8337
Pomacentridae	...	...	.9823
Labridae	11	.2234	1.6044
Scaridae	...	...	1.4407
Zeidae	...	...	.0982
Caproidae	...	...	.0655
Ephippidae	...	...	.0982
Chaetodontidae	...	...	.6549
Zanclidae	...	...	.0327
Teuthididae	...	...	.2947
Triacanthidae	...	...	.0327
Balistidae	...	...	.5239
Monacanthidae	3	.0609	.3602
Ostraciidae	...	...	.1310

Identifications of Pisces—Continued

Group	Number of identifications	Percentage of identifications among those of all fishes	Percentage of species of this group among North American fishes
Tetraodontidae	...	...	.6221
Canthigasteridae	...	...	.0655
Diodontidae	1	.0203	.3602
Molidae	...	...	.0655
Scorpaenidae	...	...	2.6523
Anoplopomatidae	...	...	.0655
Hexagrammidae	4	.0812	.3274
Cottidae	188	3.8188	4.2567
Ramphocottidae	...	...	.0327
Agonidae	2	.0406	1.1788
Cyclopteridae	...	...	.2947
Liparididae	...	...	1.2443
Triglidae	1	.0203	.8186
Peristediidae	...	...	.1310
Cephalacanthidae	...	...	.0327
Callionymidae	...	...	.1310
Gobiidae	10	.2031	2.8487
Echeneididae	...	...	.2292
Malacanthidae	...	...	.1637
Opisthognathidae	...	...	.3602
Bathymasteridae	...	...	.0982
Chiasmodontidae	...	...	.0655
Chaenichthyidae	...	...	.0327
Trichodontidae	...	...	.0655
Dactyloscopidae	...	...	.3274
Uranoscopidae	2	.0406	.1637
Batrachoididae	17	.3453	.3274
Gobiesocidae	1	.0203	.8841
Blenniidae	16	.3250	4.5187
Cryptacanthodidae	...	...	.0982
Anarhichadidae	1	.0203	.1965
Cerdalidae	...	...	.0982
Ptilichthyidae	...	...	.0327
Scytalinidae	...	...	.0327
Zoarcidae	...	...	1.0805
Derepodichthyidae	...	...	.0327
Ophidiidae	...	...	.5566
Lycodapodidae	...	...	.1310
Fierasferidae	...	...	.0982
Brotulidae	...	...	.8841
Bregmacerotidae	...	...	.0655
Merlucciidae	...	...	.0982
Gadidae	31	.6297	1.1788
Macrouridae	...	...	1.0805

Identifications of Pisces—Continued

Group	Number of identifications	Percentage of identifications among those of all fishes	Percentage of species of this group among North American fishes
Regalecidae	...	...	.0327
Trachypteridae	...	...	.0982
Stylephoridae	...	...	.0327
Pleuronectidae Soleidae	30	.6093	3.7983
Lophiidae	...	...	.0327
Antennariidae	...	...	.4912
Ceratiidae	...	...	.3274
Ogcocephalidae	...	...	.3274

Total number of identifications of fishes, 4,923; percentage of identifications among those of all vertebrates, 36.9565; percentage of species in this class among those of all nearctic vertebrates, 61.3253.

Commenting on this table it is obvious that a wide range of fishes is preyed upon, and that the families known to be most abundant in individuals almost invariably are those most extensively consumed by the birds. As to the bearing of this data on protective adaptations, we see the spined catfishes well represented, more so in fact than the equally abundant and only negatively if at all defended suckers. No fewer than 36 small catfishes were found in the stomach of a single belted kingfisher. The very spiny sticklebacks are eaten enough to show that their spines are no deterrent to the attacks of birds; no fewer than 150 of these little fishes have been taken from the stomach of a great blue heron. Advancing to the true prickly-scaled and spiny-finned fishes, we note that Centrarchids (sunfishes, bass, etc.) and perches are freely taken. High counts of sunfishes in stomachs are 12 in that of a least bittern, 14 in an anhinga, and 18 in a little green heron. Twenty yellow perch have been eaten at a meal by the least bittern and the great blue heron and no fewer than 25 darters by the little green heron. The Cottidae or sculpins often have a highly developed armature of spines about the head, but there is no evidence that it protects them from birds. Flatfishes (Pleuronectidae) represent almost the acme of protective coloration, especially of power to simulate the background, but they seem to be proportionally represented in our table. One double-crested cormorant had eaten 16 *Symphurus plagiusa*.

The unidentified fishes were distributed among approximately 165 species of birds to which a considerable number would have to be added to give the total number of fish-consuming species. A family of fishes that almost everything "picks on," such as the minnows (Cyprinidae), was represented in the stomachs of 44 species of birds. Numbers up to 50 of these little fishes were found in stomachs of the belted kingfisher and the hooded merganser, and in the case of young of the common carp a high count of 106 was made from the stomach contents of a glossy ibis. Thirty-nine species of birds are known to prey upon the common killifishes and their allies; and numbers were taken from many stomachs, the maximum being 526 from a little blue heron.

Other enemies.—Fishes have no more destructive enemies than the predacious element among their own kind. Among the highly predatory marine forms may be mentioned the dogfishes and other sharks, swordfish, bluefish, squeateague, conger eel, and the angler, and among fresh-water fishes, the gars, sculpins, trout, amia, pikes, and bass. In a study of the fisheries of Buzzard's Bay, Mass., Field estimated that two species of sharks destroy more than 500,000 fishes annually in that body of water. Pearse found fishes to compose 12.3 per cent of the food of 32 species of their class in Wisconsin lakes. Forbes notes that the principal piscivorous fishes of Illinois, those which obtain three-fourths or more of their total subsistence from their fellow fin-bearers, are *Lota, Stizostedion, Esox, Micropterus, Ictalurus, Leptops,* and *Lepidosteus.* Six other species are listed as taking from 25 per cent to 65 per cent of fish food.

Predators devour fishes in all stages, and there are numerous special enemies of fish spawn; worst among these are other fishes such as the suckers, sculpins, minnows, sticklebacks, killifishes, top minnows, and trout.

Not many enemies of fishes are numbered among our batrachians and reptiles, those worthy of note including only the bullfrog, *Necturus* and *Cryptobranchus* of amphibians; the king, garter, and water snakes, copperhead, rattlesnake, and cottonmouth moccasin among snakes; and the painted terrapin, and snapping and soft-shelled turtles.

Some mammals are important enemies of fishes but the number is not large; we may mention the raccoon, mink, otter, seals, sea-lions, porpoises, and whales.

The young of fishes especially fall a prey to a variety of insects, as the larvae of aquatic beetles and of dragonflies, and to several kinds of water bugs and to hydras. Insects also, and crawfishes and leeches prey upon the eggs of fishes, and squids are said to be among the most destructive foes of adult fishes. Parasites of fishes abound and are recruited from the ranks of such diverse groups as bacteria, protozoans, cestodes, trematodes, and crustaceans. Fishes are destroyed in large numbers sometimes by fungoid diseases; and enormous numbers of them perish by being stranded in pools, overflowed by high tides or freshets, which later dry up.

Discussion.—Forbes in his discussion of the "Food Relations of Fresh-water Fishes" notes that: "The soft-finned fishes were not very much more abundant, on the whole, in the stomachs of other species than were those with ctenoid scales, spiny fins, and other defensive structures,—an unexpected circumstance which I cannot at present explain" (p. 479). The natural comment upon this remark is that the fact detailed does not need to be explained, only accepted, theoretical bias being cast aside. He goes on to say: "Only the catfishes seem to have acquired defensive structures equal to their protection, the predatory apparatus of the carnivorous fishes having elsewhere outrun in development the protective equipment of the best-defended species" (p. 480). Examining the basis for this statement we find that Forbes examined the stomachs of about 900 adult or nearly adult fishes, and that he found catfishes in five of these stomachs; darters were identified only four times, whitefish only twice, and round suckers only three times, yet all of these are groups which equal or exceed catfishes in abundance. There is no reason therefore for saying their defenses are unusually efficient; from the table on p. 113 we see that birds take catfishes in due proportion.

Some kind of protectedness is claimed for practically every kind of fish, yet we see that all groups of them are devoured by natural enemies, and where data is available, predation seems to be very much in proportion to abundance. This principle is especially evident in depredations upon fishes if carried back through the life history of these animals; young fishes are more abundant than adults and they are greedily devoured by many piscivorous animals; while fish eggs, most abundant of all, are sought by a perfect swarm of predators. The grand principle of predation proportional to population is well supported by the known relations of fishes and their foes.

AMPHIBIA (SALAMANDERS, TOADS, FROGS)

Protective adaptations.—All amphibians have skin glands that secrete a slime which some have thought to function partly as a defense. Toads in particular, frogs to a lesser extent, possess poison glands also, and "experiments have proved that toad poison injected into the system will kill any vertebrate, the dose being proportionate to the size of the animal." (Dickerson, Mary C., The frog book, p. 17, 1906.) Some amphibians have warning colors, but it is noticeable that the nearctic species having such coloration (certain *Ambystoma*) do not possess especially noxious secretions, while our toads are not at all warningly colored. The real defense of most amphibians lies in their habits, such as aquatic life, nocturnal activity, and lying in seclusion in burrows or under logs and rocks. Most of the species are very fecund also.

Bird enemies.—The extent to which the various families of Amphibia have been identified from the stomachs of nearctic birds is shown in the subjoined table.

Identifications of Amphibia

Group	Number of identifications	Percentage of identifications among those of all amphibians	Percentage of species of this group among North American amphibians [1]
Unidentified	132	13.2396	...
Urodela (further unidentified)	124	12.4372	...
Necturidae	4	.4012	1.4184
Typhlomolgidae	...	...	.0709
Amphuimidae	...	...	1.4184
Cryptobranchidae	...	...	.0709
Salamandridae	1	.1003	2.1276
Ambystomidae	16	1.6048	14.8932
Plethodontidae	8	.8024	31.9140
Sirenidae	...	...	1.4184
Anura (further unidentified)	40	4.0120	...
Discoglossidae	...	...	.0709
Scaphiopodidae	...	...	2.8368
Bufonidae	60	6.0180	9.9288
Hylidae	77	7.7231	14.1840
Leptodactylidae	...	...	2.8368
Ranidae	535	53.6605	12.0564
Brevicipitidae	...	...	2.8368

While the Ranidae are more abundant and accessible to birds than most of the other amphibians, even so they seem considerably overrepresented in the preceding tabulation, a circumstance that is explained in part by the fact that greater numbers proportionally of the stomachs of aquatic birds have been examined than of any other group.

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[1] Computed from Stejneger, L., and Barbour, T., A check list of North American amphibians and reptiles, pp. 5-40, 1917.

Fifty-three species of birds are recorded as preying on Ranidae, of which the common crow is the most voracious (numbers as high as 24 and 29 individual frogs being counted in stomachs of this species), and has the largest number of records (197). Thirty-four frogs were found in the stomach of one little blue heron.

Among 14 species of toad eaters, the following are most important: common crow 16 records, red-tailed hawk 10, red-shouldered hawk 9, and broad-winged hawk 9. The most frequent consumer of salamanders also is the common crow with 83 records.

Total number of identifications of amphibians, 997; percentage of identifications among those of all vertebrates, 7.4844; percentage of species in this class among those of all nearctic vertebrates, 2.8313.

Other enemies.—Fishes occasionally eat the eggs of toads and frequently devour tadpoles of both toads and frogs, and the larger predacious fresh-water fishes are fond of frogs. The bullfrog especially preys upon other frogs and the gopher frog is a special enemy of toads. The Anura more or less frequently are cannibalistic upon the young of their kind, while larvae of salamanders regularly devour their brethren. Aquatic salamanders also eat the eggs and larvae of frogs. Snapping turtles, soft-shelled turtles, and alligators prey upon frogs, but it is particularly among snakes that the most deadly enemies of the Anura occur. The garter snakes and hog-nosed snake are especially fond of toads, while snakes in general eat frogs and also salamanders. In their account of the "Snakes of Okefinokee Swamp," Wright and Bishop report that: "With the larger snakes, the food most generally sought is Anura or Amphibia in general. It is *par excellence* the food of the aquatic snakes, and with these four or five species it is usually some species of *Rana*, though *Acris, Chorophilus* or *Hyla* may rarely appear as their prey. Equally important are frogs in the food of the larger land snakes, five species being addicted to them. With these the southern and oak toads (*Bufo*) are easily of first importance, with the tree frogs (*Hyla*) and the narrow-mouthed frog (*Engystoma*) occupying second and third places. In fact, these 10 snakes prefer the soft-bodied frogs and toads to any other food of the swamp (reptilian eggs not considered)." (Proc. Acad. Nat. Sci. Philadelphia, vol. 67, p. 147, Apr. 1915.)

Among mammals the skunk is known to be fond of toads, and coyotes, skunks, weasels, minks, otters, wildcats, and the brown rat feed upon frogs. No doubt most of these animals will take salamanders also when the opportunity occurs; the little spotted skunk and coyote are definitely known to do so, one stomach of the latter animal yielding 15 *Ambystoma*. The mongoose was found to feed commonly on toads and frogs in three separate investigations of its food habits in Trinidad.

Leeches prey upon both eggs and young of amphibians and there are numerous insects which destroy tadpoles. Such are the giant water bugs, backswimmers, water scorpions, predacious diving beetles, and their larvae, and the nymphs of dragonflies. Finally, it should be mentioned that myriads of amphibian eggs and young perish because of the unwise choice by their parents of too temporary bodies of water for their egg-laying.

Discussion.—The relations of predators to amphibians throw an interesting light on the efficiency of protective adaptations in averting the attacks of foes. Clearly the Ranidae or frogs are more preyed upon than any other group, certainly much more so than the toads. The theorist on adaptations attributes this to the superior special defenses of toads, but with no doubt whatever the difference in amount of predation on these two groups is a direct reflection of their relative abundance.

If toads really were specially protected, if their so-called defenses actually saved them from a certain proportion of predatory attacks, should they not increase continually relative to the Ranidae? The fact that they do not is the best proof that could be asked that their "special defenses" do not actually function in nature. In short there is no reason to believe in the case of amphibians but that the attacks of predatory enemies bear a close relation to abundance and availability of the various orders and families. Where a certain group appears to have an advantage in escaping certain foes, to a degree, it invariably proves that it suffers extraordinarily from attacks of other enemies.

REPTILIA (TURTLES, LIZARDS, SNAKES)

Protective adaptations.—Although turtles have the direct defenses of their shells, jaws and claws, several of the species have also a strong musky odor, and some exhibit warning colors. Numerous lizards have cryptic coloration; one of our species is poisonous and one has the faculty of changing its color considerably. Many lizards drop their tails easily, a device said to aid them in eluding enemies. The horned-toads besides their protective coloration have more or less prominent spines on the back of the head. Many snakes exhibit cryptic coloration and a number of them have offensively odorous secretions. Certain serpents practice intimidatory actions and a considerable number of our species are dangerously venomous.

Bird enemies.—Following is a tabulation of the records of Reptilia found in the stomachs of nearctic birds. The total number 695 seems proportional to the abundance of animals of this group in the United States.

Identifications of Reptilia

Group	Number of identifications	Percentage of identifications among those of all reptiles	Percentage of species of this group among North American reptiles[1]
Unidentified	21	3.0215	...
Crocodylidae	1	.1438	.6494
Lacertilia (further unidentified)	140	20.1432	...
Gekkonidae	...	...	.9741
Eublepharidae	...	...	.6494
Iguanidae	47	6.7624	22.0796
Anguidae	2	.2878	2.9223
Anniellidae	...	...	.6494
Helodermatidae	...	...	.0325
Xantusiidae	...	...	1.2988
Teiidae	5	.7194	4.8705
Scincidae	26	3.7409	4.8705
Ophidia (further unidentified)	250	35.9700	...
Bipedidae	...	...	.0325
Leposternidae	...	...	.0325
Leptotyphlopidae	...	...	.6494
Boidae	...	...	.9741
Colubridae	111	15.9707	35.0676
Elapidae	...	...	.6494
Crotalidae	1	.1438	5.8446
Chelonia (further unidentified)	84	12.0859	...
Kinosternidae	2	.2878	2.2729
Chelydridae	1	.1438	.6494
Testudinidae	3	.4316	9.7410
Cheloniidae	...	...	2.2729
Dermochelidae	...	...	.6494
Trionychidae	1	.1438	1.2988

In commenting on the foregoing table the obvious fact is recalled that our birds can hardly assume the rôle of predators upon turtles except in the case of rather small young of these animals. This limitation considered, 91 records seems fully as many as could be

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[1] Computed from Stejneger, L., and Barbour, T., A check list of North American amphibians and reptiles, pp. 41-125, 1917.

expected. Forty-five species of birds participated in the lizard-eating, including some surprisingly diminutive ones such as the canyon and Carolina wrens and the white-eyed vireo. The road-runner, crows, jays, butcherbirds, and the Carolina wren took lizards most frequently. The chameleon, despite its powers of color change, was identified more often than any other species of lizard, namely, 24 times in the stomachs of 10 species of birds. One swallow-tailed kite had eaten seven specimens at a meal. Horned-toads and swifts, notwithstanding their defenses, which as it happens are diametrically opposed in character, were "among those present" in the stomachs.

In contrast to the comparatively wide distribution of the lizard determinations, those of snakes were shared by only 26 species of birds. Crows, hawks, and owls were the most important of these predators; and it is worth mentioning that the little Carolina wren again unexpectedly appears in the list. The superlatively cryptic green snake (*Cyclophis aestivus*) was eaten by red-shouldered and broad-winged hawks; the swift racers (*Bascanion*) by five species of hawks and the crow; the desperately bluffing hog-nosed snakes by the red-tailed and Swainson's hawks; the stinking garter and water snakes by several kinds of birds; and the redoubtable and warningly colored king snakes by the red-shouldered hawk. A great blue heron had swallowed a water snake (*Natrix fasciatus*) slightly over 25 inches long. The only venomous snake identified in the stomachs was *Crotalus confluentus* from a great horned owl but field observers credit another of our birds, the road-runner, with occasional depredations on rattlesnakes.

Total number of identifications of reptiles, 695; percentage of identifications among those of all vertebrates, 5.2173; percentage of species in this class among those of all nearctic vertebrates, 6.1847.

Other enemies.—While some of the larger predatory fresh-water fishes may occasionally devour a young turtle or small snake, actual records of the occurrence have not come to hand. The only one of our amphibians known to be a reptile eater is the bullfrog, which has been observed to eat snakes and newly-hatched turtles and alligators. Reptiles have numerous destructive enemies among their own ranks. Snapping turtles eat snakes; several kinds of snakes eat turtle eggs and a few the young; a few species of lizards prey upon other lizards, and a number of snakes devour both these animals and their eggs. Snakes are the worst enemies of snakes, such species as the racers, king snakes, ring-necked snakes, coral snakes, water moccasin, and copperhead being conspicuous in this respect. The king snakes are immune to the poison of the venomous serpents and kill them whenever they run across them. Among mammals, skunks, raccoons, and bears dig up and devour the eggs of turtles; skunks, foxes, and wildcats eat snakes and lizards; the badger is known to feed upon tortoises and snakes, the coyotes on horned-toads and garter snakes, the opossum on horned-toads, and ground squirrels and grasshopper mice upon lizards.

Discussion.—The reptiles are not a very numerous group in our fauna and it would appear that they have natural enemies in due proportion. While some of the turtles are monarchs of the waters they inhabit when adult, yet their young must run the gauntlet of numerous enemies which cut the number down so that there are no indications whatever of an increase in the number of these species. So it is apparently with all the forms that when adult seem too large to have many enemies to fear; they are small and relatively helpless in the earlier stages of their life, and it is then that predators do great execution. In the class of reptiles, fratricide in almost every direction seems to be one of the most important elements of natural control. That such control is effectively exercised, the relatively stationary character of the reptile population sufficiently attests.

AVES (BIRDS)

Protective adaptations.—Much has been written about protective coloration in the bird world, including the nests, the eggs, the sitting bird upon the nest, and later the nestlings, the fledglings with their special plumages, and extending to the adults of hundreds of species, some of which (Anatidae) have a special protective dress, the eclipse plumage, during the season when the flight feathers are moulted. The ringed plovers of numerous species are said to have ruptive color patterns tending to break up the outline of the birds and render them inconspicuous. (The phylogenetic significance of this group character apparently is ignored.)

Crests of birds in some cases are said to be used to frighten their enemies, as are various sudden displays of contrastingly colored feathers elsewhere. Boldly marked birds of colors held to be warning in other classes of animals are numerous and the unusual often intense and striking coloration of the lining of the mouth of certain nestlings is held to be warning in effect. It has even been claimed that the color of some bird eggs advertises their low digestibility and that they are therefore avoided by all but ravenously hungry predators.

Bird enemies.—Birds, not content with preying upon animals of every class from protozoans to mammals, also draw upon their own kind to the extent of a fourth (26.6 per cent numerically) of all their vertebrate food. The following table shows the distribution to families and two more inclusive groups of the determinations that have thus far been made of birds in the stomachs of nearctic birds.

Identifications of Aves

Group	Number of identifications	Percentage of identifications among those of all birds	Percentage of species in this group among nearctic birds [1]
Birds (further unidentified)	301	8.4669	...
Egg-shell	463	13.0327	...
Colymbidae	6	.1688	.7490
Gaviidae	...	...	.6242
Alcidae	3	.0844	2.7465
Stercorariidae	...	...	.4994
Laridae	3	.0844	5.2433
Rynchopidae	...	...	.1248
Diomedeidae	...	...	.6242
Procellariidae	...	...	3.8700
Phaethontidae	...	...	.3745
Sulidae	...	...	.7490
Anhingidae	...	...	.1248
Phalacrocoracidae	...	...	.7490
Pelecanidae	...	...	.2497
Fregatidae	...	...	.1248
Anatidae	26	.7314	7.2407
Phoenicopteridae	...	...	.1248
Plataleidae	...	...	.1248
Ibididae	...	...	.4994
Ciconiidae	...	...	.2497
Ardeidae	2	.0563	1.7478
Gruidae	...	...	.3745
Aramidae	...	...	.1248
Rallidae	19	.5345	1.9974
Phalaropodidae	3	.0844	.3745
Recurvirostridae	2	.0563	.2497
Scolopacidae	53	1.4908	5.2433
Charadriidae	5	.1406	1.7478
Aphrizidae	...	...	.4994
Haematopodidae	...	...	.4994
Jacanidae	...	...	.1248
Odontophoridae	23	.6470	.8739
Tetraonidae	26	.7314	1.7478
Phasianidae	265	7.4542	...
Meleagridae	...	...	.1248

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[1] Computed from Check list of North American birds, prepared by a Committee of the American Ornithologists' Union, 3rd ed. (rev.), 430 pp., 1910.

Identifications of Aves—Continued

Group	Number of identifications	Percentage of identifications among those of all birds	Percentage of species in this group among nearctic birds
Cracidae	...	...	.1248
Columbidae	11	.3094	1.6229
Cathartidae	...	...	.3745
Buteonidae	...	...	2.8713
Falconidae	14	.3938	1.4980
Pandionidae	...	...	.1248
Aluconidae	...	...	.1248
Strigidae	15	.4219	2.3720
Psittacidae	...	...	.1248
Cuculidae	6	.1688	.8739
Trogonidae	...	...	.1248
Alcedinidae	...	...	.3745
Picidae	51	1.4346	2.9962
Caprimulgidae	1	.0281	.7490
Micropodidae	17	.4782	.4994
Trochilidae	...	...	2.2471
Cotingidae	...	...	.1248
Tyrannidae	10	.2813	3.8700
Alaudidae	12	.3375	.2497
Corvidae	20	.5626	2.8713
Sturnidae	2	.0563	.1248
Icteridae	111	3.1223	2.3720
Fringillidae	992	27.9040	11.6101
Tangaridae	11	.3094	.4994
Hirundinidae	76	2.1378	1.6229
Bombycillidae	34	.9564	.2497
Ptilogonatidae	...	...	.1248
Laniidae	1	.0281	.2497
Vireonidae	88	2.4754	1.4980
Coerebidae	...	...	.1248
Mniotiltidae	488	13.7270	6.8662
Motacillidae	7	.1969	.8739
Cinclidae	...	...	.1248
Mimidae	45	1.2658	1.3732
Troglodytidae	17	.4782	1.7478
Certhiidae	4	.1125	.1248
Sittidae	15	.4219	.4994
Paridae	38	1.0689	1.8726
Chamaeidae	1	.0281	.1248
Sylviidae	25	.7032	.7490
Turdidae	243	6.8353	1.8726

About one-eighth (13.02 per cent) of all the records are for bird eggs, and the number of species feeding upon eggs is so considerable and represents so great a variety of birds (55 species) that the late Prof. F. E. L. Beal, taking these facts in connection with his field observations, was constrained to express the belief that scarcely a species of bird exists that upon good opportunity, can resist the temptation to eat another bird's eggs. Numbers of identifications such as 6 for the yellow-billed cuckoo, 10 for the brown towhee, 12 for the Baltimore oriole, 10 for the California towhee, and 11 for the bank swallow prove that egg or at least egg-shell eating is not confined to birds of the recognized predatory groups. Probably a number of the records are due to birds swallowing bits of their own egg-shells. On the other hand eggs may be punctured as by the house wren, or eaten without swallowing any of the shell, occurrences not likely to be registered in the evidence brought to light by stomach examination.

Of the records for predation upon the various families of birds, it may be said that the high number for Phasianidae represents domestic poultry almost entirely, and that of the other families, the two—sparrows and warblers—undoubtedly most numerous in individuals are those which bear the brunt of predatory attack. The rather high number of determinations of Turdidae reflect the abundance of the robin which contributed nearly 45 (43.6 per cent) of the total. The Icteridae, next in line, are birds of great abundance, which might be expected to rank still higher among the avian contributors to the subsistence of their predatory relatives. However, there is no evidence that they are at all immune to attack, as the great flocks of blackbirds wintering in our southern latitudes are constantly harried by predacious birds in variety and force.

The sparrows, most persecuted of all, because most available, represent almost the acme of protectively colored birds; the bob-whites (16 records), ruffed grouse (11), and their allies, also cited, as marvels of cryptic coloration are certainly eaten freely considering their relative numbers. It is of interest that birds of prey by no means spare each other, and it seems that a slight advantage in size is all that is needed to induce this strained predation; indeed there are records of intra-specific cannibalism. The pugnacious kingbird and other members of the family of tyrant flycatchers do not escape: the aerially expert swifts and swallows pay their due toll; and the green-coated vireos, best blended with foliage of any of our birds, are freely eaten.

Birds "warningly colored" that are represented in the dietary of other birds as illustrated by our tabulations include the bobolink (19 records), Baltimore oriole 4, orchard oriole 3, lark bunting 6, cardinal 3, rose-breasted grosbeak 1, black-headed grosbeak 3, scarlet tanager 11, Blackburnian warbler 5, bay-breasted warbler 12, myrtle warbler 16, magnolia warbler 16, Canadian warbler 13, Wilson's warbler 10, hooded warbler 1, and the robin 106. These birds certainly have the colors and arrangement of colors said to be warning in the case of other animals, but brought home in the instances of these familiar and practically defenseless species, for none of which can any degree of inedibility be assumed, and in the light of the fact that all are eaten, some freely, some less so, in relation to their numbers, the theory of warning coloration becomes a wraith of the imagination so tenuous that one cannot understand why it ever received serious consideration.

Total number of identifications of birds, 3,555; percentage of identifications among those of all vertebrates, 26.6870; percentage of species in this class among those of all nearctic vertebrates, 16.0843.

Other enemies.—Fishes are not recorded as serious enemies of birds, but it is probable that sharks and some other highly predacious forms take some toll of birds that rest on the surface of the ocean. The goosefish is known to have eaten seven wild ducks at a meal and to have attacked such large birds as geese and loons. In fresh-water, bass have been observed to capture swallows. (Fins, feathers, and fur, p. 8, Dec. 1921.) The bullfrog is the only one of our amphibians known to eat birds, but records of its so doing are fairly numerous and some of the birds taken are surprisingly large (*e. g.* woodcock).

Among the snakes we find very serious enemies of birds, some of the expert climbing species especially, making birds, their eggs and young a considerable part of their diet. Most noteworthy in this respect are the pilot snake and black snake. Other bird-eaters are the garter, house, hog-nosed, king, and all of the Crotaline snakes.

The larger predacious mammals are very fond of birds and must be numbered among their worst enemies. Such are the opossum, wild cats, foxes, coyotes, raccoon, badger, and skunks. Smaller species as the weasels and mink are no less destructive and even the highly vegetarian squirrels never lose an opportunity to devour the eggs and young of birds. The red or pine squirrels are universally acknowledged to be among the most destructive foes of birds. The domestic cat, large numbers of which lead a more or less feral life, possibly is the most deadly single enemy of birds.

Recently much evidence has been gathered showing that the larvae of certain flesh flies (family Muscidae, sens. lat.) parasitize the nestlings of various birds, this activity resulting in the destruction of numerous broods. Birds have other external as well as internal parasites also, the relation of which to mortality is not well known. An occasional bird falls a victim to mussels or other bivalves, to crayfishes, and to mantids and spiders.

Discussion.—" Warningly colored " nearctic birds, according to our tabulations, are eaten along with the others, the common ones frequently, the rarer ones to a lesser extent. Our most extensive family and the one most numerous in individuals, occupies the logical, if unenviable niche, as the most important contributor to the subsistence of predatory species. This family, the finches, includes many of the most " protectively colored " species. Fortunately there is other direct evidence of the way in which nearctic predators react to protective coloration. I refer to Dr. Raymond Pearl's paper on the " Relative Conspicuousness of Barred and Self-colored Fowls " (Amer. Nat., vol. 45, pp. 107-117, Feb., 1911). Natural enemies captured in one year 325 individuals out of a total of 3,443, a flock which contained both barred and solid-colored fowls. By all theories of protective coloration, the latter are the more conspicuous and should pay a higher toll to predatory enemies. Of the total number of birds 10.05 per cent were self-colored and of all the eliminated birds 10.77 per cent were self-colored. Thus these monochrome birds were taken almost exactly in proportion to their numbers in the whole flock. This is precisely the result that would be expected by those who have learned by study of the subject that availability is the one strongest factor in choice of food by predators. With availability as the controlling factor it follows that in the long run, and on the average, losses to predators will be very closely in proportion to the relative abundance of the group concerned.

Mammalia (Mammals)

Protective adaptations.—Many of the mammals are conceived to be very perfect exemplifications of protective or cryptic coloration. A few are credited with noxious qualities, accompanied in the case of the skunks only, in our fauna, by warning coloration. The short dense fur of moles and shrews is said to be a deterrent to predators and these animals are thought to be protected by a strong musky secretion also; shrews have even been credited with poisonous bites. However the most potent defenses of mammals in general against birds are their large size, and their teeth and claws.

Bird enemies.—Despite the size and direct means of defense of many species, mammals pay a heavy toll to bird predators. In our complete tables, the group without doubt is over-represented, owing to the fact that stomachs of the hawks and owls have been kept examined practically up to date. However this fact probably does not materially affect the relative numbers of identifications for the different families, as shown in the following table for mammals alone.

Identifications of Mammalia

(Land mammals only)

Group	Number of identifications	Percentage of identifications among those of all mammals	Percentage of nearctic species in this group[1]
Further unidentified (in many cases carrion)	331	10.5046	...
Carrion (identified to species)	18	.5712	...
Didelphiidae	2	.0635	.2958
Talpidae	22	.6982	1.4790
Soricidae	274	8.6957	6.5076
Phyllostomidae	...	...	.2958
Vespertilionidae	19	.6030	3.5496
Molossidae	...	...	.1479
Ursidae	...	...	3.2538
Canidae	1	.0317	5.6202
Procyonidae	...	...	.5916
Mustelidae	1	.0317	8.5782
Felidae	1	.0317	...
Rodentia (further unidentified)	86	2.7293	...
Muridae	1,816	57.6326	24.1077
Geomyidae	31	.9838	7.9866
Heteromyidae	16	.5078	8.5782
Zapodidae	14	.4443	1.7748
Erithizontidae	...	...	.2958
Aplodontiidae	1	.0317	.7395
Sciuridae	173	5.4903	14.6421
Petauristidae	15	.4760	.7395
Castoridae	...	...	.2958
Ochotonidae	...	...	1.7748
Leporidae	330	10.4729	2.9580
Dasypodidae	...	...	.1479
Tayassuidae	...	...	.1479
Cervidae	...	...	3.9933
Antilocapridae	...	...	.1479
Bovidae	...	...	1.3311

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[1] Compiled from Miller, Gerrit S., Jr., List of North American land mammals in the U. S. National Museum, 1911, U. S. Nat. Mus. Bull. 79, 455 pp., 1912.

Let us now take up some of the groups of interest in the order of their appearance in the tabulation. From the large number (274) of records for shrews it would appear certain that the alleged special defenses of these animals are no protection against birds. Thirteen species of shrews were identified in the stomachs; 27 species of birds are known to prey upon our common short-tailed shrew and 23 upon unidentified species of *Sorex*. Shrews are by no means gregarious, nevertheless five specimens of *Sorex personatus* were taken at a meal by a great gray owl. Considering their almost exclusively underground life, moles were captured fully as often as would be expected; the number of species of birds preying upon them is 12.

Bats, again on account of their nocturnal activity, are not greatly exposed to the attacks of birds. Six predators upon them are recorded in our tabulation with a total of 19 identifications. While the Mustelidae are provided with unusually strong musky scents, they are also rather above the size for many birds to attack. The single determination in our table, attributed to a crow, might perhaps be more correctly added to the records of carrion. Skunks, of this family, customarily cited as examples of animals having noxious qualities and warning coloration to advertise them certainly are too large for all except a very few species of our raptors to conquer. However there are a number of published and other records of the great horned owl preying upon skunks.

Muridae (mice and rats) are secretive, elusive animals with what would be called highly protective coloration, but this does not prevent their being the staple mammal food of birds. Meadow mice, perhaps our most ubiquitous rodents, are eaten by the largest number of species of birds, namely 44. Twenty-six species of birds are known to feed on the house mouse and 35 upon deer mice (*Peromyscus*). We have records of five species of birds preying upon our largest member of this family, the muskrat, and eight upon the smallest (*Reithrodontomys*).

Pocket gophers, like the moles, spend most of their lives underground and this fact limits the opportunities of birds for capturing them, yet there are 31 records for 11 species of birds; nocturnal and burrowing habits shield also the pocket mice and kangaroo-rats. Captures in these groups probably are in proportion to their reduced availability. Jumping mice (14 records), a more diurnal group, seem to be proportionately represented.

Erithizontidae (porcupines) are entirely beyond the size of prey practicable for birds, though possibly some of them are captured when young. Mountain-beavers also are rather large and are inaccessible to any but owls, of which the great horned owl contributed our only record of their being eaten.

The large number of determinations of members of the squirrel family, cover, it must be recalled, such diverse groups as the spermophiles, prairiedogs, groundhogs, tree squirrels, and chipmunks. There are only two records of the groundhog, a very large rodent, one being captured by a goshawk and the other by a golden eagle. The number of identifications (15) of the chiefly nocturnal flying squirrels seems as large as could be expected. The cryptically colored rabbits are exceedingly common and live fully exposed to predacious birds, factors which go far toward accounting for the very large number of records of their being eaten. The remaining families in the list all consist of animals so large that only a few of the most formidable birds can prey upon them, and then only upon the young. There are observations of such occurrences, but it so happens that our records of stomach contents do not include any of them.

Total number of identifications of mammals, 3,151; percentage of identifications among those of all vertebrates, 23.6542; percentage of species in this class among those of all nearctic vertebrates, 13.5743.

Other enemies.—Fishes have few opportunities to capture mammals, but trout have been known to feed upon meadow mice and lemmings, and it is probable that other highly predacious fresh-water fishes occasionally get small mammals that venture near or in the water. The bullfrog is the only one of our amphibians known to eat mammals, an occasional mouse falling to its lot. The snapping turtles also get some mice and sometimes even capture animals as large as rabbits. Among snakes we find many habitual predators upon mice and other small mammals. Some results of studies of the food of snakes by the Pennsylvania Division of Zoology may be briefly cited: Pilot snake, mice 22 per cent of the diet, squirrels 11 per cent, weasels 4 per cent; black snake, mice 26 per cent, rabbits 4 per cent, other mammals 7 per cent; milk snake, mice 71 per cent, other mammals 11 per cent; copperhead, mice 41 per cent, shrews 4 per cent, other mammals 8 per cent. In the case of the timber rattlesnake, mice, rats, and rabbits composed nearly the whole diet. This is known to be true also of most of our venomous snakes.

The worst foes of mammals, however, are their own kind, and the diversity of their predatory habits may be indicated by brief references to their mammal prey. Opossums take limited numbers of small mammals, while raccoons and skunks prey more extensively upon them, especially upon mice and ground squirrels. The bob cats or lynxes are fond of mice, ground squirrels, rabbits, and other rodents, occasionally prey upon small domestic stock, and are known to eat skunks and porcupines. The mountain-lion specializes upon deer, but eats a variety of wild mammals, including foxes, skunks, coons, porcupines, and bob cats. House cats take mice, rats, moles, shrews, and rabbits. Coyotes and wolves prey upon the young of deer and domestic stock, and upon prairie dogs, spermophiles, and other small rodents. On the bill-of-fare of our various species of foxes are shrews, mice, ground squirrels, pocket gophers, kangaroo-rats, and rabbits. Badgers also take all of these mammals and in addition, prairiedogs and mountain-beaver. The black-footed ferret is a special enemy of the prairiedog, and relishes rabbits also. Weasels are ferocious enemies of small mammals in general, and for their size, shrews are fiendish predators. They commonly overpower and devour other shrews and mice of their own or even of slightly greater bulk. The polar bear preys especially upon seals, and the killer whales also destroy these animals, as well as wearing down and devouring the largest of all mammals, whales.

Discussion.—Limitations due to relative sizes allowed for, we see the same phenomenon in the case of mammals as in those of other elements of bird food, namely that the more available (this usually meaning abundant) groups are preyed upon most extensively, while those which are less abundant or whose habitat is somewhat out of the domain of birds are not so often captured. We see that the burrowing moles and pocket gophers escape with moderate losses, but that the abundant mice, and the both common and relatively easier found rabbits suffer severely. It is evident also that the mammals outside the range of prey of birds have serious enemies, chiefly other mammals; and it is further evident that, taking all mammal enemies into consideration, they are most numerous in the case of so abundant and ubiquitous a group as the mice, and proportionally less numerous for other less abundant families.

DISCUSSION

Availability is a mighty factor in the choice of food by birds. Within the limits imposed by special habitats, bodily modifications, and the relative sizes of predator and prey, birds are prone to feed upon what is abundant and easily obtained. Not only is this very natural procedure the everyday order, but it is conspicuously exemplified by the characteristic flocking[1] of birds to the scene of insect outbreaks or of other occurrences of unusual abundance of food.

Constant seeking of the available leads to a wide distribution of predatory attack because of seasonally or otherwise variable abundance or availability of many of the food organisms, further on account of the greater or lesser restriction of predators to specific habitats in each of which the range of food items is different, and because of the specialization of various predators in methods of seeking food.

That the predatory attacks of birds are amazingly distributed over the entire animal kingdom, preceding pages bear witness. If it be asked whether birds eat bats or moles, flyingfishes or hermit crabs, dragonflies or mole crickets, sea-urchins or bryozoans, the answer is ever in the affirmative. Given an animal group comprising only a small number of species we find that there are only a few records of birds preying upon it. Given one of large numbers of species we invariably find it is an important item of bird food. If the validity of depending upon the number of species as an index of frequency be questioned, no matter. The tendency for feeding to be distributed over the whole range of the available food organisms and in at least rough proportion to the known abundance of the various groups, is beyond dispute.

This principle, predation in proportion to population, stands out clearly in the tabulations of the animal food of nearctic birds here presented and discussed. Compared to it the effect of the so-called protective adaptations on character of food is negligible. If these adaptations controlled choice of bird food to a significant extent, discrimination would everywhere be evident; finding indiscriminancy, on the contrary, we must conclude that the ruling criterion in choice of food is availability.

Indiscriminancy of Predators other than Birds

Nearctic birds, as a group, are little influenced by the protective adaptations of available prey. Let us see what can be said of other classes of predators.

Odonata.—In a general article on "Predacious Insects and their Prey," Prof. E. B. Poulton says of a tabulation of dragonfly victims: "Short as it is, the list is extremely interesting, and raises the expectation that dragonflies will be found to prey rather largely upon

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[1] American instances are summarized in the following paper: McAtee, W. L., The rôle of vertebrates in the control of insect pests, Smithsonian Rep. 1925, pp. 415-437, 7 pls., 1926.

specially defended groups of insects." (Trans. Ent. Soc. London 1906, p. 401, 1907.)

Agnatha, Plecoptera, et al.—In a report which deals with the food of stoneflies, mayflies, caddisflies, and Diptera in trout streams, Muttkowski and Smith state that "Aquatic insects in rapid streams are opportunists as regards food and eat whatever becomes available."[1]

Orthoptera.—Professor Poulton in the paper referred to says of the prey of these insects: "The proportion of specially protected forms was very high." (Op. cit., p. 408.)

Rhynchota.—Quoting from Poulton again, he says of bugs, "So far as it is possible to judge from the . . . . table it appears that Hemiptera will prove to be extremely dangerous foes to the specially protected groups." (Op. cit., p. 403.)

Diptera.—Writing of the food of the larvae of aquatic midges, A. L. Leathers says:[2] "The organisms found were so similar, both in number and variety, to those available in a given locality that there seemed to be little or no sorting in their method of feeding."

Professor Poulton remarks on robber flies that "A study of the table at once shows that the Asilidae are most indiscriminate in their attacks. The stings of the Aculeates, the distasteful qualities of Danainae and Acraeinae, and of the odoriferous Lagria, the hard chitinous covering of Coleoptera, the aggressive powers of Odonata, are alike insufficient protection against these active and voracious flies." (Trans. Ent. Soc. Lond. 1902, p. 336.)

Parasites.—"Certain species and groups of species [of insects] . . . . have, as far as we know, relatively few parasites in any region. . . . . This is sometimes considered to be due to the possession of protective devices of certain kinds, but the explanation is not satisfactory. Neither systems of colorations, nor nettling hairs, nor an armour of chitinised plates, nor rapidity of movement, nor the existence of toxic principles in the blood prevent insects from being decimated by parasites."[3]

Miscellaneous insects.—"Many groups of predacious insects also appear especially to attack the conspicuous, easily-captured prey provided by the groups with warning colours. This has been observed in

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[1] Muttkowski, R. A., and Smith, G. M., The food of trout stream insects in Yellowstone National Park, Roosevelt Wild Life Ann., vol. 2, no. 2, p. 261, Oct., 1929.

[2] Bull. U. S. Bur. Fisheries, vol. 38, Doc. no. 915, p. 3, 1922.

[3] Thompson, W. R., On natural control, Parasitology, vol. 21, no. 3, p. 279, Sept., 1929.

the case of the predacious asilid flies, Dragonflies, Hemiptera, Mantidae, and Locustidae." (Poulton, E. B., Essays on evolution, p. 318, 1908.)

Arachnida.—" Spiders are for the most part not very particular as to the insects they catch." (Bristowe, W. S., Proc. Zool. Soc. Lond., 1929, p. 643.)

" It is quite probable . . . . that certain species of spiders, together with Mantides and other predacious insects, will be found to be among the chief, perhaps the chief non-parasitic enemies of aposematic insects." (Poulton, E. B., Trans. Ent. Soc. Lond. 1902, p. 327.)

Pisces.—" In general, fish are opportunists as far as their food is concerned. They eat what animal food is available, regardless of the origin." [1]

The closeness with which the brook trout is guided by availability in its choice of food is indicated in the following table by Dr. P. R. Needham based on studies near Ithaca, N. Y.:

Comparison of Available Aquatic Fish Foods in Stream Bottoms and Aquatic Foods Consumed by Trout [1]

Order	Available aquatic foods		Consumed aquatic foods	
	Number	Per cent	Number	Per cent
Mayfly nymphs	2,316	36.90	356	30.12
Caddisfly larvae and pupae........	1,335	21.27	528	44.67
Stonefly nymphs..................	921	14.67	41	3.47
Fly larvae and pupae............	869	13.84	187	15.82
Beetle larvae	476	7.58	33	2.79
Crayfish and shrimps............	235	3.74	14	1.18
Miscellaneous	125	1.99	23	1.94
Totals	6,277	99.98	1,182	99.99

[1] Quantitative studies of the fish food supply in selected areas, Suppl. 18th Ann. Rep. New York Conserv. Dep. 1928, p. 227, 1929.

Further testimony to the effect of availability on the food of fishes is contained in Muttkowski's study [2] of " The Fauna of Lake Mendota " in which he shows that insects form about 60 per cent by bulk

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[1] Muttkowski, R. A., The ecology of trout streams in Yellowstone National Park, Roosevelt Wild Life Ann., vol. 2, no. 2, p. 229, Oct., 1929.

[2] Muttkowski, R. A., Trans. Wisconsin Acad. Sci. Arts and Letters, vol. 19, pp. 374-482, 1918.

of the macrofauna of the lake and about that proportion of the total diet of the fishes.

Some of the above remarks tending to emphasize feeding on protected forms are special pleading because their authors felt under the necessity of proving "protected" insects do have enemies. The various groups of predators thus referred to, however, prey upon other than the specially protected insects, just as birds do, and examined in that light, the comment "indiscriminate" would in most cases fit their food habits. An adaptation of Poulton's tabulation for robber flies illustrates the point.

Name of prey	Number of records	Percentage of records	Percentage of species in this group among the whole number of insect species known
Orthoptera	13	5.70	2.94
Rhynchota	12	5.26	8.58
Neuropteroidea	7	3.07	.71
Lepidoptera	32	14.03	15.61
Coleoptera	40	17.54	46.20
Diptera	57	25.00	11.44
Hymenoptera	67	29.34	17.17

This does not look very different from tabulations for birds, and clearly illustrates the same propensity demonstrated for that class, namely of preying largely upon the groups most numerous in species, and presumably therefore in individuals—in other words upon what is most available.

That availability does largely govern choice of food is the very thing that creates problems in wild life economics. When man invades the domain of wild life and in the various phases of his husbandry makes available large supplies of new foods, they are immediately attacked and up to a certain limit the enemies steadily increase in variety and abundance. It is needless to cite examples of this universal phenomenon from the vegetable kingdom. All may not realize, however, that it prevails also in the animal world. The temerity of the pioneer establishing an orchard in a clearing in the foothills where the crop is largely harvested by wild life, is paralleled by that of the sheep raiser who grazes his herds in mountain meadows where they are attacked at once by wolves, coyotes, wild cats, bears, and other predators. Man's taking the domestic fowl wherever he goes furnishes material for further demonstration of the supreme influence of availability. The chicken, a native of Asia should have no "natural enemies" in other parts of the world, nevertheless in America for instance, a large number of predators, including hawks, owls, crows, jays, skunks, weasels, and foxes eagerly welcomed the new food.

More Theoretical Aspects of Indiscriminancy by Predators

The experience we have when we place inviting food supplies in abundance before the birds indicates what must happen in nature under similar circumstances. If we imagine a world of food available to predators we must realize that the elements composing it will be utilized very much in proportion to their abundance. This is only what would be expected if there is or ever was such a thing as the oft-mentioned "balance of nature." To preserve a balance, natural checks must be in proportion to population. If they were not apparently so, no balance would have been observed and the term balance of nature would never have been invented.

Distribution of predation in proportion to population also is what we should expect if the theory of adaptive radiation, or the occupation of every possible ecologic niche is correct. Given the world of prey to exploit it is inevitable that predation will extend in all possible directions. No source of food will be left untouched if by any possibility it can be drawn upon. Under so searching a campaign for food each inevitably will be utilized in proportion to its abundance.

That this principle actually is at work is well shown by a series[1] of studies by Harry B. Weiss which indicate that regardless of locality there is a more or less fixed set of ratios between types of food habits of insects. Thus from several widely separated areas the insect population groups into from 45 to 55 per cent of phytophagous species, from 15 to 27 per cent of saprophagous, from 14 to 19 per cent harpactophagous, from 10 to 12 per cent parasitic, and from 1 to 4 per cent of species of miscellaneous feeding habits.

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[1] Insect food habits and vegetation. Ohio Journ. Sci., vol. 24, no. 2, pp. 100-106, Mar., 1924.

Ratios between the food habits of insects. Ent. News., vol. 35, no. 10, pp. 362-364, Dec., 1924.

Notes on the ratios of insect food habits. Proc. Biol. Soc. Wash., vol. 38, pp. 1-4, Jan., 1925.

Insect food habit ratios on Quelpart Island. Psyche, vol. 32, no. 2, pp. 92-94, Apr., 1925.

The similarity of insect food habit types on the Atlantic and Western Arctic Coasts of America. Amer. Nat., vol. 60, no. 1, pp. 102-104, Jan.-Feb., 1926.

Weiss' table summarizing these interesting data is substantially quoted as follows:

	Number of species	Phytophagous. Per cent	Saprophagous. Per cent	Harpactophagous. Per cent	Parasitic. Per cent	Pollen feeders, misc. species. Per cent
Quelpart Island	577	55	15	19	10	1
Western Arctic Coast of N. A.	400	47	27	14	10	2
State of N. J.	10,500	49	19	16	12	4
State of Conn.	6,781	52	19	16	10	3

The similarity of the figures whether for the States of New Jersey or Connecticut, for the Pacific Coast of Arctic America, or from far flung Quelpart Island (Corea) shows that there is at work some principle controlling choice of food that overrides whatever effect the so-called protective adaptations may have.

It is almost certain that the constancy of the ratios is due to a tendency (one might well say a compulsion) toward distribution of predatory and parasitic attack. This distribution is one that lays every group under tribute, that takes toll from each so long as the tax is more easily collected there than elsewhere, but when that condition fails turns toward more easily available supplies.

Predation is thus kept proportional to population and practical indiscriminancy as to factors other than availability must result.

INDISCRIMINANCY OF NATURAL CHECKS OTHER THAN PREDATORS

It will not be questioned, we believe, that from the standpoint of protective adaptations such checks as parasites, bacterial and fungal diseases, heat, cold, and other climatic factors, are indiscriminate in action.

RELATIVE IMPORTANCE OF NATURAL CHECKS

Years ago Chittenden writing of "Insects and the Weather"[1] stated: "It also appears to me what has been observed by Mr. Marlatt in the case of scale insects . . . . is true in general, viz., that favorable or unfavorable climatic conditions are of greater importance in

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[1] Bull. 22, n. s., U. S. Div. Ent., pp. 51-64, 1900.

determining the abundance or scarcity of insects as a whole than are other natural checks such as parasitic and other enemies, or even fungous or bacterial diseases" (p. 63).

Recent studies have only crystallized long-held views to the effect that the grand overwhelming factors of insect control are climatic.[1] Thus Uvarov in discussing "Weather and Climate in their Relation to Insects,"[2] says:

> Apart from the seasonal rhythm in the appearance and activities of insects, there is a more or less strongly marked periodic fluctuation of a species from year to year. Only relatively few insect pests are equally numerous and injurious every year, while most of them are practically negligible, except in certain years, when mass outbreaks occur. It would be out of place to discuss here all the causes for these periodic fluctuations, but I would like to point out that recent researches in this direction tend to throw some doubt on the commonly accepted idea that the chief controlling factor is the parasites, since a number of cases have become known in which the factors normally keeping an insect species down are almost entirely of meteorological order. This has been admitted for the cotton boll weevil in America (Hunter and Pierce, 1912), for the corn-borer in Europe (Thompson and Parker, 1928), for the almond sawfly in Palestine (Bodenheimer, 1928), for the cotton seed bug in Egypt (Kirkpatrick, 1923), for plague fleas in India (Hirst, Rogers), for vine-moths in Europe (Stellwaag, 1925), and for some other notorious pests.

Again Bodenheimer in answering[3] the question "Welche Faktoren regulieren die Individuenzahl einer Insektenart in der Natur?" states that parasites, predators, and scarcity of food, are rarely or only secondarily of regulatory significance, but that climatic factors are the real controlling influences.

Accepting the great superiority of meteorological phenomena as regulative factors we may make some inquiry as to the relative importance of other controlling agencies. Diseases sometimes are dramatically destructive, but they rarely have a steady regulatory influence.

Among parasitic and predacious organisms it must be presumed, except for specific limiting factors, that their effectiveness as control agencies will be more or less in keeping with their total numbers. Thus we can deduce from a table such as that on page 9 that most

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[1] This statement has general validity, for insects are nine-tenths of the terrestrial animals above the size of nematodes, and probably a large proportion of the smaller animals, as well as part of the tenth of larger size are subject to similar checks.

[2] Uvarov, B. P., Conference of [British] Empire meteorologists, 1929, Agricultural Section, pp. 17-18.

[3] Bodenheimer, F. S., Biol. Zentralbl., vol. 48, pp. 714-739, 1928.

of the groups can play only minor rôles in the whole drama of predation, and that insects must occupy the center of the stage, regardless even of the superior individual size of the chordates.

To put the case in other language we may quote from David Sharp,[1] "Insects form by far the larger part of the land animals of the world; they outnumber in species all the other terrestrial animals together, while compared with the vertebrates their numbers are simply enormous" (p. 83).

"Insects derive their sustenance primarily from the vegetable kingdom. So great and rapid are the powers of assimilation of the Insect, so prodigious its capacity for multiplication, that the mammal would not be able to compete with it were it not that the great horde of six-legged creatures has divided itself into two great armies, one of which destroys the other" (p. 521).

SUMMARY

The hypotheses about protective and warning colors and mimicry are part of the Natural Selection group of theories. These coloration phenomena and other protective adaptations are supposed to have been developed and perpetuated by the selective value they had in shielding their possessors from attack by predators.

Preceding sections of this discussion call attention to the evidence that one group of predators after another is known either to prey habitually upon "specially protected" groups, or to be so largely guided in choice of food by availability as practically to ignore protective adaptations.

The former is admitted to be true of dragonflies, robber flies, mantids, predacious locustids and Hemiptera, parasitic insects, and of spiders, while the latter is stated to be characteristic of the aquatic immature forms of mayflies, stoneflies, caddisflies, and two-winged flies, and of fishes. Data cited throughout the main body of the present paper show a high degree of indiscriminancy also on the part of amphibians and reptiles.

In fact this general indiscriminancy on the part of predators is so evident that even ardent advocates of the selection theories have been impressed by it and one of them, G. A. K. Marshall, in a paper on the "Bionomics of South African Insects" says:[2]

> If the view advocated by many, that birds cannot be reckoned among the principal enemies of butterflies in the imago state, be true, then I consider that we may practically abandon the whole theory of mimicry as at present applied to the Acraeinae and Danainae of South Africa at all events, for from what I

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[1] Cambridge Nat. Hist., vol. 5, 1910.

[2] Trans. Ent. Soc. London, 1902, p. 356.

> have observed of these insects, I am convinced that their warning coloration cannot have reference to either Mantises, Asilidae, or lizards, which are practically the only other enemies that can be taken into account. . . . . That they [birds] have been the chief, if not the only agents in the production of mimicry whether Batesian or Müllerian I have little doubt.

In other words selectionists practically rest their case on the reactions of birds to protective adaptations. The principal object of the present paper has been to show what those reactions are so far as nearctic birds are concerned, and there is no reason to suspect that the results are otherwise than typical for birds of the world.

The most outstanding feature of the records of the animal food of nearctic birds undoubtedly is the marvellous distribution of them through the phyla, orders, and subordinate systematic groups. Within size limits, animals of practically every kind accessible to birds are preyed upon, and as we consider the records for group after group a tendency for the number of captures to be in proportion to the abundance of the animals concerned is unmistakable. Availability undoubtedly is the chief factor involved in the choice of food, and predation therefore tends to be in proportion to population.

Considering bird predation alone this principle leads to a high degree of indiscriminancy in attack upon the whole kingdom of animal life. The combined attack of birds plus all other predators still more closely approaches complete indiscriminancy. In other words there is utilization of animals of practically every kind for food approximately in proportion to their numbers. This means that predation takes place much the same as if there were no such thing as protective adaptations. And this is only another way of saying that the phenomena classed by theorists as protective adaptations have little or no effectiveness.

Natural Selection theories assume discrimination in the choice of prey. The principle of proportional predation so obvious from the data contained in this paper vitiates those theories for it denotes indiscrimination, the very antithesis of selection.

Finally so far as the types of adaptations discussed in this paper are concerned the influence of such factors as disease and climatic factors, the last the most important of all in reducing animal populations, is completely indiscriminate.

The total mortality of animal groups is known normally to be in strict proportion to their numbers, *i. e.*, a pair of the new generation remains, to replace a pair of the old and it is apparent elimination of all but that pair is very largely due to agencies indiscriminate in their action. There would seem, therefore, to be no discriminative eliminating forces of sufficient strength to bear the very great burden put upon them by natural selection theories.

BIBLIOGRAPHY

A complete bibliography of the subject matter of this paper would fill volumes and nothing like it is attempted here. Articles on food habits cited are chiefly those from which notes supplemental to our tabulations were gleaned; few of foreign origin are included. The citations relating to enemies of various groups are illustrative only, not exhaustive, and some of exotic origin are used where helpful in indicating the wide distribution of predatory attack.

The bibliography is primarily one of predation and so far as possible entries are distributed according to the thing eaten. When the feeding habits are varied, entries are filed according to the group the diet of which is reported upon. Titles classifiable under either of these criteria are arranged according to the phyla or orders to correspond with divisions of the text. Those unclassifiable are grouped at the beginning of the bibliography as Miscellaneous.

MISCELLANEOUS

Blegvad, H.

1915. Food and conditions of nourishment among the communities of invertebrate animals found on or in the sea bottom in Danish waters. Rep. Danish Biol. Sta. to the Board Agr., vol. 22, 1914, pp. 41-78. Notes on food and enemy relations of many groups.

Clark, A. H.

1925. Life in the ocean. Smithsonian Rep. 1923, pp. 369-394. Chiefly a discussion of food relations, many notes from which are used in this paper.

Ewing, H. E.

1929. A manual of external parasites. 225 pp., 96 figs. Includes information on the hosts attacked by mites, ticks, Mallophaga, Anoplura, and fleas.

Force, Edith R.

1925. Notes on reptiles and amphibians of Okmulgee County, Oklahoma. Copeia, no. 141, p. 26, Apr. Notes on examinations of the stomachs of 6 species.

Kjerskog-Agersborg, H. P.

1920. The utilization of echinoderms and of gasteropod mollusks. Amer. Nat., vol. 54, pp. 414-426, Sept.-Oct. Notes on these forms as food of fishes; short bibliography.

McAtee, W. L.

1918. Bird enemies of brine shrimps and alkali flies. The Auk, vol. 35, no. 3, p. 372, July. Eight species of birds mentioned as feeding extensively on both. Doctor Wetmore states: "The toll taken by birds from the brine shrimp and alkali fly larvae and pupae during the course of a season constitutes a mass of individuals almost beyond comprehension."

McIntosh, W. C.

1899. The resources of the sea as shown in the scientific experiments to test the effects of trawling and of the closure of certain areas off the Scottish shores. 248 pp., 32 tables, many pls. Notes on food of fishes, and other marine animals.

Pratt, Henry S.

1923. Preliminary report on the parasitic worms of Oneida Lake, New York. Roosevelt Wild Life Bull., vol. 2, no. 1, pp. 55-71, Oct. Parasites of fishes, birds, reptiles, frogs, and mollusks.

Weed, C. M.

1884. The food relations of birds, frogs, and toads. Ent. Lab. Mich. Agr. Coll., pp. 20-29. Catbird 3 stomachs, robin 6, bluebird 2, crow blackbird 2, spotted frog 8, green frog 4, and toad 7.

Yonge, C. M.

1928. Feeding mechanisms in the invertebrates. Biol. Rev., vol. 3, no. 1, pp. 21-76, Jan. Notes on numerous food and enemy relationships. Full bibliography.

PROTOZOA

See entries under Miscellaneous, Blegvad, McIntosh, Yonge.

PORIFERA

See entries under Miscellaneous, Blegvad, McIntosh, Yonge.

COELENTERATA

See entries under Miscellaneous, Blegvad, McIntosh, Yonge.

PLATYHELMINTHES

Gamble, F. W.

1910. Platyhelminthes and Mesozoa, Cambridge Nat. Hist., vol. 2, pp. 1-120. " Turbellaria are carnivorous. . . . . Land Planarians feed on earthworms, molluscs and wood-lice; fresh-water Planarians on Oligochaet worms, water-snails, and water-beetles; marine forms devour Polychaet worms and molluscs. . . . . Certain Rhabdocoelida are mess-mates of Molluscs and Echinoderms, and a few others are truly parasitic—a mode of life adopted by all Trematodes save Temnocephala" (p. 4).

Stiles, Ch. Wardell.

1902. Frogs, toads, and carp (*Cyprinus carpio*) as eradicators of fluke disease. 18th Ann. Rep. U. S. Bur. Animal Industry, 1901, pp. 220-222, figs. 197-203. Carp apparently destroying large numbers of *Fasciola hepatica*.

NEMATHELMINTHES

Van Zwaluwenburg, R. H.

1928. The interrelationships of insects and roundworms. Bull. Exp. Sta. Hawaiian Sugar Planters' Assoc., Ent. Ser. vol. 20, 68 pp., Jan. Some are primary parasites of orthoptera and bumble bees.

TROCHELMINTHES

Hartog, M.

1910. Rotifera, Gastrotricha, and Kinorhyncha. Cambridge Nat. Hist., vol. 2, pp. 197-238. They devour algae, Infusoria, and other rotifers (p. 212).

MOLLUSCOIDA

Osburn, Raymond C.

1921. Bryozoa as food for other animals. Science, n. s., vol. 53, pp. 451-453, May 13. Two species of ducks and 10 of fishes noted as predators upon bryozoa.

ECHINODERMATA

Clark, Hubert Lyman.

1920. Echinoderms in birds' stomachs. Science, n. s., vol. 51, pp. 594-595, June 11. Ducks and gulls feeding on holothurians and brittlestars.

Dawson, J. W.

1867. The food of the common sea urchin. Amer. Nat., vol. 1, no. 3, pp. 124-125, May. Minute seaweeds mixed with diatoms and remains of small sponges.

ANNULATA

Benham, W. B.

1910. Chaetognatha. Cambridge Nat. Hist., vol. 2, pp. 186-194. "The food of the Chaetognatha consists of floating diatoms, Infusoria, small larvae, and . . . . Copepods, small Amphipods, larval fishes"; they are also cannibalistic (p. 190).

1910. Polychaeta. Cambridge Nat. Hist., vol. 2, pp. 245-344. "The Nereidiformia are mostly carnivorous, and feed on small Crustacea, Mollusca, sponges, and other animals; and Polynoids are even said to eat one another." The Terebellids and Cryptocephala feed on minute organisms strained from water; the deep sea forms feed on Radiolaria and Foraminifera (p. 296).

Blair, W. N.

1927. Notes on *Hirudo medicinalis,* the medicinal leech, as a British Species. Proc. Zool. Soc. London 1927, pp. 999-1,002. The larvae live on frog-tadpoles and fish, and the adults on horses and cattle.

Miller, John A.

1929. The leeches of Ohio. Distribution of the species together with what is known of their occurrence, food, and habitat. Ohio State Univ. Contr. vol. 2, Stone Labr., 38 pp. Feed on turtles, fishes, frogs, mammals, snails, worms, and insect larvae.

Moore, J. Percy.

1923. The control of blood-sucking leeches, with an account of the leeches of Palisades Interstate Park. Roosevelt Wild Life Bull., vol. 2, no. 1, pp. 9-53, 1 pl., 17 figs., Oct. Natural enemies of leeches include domestic and wild ducks, herons, kingfishers, crows, rats, minks, turtles, snakes, frogs, newts, fishes, crayfishes, dragonflies, and other predacious insects and leeches (pp. 29-30, 36).

CRUSTACEA

Bonnot, Paul.

1930. Crayfish. California Fish and Game, vol. 16, no. 3, pp. 212-216, figs. 65-67, July. Scavengers, will eat anything organic either alive or dead; destroy fish spawn. Are preyed upon by many fishes, other crayfishes, salamanders, snakes, turtles, kingfishers, raccoons, and man.

Breder, C. M., Jr.

1922. Notes on the summer food of *Chilomycterus schoepfi* Walbaum. Copeia, no. 104, pp. 18-19, Mar. 20. Analysis of contents of 26 stomachs; chiefly crabs.

Cott, Hugh B.

1929. The Zoological Society's Expedition to the Zambesi, 1927: No. 2, Observations on the natural history of the land-crab *Sesarma meinerti,* from Beira, with special reference to the theory of warning colours. Proc. Zool. Soc. London, 1929, pp. 679-692, pl. 1, figs. 1-4. "Crabs have numerous enemies; they are preyed upon by many small mammals, such as jackals, civets, and mongooses, but more especially by birds." Pelicans, secretary-birds, herons, ibises, storks, owls, hawks, gulls, and waders (p. 689).

Embody, George C.

1910. A new fresh-water amphipod from Virginia, with some notes on its biology. Proc. U. S. Nat. Mus., vol. 38, pp. 299-305, 17 figs., June 18. Notes on 3 species of fish eating this *Eucrangonyx,* p. 305.

Forbes, S. A.

1880. On the food of young fishes. Bull. Ill. State Lab. Nat. Hist., vol. 1, no. 3, pp. 66-79, Nov. Notes on stomach examinations; entomostraca the most important food.

1883. The first food of the common white fish. Bull. Ill. State Lab. Nat. Hist., vol. 1, no. 6, pp. 95-109, May. Entomostraca.

Hankinson, T. L.

1914. Young whitefish in Lake Superior. Science, n. s., vol. 40, pp. 239-240, Aug. 14. Notes on food, chiefly entomostraca.

Kendall, W. C.

1923. Fresh-water Crustacea as food for young fishes. Rep. U. S. Comm. Fisheries, 1922, app. 1, 32 pp., 10 figs. Copepods and ostracods in part carnivorous; Malacostraca and isopods, and amphipods, scavengers; crayfishes, carnivorous. Enemies of amphipods include fishes, birds, insects, Hydra, and the plant Utricularia; crustaceans important food for young fishes. Bibliography.

Klugh, A. B.

1927. The ecology, food-relations, and culture of fresh-water Entomostraca. Trans. Royal Can. Inst., vol. 16, pt. 1, pp. 15-98, May. The chief enemies of entomostracans are fish, dragonfly nymphs, and Hydra. They are eaten also by Corethra, young larvae of Dytiscus, tadpoles of *Rana sylvatica,* and by the entomostracans *Leptodora kindtii* and *Cyclops fuscus.* Their chief food is planktonic *Chlorophyceae.* A long bibliography.

McAtee, W. L.

1913. Some bird enemies of amphipods. The Auk, vol. 30, no. 1, pp. 136-137, Jan. Amphipods preyed upon by 30 species of birds, including 6 species of shorebirds and 14 ducks.

MYRIAPODA

Sinclair, F. G.

1910. Myriapoda. Cambridge Nat. Hist., vol. 5, pp. 29-80. Food of millipeds, vegetable, of centipeds, animal, including diptera, other insects, worms, other centipeds. Centipeds eaten by South American Indians.

MISCELLANEOUS INSECTS

BAIRD, A. B.

1923. Some notes on the natural control of the larch sawfly and larch case bearer in New Brunswick in 1922. Proc. Acadian Ent. Soc., vol. 8, 1922, pp. 158-171. *Lygaeonematus erichsonii.* Birds ate about 10 per cent and tachinid flies parasitized about 15 per cent of the larvae; a pentatomid, ants, and coccinellids were minor predators; hymenopterous parasites of the cocoons were scarce, but shrews consume about 40 per cent of them; natural enemies account for about 75 per cent of each brood.

Coleophora laricella. Birds sometimes consume 75 per cent but on the average about 25 per cent of the larvae; ants and pentatomids take a few; hymenopterous parasites of the pupal stage were of slight importance.

BEAL, F. E. L., McATEE, W. L., and KALMBACH, E. R.

1927. Common birds of Southeastern United States in relation to agriculture. Farmers' Bull. 755, U. S. Dep. Agr. (rev.), 43 pp. 22 figs. In the introduction are statements about the bird enemies of certain groups of insects as 66 species vs. the cotton-boll weevil, 41 for the cottonworm, corn ear worm 12, white grubs 57, wireworms 128, billbugs 55, armyworm 43, cutworms 88, chinch bug 24, corn leaf beetle 22, corn root worm 26, leafhoppers 100, clover leaf weevil 25, clover-root borers 74, cucumber beetle 19, sweet-potato flea beetle 28, grapevine flea beetle 23, bean leaf beetle 19, rice weevil 20, potato beetle 26, periodical cicada 33, and horse flies 40.

CLARINVALL, AM.

1928. De la disparition brusque des invasions d' insects. Bull. Soc. Centr. Forest. Belgique, vol. 31, pp. 266-278, 316-335, and 378-392, 9 figs. Lack of food, climatic factors, natural enemies, and disease; the last three causes are given special attention; parasitic Hymenoptera and Diptera receive much comment and predators of the following groups are discussed: mammals, birds, Neuroptera, Coleoptera, Diptera, and Hymenoptera.

FORBUSH, E. H.

1900. Birds as protectors of woodlands. Massachusetts Crop Rep., July, 1900, pp. 26-39. Contains lists of birds feeding on gipsy moth, 46 species; brown-tail moth, 29; forest tent caterpillar, 25; orchard tent caterpillar, 32: cankerworms, 51; tussock moth, 9; may beetles, 8; and plant lice, 34.

GIRAULT, A. A.

1907. Hosts of insect egg-parasites in North and South America. Psyche, vol. 14, pp. 27-39, Apr. Coleoptera, 9 species, 10 egg parasites; Diptera, 1 species, 1 egg parasite; Hemiptera, 28 species, 43 egg parasites; Hymenoptera, 9 species, 11 egg parasites; Lepidoptera, 51 species, 68 egg parasites; Neuroptera, 1 species, 2 egg parasites; Orthoptera, 26 species, 47 egg parasites.

1911. Hosts of insect egg-parasites in North and South America, II. Psyche, vol. 18, no. 4, pp. 146-153, Aug. Coleoptera, 6 species, 6 parasites; Hemiptera, 10 species, 16 parasites; Hymenoptera, 2 species, 4 parasites; Lepidoptera, 15 species, 22 parasites;

Neuroptera, 1 species, 1 parasite; Odonata, 2 species, 5 parasites; Orthoptera, 4 species, 4 parasites; Platyptera, 1 species, 1 parasite.

McAtee, W. L.

1911. Economic ornithology in recent entomological publications. The Auk, vol. 28, no. 1, pp. 138-142, Jan. Clover root curculios (*Sitones hispidulus*) are recorded as being taken by 24 species of birds. Sorghum midge (*Contarina sorghicola*) apparently eaten by hummingbirds. New Mexico range caterpillar (*Hemileuca oliviae*)—preyed upon by robins. Crane flies (Tipulidae)—86 species of nearctic birds are known to feed upon tipulids and their eggs. Pentatomidae are eaten freely by a great variety of birds. Yellow bear caterpillar (*Diacrisia virginica*)—two species of birds, the black-billed cuckoo and the bob-white, are recorded as enemies. Mosquitos are preyed upon by more than 20 species of North American birds.

1911. Economic ornithology in recent entomological publications. The Auk, vol. 28, no. 2, pp. 282-287, Apr. Oakpruner (*Elaphidion villosum*) is recorded as preyed upon by four species of birds. Potato beetle (*Leptinotarsa decemlineata*)—21 species of birds are recorded as enemies of this pest. Hop flea beetles are eaten by killdeers and cliff swallows. Gipsy moths are recorded as being taken by 46 species of birds and brown-tail moths by 31. Alfalfa leaf weevil (*Phytonomus murinus*)—the English sparrow and the black-headed grosbeak are recorded as feeding on this weevil.

1911. Economic ornithology in recent entomological publications. The Auk, vol. 28, no. 4, pp. 505-509, Oct. Millipeds are recorded as being eaten by 83 species of birds, certain beetle larvae, toads, armadillos and skunks. Cutworms are eaten on sight by practically all birds that glean their food from the ground or from low vegetation. Flea beetles are eaten by various species of birds, in the case of *Crepidodera* by 26 species. Harlequin bug (*Murgantia histrionica*) is kept in check locally by the English sparrow. Cabbageworm (*Pontia rapae*) eaten by English sparrow. Codling moth—mortality during the winter as high as 90 per cent caused chiefly by birds, the beetle larvae, *Tenebrioides* sp., and diseases. Larch sawfly (*Nematus erichsoni*)—red-eyed vireos and cuckoos reported as feeding upon larvae of this insect.

1912. Economic ornithology in recent entomological publications. The Auk, vol. 29, no. 3, pp. 416-417, July. Billbug (*Sphenophorus callosus*) recorded as taken by nighthawks. False wireworms (*Eleodes*) preyed upon by 13 species of birds. Agricultural ant (*Pogonomyrmex barbatus molefaciens*)—eight species of birds recorded as foes. Alfalfa weevil recorded as taken by 31 species of birds, notable mention being made of the English sparrow.

1913. Economic ornithology in recent entomological publications. The Auk, vol. 30, no. 1, pp. 128-132, Jan. Boll weevils preyed upon by 53 species of birds. A rice weevil (*Lissorhoptrus simplex*)—the only natural enemies recorded are two species of birds. Plum curculio—seven species of birds recorded as enemies. Leafhoppers known to be preyed upon by more than 120 kinds of birds, numerous species taking them in abundance. Nabidae, Lygaeidae, and spiders also mentioned as enemies.

1913. Economic ornithology in recent entomological publications. The Auk, vol. 30, no. 4, p. 602, Oct. Eight species of birds observed feeding on the larvae of the fruit tree leafroller (*Archips argyrospila*). May beetles and their larvae (*Lachnosterna*) preyed upon by 60 species of birds, the crow and crow blackbird probably being the most important enemies.

1914. Economic ornithology in recent entomological publications. The Auk, vol. 31, no. 3, pp. 421-422, July. Sugar-beet wireworm (*Limonius californicus*)—the California shrike an important enemy. *Crambus caliginosellus*—the quail and the kingbird noted feeding on this species. *Crambus laqueatellus*—the wood pewee observed taking large numbers. Rose aphid (*Macrosiphum rosae*)—house finch and white-crowned sparrow feeding on these aphids. Chinch bug—17 species of birds recorded as foes.

1915. Economic ornithology in recent entomological publications. The Auk, vol. 32, no. 2, pp. 253-254, Apr. Wireworms (*Elateridae*) are recorded as being taken by 90 species of birds. Grasshoppers—upward of 100 species of birds are known to feed upon these insects. Alfalfahopper (*Stictocephala festina*)—four species of birds recorded as enemies. Midges (*Chironomus*) are recorded as preyed upon by six species of birds.

1915. Bird enemies of forest insects. Amer. Forestry, vol. 21, no. 6, pp. 681-691, June. Bark beetles are preyed upon by more than 45 species of birds. Round-headed and flat-headed wood borers—the larvae of these insects are recorded to be eaten by all kinds of woodpeckers. Flat-headed apple tree borers are recorded as taken by the downy woodpecker. Carpenter ants—fully 50 species of birds are known to eat these insects. An average of nearly 30 per cent of the food of woodpeckers is recorded as being ants. No fewer than 46 kinds of birds are known to feed upon the gipsy moth in one or another of its stages. Thirty-one species of birds are recorded as enemies of the brown-tail moth. Orchard tent caterpillars are preyed upon by 43 species of birds, forest tent caterpillars by 32 and cankerworms by more than 50. Snow-white linden moth—the English sparrow is recorded as an important check on this insect. Plant lice are preyed upon by most small birds. Scale insects are known to be taken by more than 60 species of birds. Cicada—fishes and tortoises when opportunity presents, frogs, toads, lizards, squirrels, and a multitude of birds prey upon these insects.

1915. Economic ornithology in recent entomological publications. The Auk, vol. 32, no. 4, pp. 520-521, Oct. Katydids—birds recorded as important foes, special mention being made of chipping sparrows. *Calosoma sycophanta*—crows and hairy woodpeckers recorded as enemies of this beetle. Armyworm—more than 20 species of birds recorded as foes.

1915. Birds that feed upon pecan insects. Proc. Nat. Nut Growers' Assoc., pp. 40-41, Dec. 1. Pecan leaf caterpillar—birds known to feed upon pests of this genus (*Datana*) are robins, starlings, and two species of cuckoos. Fall webworm—four species of birds noted as enemies of this pest. Pecan weevil—64 kinds of birds are known to feed upon these beetles and congeners. White ants—of the 27 species of birds feeding on white ants, a flicker is recorded to have taken 1,100. Oakpruners are known to be preyed upon by four species of birds. *Cyllene*—five species of birds are recorded as enemies. Bark beetles are devoured by more than 45 kinds of birds. Plant lice and scale insects each are taken by 60 or more species of birds.

1916. Economic ornithology in recent entomological publications. The Auk, vol. 33, no. 2, pp. 216-217, Apr. Twelve-spotted cucumber beetle—27 species of birds recorded as enemies. Grasshoppers—six species of birds feeding upon them during an outbreak in New Mexico. Pine moth—the hairy woodpecker recorded as the most efficient natural force in restraining the Zimmerman pine moth.

1916. Economic ornithology in recent entomological publications. The Auk, vol. 33, no. 4, pp. 448-450, Oct. Armyworm (*Cirphis unipuncta*)—crows recorded as great destroyers of this pest; cowbirds and grackles also reported doing good work. Meadowlarks and robins observed eating the larvae. The armyworm has many natural enemies, among which are insects, reptiles, birds, and mammals. Skunks and toads undoubtedly eat thousands both of caterpillars and pupae. Clover leafhoppers are recorded taken by nine species of birds. Corn and cotton wireworm (*Horistonotus uhleri*)—birds are the only enemies of this pest recorded. Velvetbean caterpillar—the "ricebird" and the mockingbird eat many of these. California green lacewing flies (*Chrysopa californica*) are recorded as taken by two species of birds, the western wood pewee and the nighthawk.

1917. Bird enemies of a few insect pests. The Auk, vol. 34, no. 2, pp. 230-231, Apr. Grasshoppers are eaten by practically all birds, exceptions being the strictly vegetarian doves and pigeons. Fall armyworm—several common wild birds recorded as important enemies. Cabbageworm—the English sparrow, chipping sparrow and house wren recorded as enemies of this pest. Velvetbean caterpillars are preyed upon by the red-winged blackbird, the mockingbird, and the field sparrow.

1918. Economic ornithology in recent entomological publications. The Auk, vol. 35, no. 2, pp. 251-253. Apr. Potato aphid (*Macrosiphum solanifolii*)—chipping sparrows, quail, and English sparrows observed feeding on this pest. Sweet-potato leaf folder (*Pilocrocis tripunctata*) reported taken by the boat-tailed grackle. Cabbage looper (*Autographa brassicae*)—boat-tailed grackle observed feeding on adults and larvae. Pecan-leaf casebearer (*Acrobasis nebulella*) larvae taken by three species of birds. Fall webworm (*Hyphantria textor*)—red-eyed vireos recorded as destroying about 40 per cent of the larvae in Nova Scotia in 1916; other bird foes noted are yellow-billed cuckoos and Baltimore orioles. Emperor moth (*Samia cecropia*)—cocoons destroyed by woodpeckers.

1918. Economic ornithology in recent entomological publications. The Auk, vol. 35, no. 4, pp. 493-495, Oct. Round-headed apple tree borer (*Saperda candida*)—entomologists record birds as enemies; the present note names five species as feeding upon the adults. Rootworms—37 species of birds recorded as enemies of *Diabrotica duodecimpunctata*, and 23 species as enemies of *Diabrotica soror*. Green plant-bugs (*Nezara* spp.) identified in stomachs of 31 kinds of birds, 100 individuals being found in the stomach of a Franklin's gull. Whitegrubs (*Lachnosterna* spp.) taken by 78 species of birds and 2 of toads.

1919. Economic ornithology in recent entomological publications. The Auk, vol. 36, no. 2, pp. 305-307, Apr. Woodpeckers noted as preying extensively upon larch bark beetles and borers. Grape root borer (*Memythrus polistiformis*)—the crested flycatcher observed feeding on the adults. Peach-tree borers (*Sanninoidea exitiosa* and *S. pictipes*)—two species of birds recorded as foes. Cankerworms preyed upon by 75 species of birds. Whitegrubs—several groups of birds named as enemies.

1920. Economic ornithology in recent entomological publications. The Auk, vol. 37, no. 2, pp. 322-325, Apr. False wireworms (*Eleodes*)—24 species of birds recorded as enemies. Lotus borer (*Pyrausta penitalis*)—red-winged blackbirds noted as foes of this pest. Roundheaded apple tree borer (*Saperda candida*)—"Woodpeckers destroy great numbers of the borers by removing them from their burrows. . . . . In some cases from 50 to 75 per cent." Ten kinds of birds recorded as enemies. Flat-headed apple tree borer—12 species of birds recorded as preying upon the adults of *Chrysobothris*. Striped cucumber beetle (*Diabrotica vittata*)—17 species of birds noted as foes. Grainbugs (*Chlorochroa* spp.) recorded as taken by eight species of birds. Whitegrubs (*Phyllophaga*) preyed upon by 81 species of birds, the common crow being the most important enemy of both adults and larvae.

1921. Economic ornithology in recent entomological publications. The Auk, vol. 38, no. 2, pp. 302-304, Apr. Spotted apple tree borer (*Saperda cretata*)—"by far the most effective natural check to the increase of this borer seems to be the woodpeckers." Clover stem borer (*Languria mozardi*)—hymenopterous parasites, toads, and five kinds of birds recorded as enemies. Beet leaf beetle (*Monoxia puncticollis*)—enemies recorded are ladybird beetles, a stink bug, parasites, toads, and birds. Cabbage flea beetles (*Phyllotreta* spp.) 12 kinds of birds noted as foes. Grapevine flea beetle (*Altica chalybea*)—eight species of birds recorded as feeding upon this insect. Clover leaf weevil (*Hypera punctata*) preyed upon by 42 species of birds.

1922. Local suppression of agricultural pests by birds. Smithsonian Rep. 1920, pp. 411-438, pls. 1-3. In more than 70 cases birds apparently exterminated one or another of 32 insect pests locally.

1923. Economic ornithology in recent entomological publications. The Auk, vol. 40, no. 1, pp. 161-162, Jan. Pale western cutworm (*Porosagrotis orthogonia*)—records the western grasshopper sparrow, horned larks, and possibly other wild birds as enemies. Green June beetle (*Cotinis nitida*)—19 kinds of birds recorded as foes; southern corn root worm (*Diabrotica 12-punctata*) taken by 40 species of birds. Potato beetle (*Leptinotarsa decemlineata*)—fed upon by 25 species of birds.

1923. Economic ornithology in recent entomological publications. The Auk, vol. 40, no. 3, pp. 557-559, July. Corn ear worm (*Heliothis obsoleta*)—17 species of birds feed on this pest; more than 50 larvae were found in a single stomach of the boat-tailed grackle. Cloverleaf weevil (*Hypera punctata*)—records 43 species of birds preying upon this weevil. European corn borer (*Pyrausta nubilalis*)—five species of birds recorded preying upon larvae and three species observed catching the moths. Tussock moth (*Hemerocampa leucostigma*)—12 species of birds known to feed upon this insect in one stage or another. Lacewing flies (*Chrysopidae*)—17 species of birds recorded as predators, most of them taking the adults, but five known to eat the larvae.

1924. Economic ornithology in recent entomological publications. The Auk, vol. 41, no. 1, pp. 191-193, Jan. American silkworm (*Samia cecropia*)—Dr. John Tothill concludes from his observations in Nova Scotia that nearly three-fourths of the caterpillars are eaten by birds (orioles, robins, etc.), and about 85 per cent of the pupae are destroyed by woodpeckers. Apple leaf skeletonizer (*Hemerophila pariana*)—chipping sparrow observed feeding on the larvae. Mormon cricket (*Anabrus simplex*)—three species of birds mentioned as enemies, but birds said to be important factors in the control of these insects.

1924. Economic ornithology in recent entomological publications. The Auk, vol. 41, no. 4, pp. 629-632, Oct. False wireworms (*Eleodes* spp.)—13 kinds of birds recorded as enemies. Argus tortoise beetle (*Chelymorpha cassidea*)—identified in the stomachs of 14 species of birds, most often in those of the starling and kingbird. Codling moth (*Carpocapsa pomonella*)—woodpeckers recorded as important enemies, special mention being made of the red-bellied. Oak sapling borer (*Goes tesselatus*)—woodpeckers noted as destroying many larvae and pupae. Larch sawfly (*Lygaeonematus erichsonii*)—four species of birds recorded as feeding upon the larvae, consuming about 10 per cent of them in New Brunswick. Larch casebearer (*Coleophora laricella*)—4 species of birds recorded as enemies. Spruce budworm (*Tortrix fumiferana*)—several species of birds and insect parasites noted as foes.

1926. Economic ornithology in recent entomological publications. The Auk, vol. 43, no. 3, pp. 396-398, July. Most common birds are enemies of the Japanese beetle (*Popillia japonica*). Green June beetle (*Cotinis nitida*)—observations show that starlings feed on the larvae and cardinals on the adults; in addition to these two birds, 22 other species are known to prey upon this pest. Striped cucumber beetle (*Diabrotica vittata*)—17 species of birds known

to feed on this beetle. The larvae or pupae of cattle grubs (*Hypoderma*) were found in stomachs of four species of birds; the robin also observed feeding on the larvae. Cankerworms (*Alsophila pometaria* and *Paleacrita vernata*)—76 species of birds listed as predators. Cabbageworm (*Pieris rapae*)—" Birds which are known to feed upon cabbage worms are the chipping sparrow, English sparrow, and house wren."

1926. Relation of birds to woodlots. Roosevelt Wild Life Bull., vol. 4, no. 1, 152 pp., 22 pls., Oct. Contains a section (pp. 101-136) on forest insect pests and their bird enemies discussed under the following heads: Plant lice (Aphididae), scale insects (Coccidae), cicadas (Cicadidae), walkingsticks (Phasmidae), flat-headed wood borers (Buprestidae), leaf chafers (Scarabaeidae), leaf beetles (Chrysomelidae), round-headed wood borers (Cerambycidae), bark beetles (Scolytidae), caterpillars (Lepidoptera), and sawflies, borer wasps, and ants (Hymenoptera).

1926. The role of vertebrates in the control of insect pests. Smithsonian Rep. 1925, pp. 415-437, 7 pls. General notes on amphibians, reptiles, and mammals as enemies of insects. Summarizes 109 cases of control and 88 of local suppression of insects by birds.

1928. Economic ornithology in recent entomological publications. The Auk, vol. 45, no. 4, pp. 526-528, Oct. Satin moth (*Stilpnotia salicis*) —five species of birds noted as enemies in Massachusetts. Western robins and bats reported as feeding on it in British Columbia. *Lygus elisus*—26 species of birds known to feed upon plant bugs of this genus. Cotton-stainers (*Dysdercus* spp.)—record of nine kinds of birds preying upon cotton stainers, and three species feeding upon other bugs of the same family. Fall armyworm (*Laphygma frugiperda*)—lists 13 species of birds as enemies, and notes that English sparrows have several times been observed to eradicate local infestations. Pale western cutworm (*Porosagrotis orthogonia*)—horned larks observed doing effective work against this pest.

Muttkowski, R. A., and Smith, G. M.

1929. The food of trout stream insects in Yellowstone National Park. Roosevelt Wild Life Ann., vol. 2, no. 2, pp. 241-263, Oct. Stoneflies, carnivorous forms prey chiefly on larvae and pupae of mayflies, caddisflies, midges; mayflies are chiefly scavengers; caddisflies: the carnivorous species are inclined to be cannibalistic, but they take also rotifers, midge larvae and pupae, and dead insects. Bibliography.

Patch, E. M.

1906. White grubs and June beetles. [In circulars, finance, meteorology, and index.] Bull. 137, Maine Exp. Sta., pp. 286-287. Enemies noted: Skunks, moles, and ground squirrels in addition to a large number of birds prey on the grubs. Besides toads and frogs and possibly insectivorous snakes, a large number of birds feed on the adult beetles. Cecropia moth, p. 294: enemies noted are chickens, turkeys, and swine. The tent caterpillar, p. 296: natural enemies of this caterpillar include birds and parasitic insects; it is also susceptible to attack by bacterial and fungus diseases.

Thompson, W. R.

1929. On the relative value of parasites and predators in the biological control of insect pests. Bull. Ent. Research, vol. 19, pt. 4, pp. 343-350, Mar. Mentions parasitic habits for 3 families of Coleoptera, the Strepsiptera, 2 families of Neuroptera, 2 of Lepidoptera, 8 of Diptera, and 19 of Hymenoptera, and predatory habits in 3 families of Orthoptera, 9 of Neuroptera, the Odonata, some Corrodentia and Thysanoptera, in 8 families of Hemiptera, the Dermaptera, 19 families of Coleoptera, the Mecoptera, 2 families of Lepidoptera, 15 families of Diptera, and 6 of Hymenoptera. Thinks value of predators has been underestimated.

Uvarov, B. P.

1928. Insect nutrition and metabolism. A summary of the literature. Trans. Ent. Soc. London, pp. 255-343. Largely technical on metabolism, but some details of food are given. There is a section on carnivorous insects, pp. 269-270. Bibliography.

APTERA

Macnamara, Charles.

1924. The food of Collembola. Can. Ent., vol. 56, no. 5, pp. 99-105, May. Feed on sap, pollen, diatoms, algae, carrion, and Collembola.

ODONATA

Burnham, Edward J.

1899. Preliminary catalogue of the Anisoptera in the vicinity of Manchester, N. H. Proc. Manchester Inst. Arts and Sci., vol. 1, pp. 32-34. Certain birds appear to feed exclusively upon these insects while they last. The dragonflies mentioned are *Macromia illinoensis* and *Tetragoneuria semiaquea*.

Calvert, Philip P.

1893. Catalogue of the Odonata (dragonflies) of the vicinity of Philadelphia, with an introduction to the study of this group of insects. Trans. Amer. Ent. Soc., vol. 20, no. 3, pp. 205-206, July-Sept. Notes on numerous bird enemies of dragonflies.

Lamborn, Robt. H.

1890. Dragonflies vs. mosquitoes, 202 pp., 9 pls. Nymphs feed on mosquito larvae, upon each other, upon water beetles, bugs, and small fishes. Not worth encouraging as mosquito enemies; fish and waterfowl also are foes of mosquitoes.

Lucas, W. J.

1908. Foe of dragonfly nymphs. Entomologist, vol. 41, p. 16. *Notonecta glauca.*

Lyon, Mary B.

1915. The ecology of the dragonfly nymphs of Cascadilla Creek (Odon.). Ent. News, vol. 26, no. 1, pp. 1-15, Jan. Notes on stomach contents of 36 specimens, midge larvae the most prominent item of food, but mayflies, *Corixids,* dytiscids, amphipods, cladocera, ostracods, hydrachnids, and snails were eaten.

Moore, J. Percy.

1900. Kingbirds eating dragonflies. Ent. News, vol. 11, p. 340. *Epiaeschna heros;* habitually captures them.

NEEDHAM, JAMES G.

1898. Birds vs. dragonflies. Osprey, vol. 2, nos. 6-7, pp. 85-86, Feb.-Mar. Review of notes by Rene Martin on European hobby and swift as enemies; *Merops persicus* lines its nest with their wings; when teneral, chipmunks, frogs, toads, snakes, ants, and birds eat them. Various birds eat nymphs.

1918. [Food of Odonata.] In Fresh-water biology, by Ward and Whipple, p. 890. Diptera and other dragonflies.

NEEDHAM, JAS. G., AND HEYWOOD, HORTENSE B.

1929. A handbook of the dragonflies of North America, 378 pp., illus. Food, flies, mosquitoes, honey bees; enemies, birds, frogs, fishes, water snakes, spiders, other dragonflies; large numbers sometimes destroyed by storms.

SHARP, DAVID.

1910. [Enemies of Odonata.] Cambridge Nat. Hist., vol. 5, pp. 424-425. Hawks, bee-eaters, other birds, fishes, snakes, newts, aquatic Coleoptera, Hemiptera, and other Odonata.

WALKER, E. M.

1924. The Odonata of the Thunder Bay District, Ontario. Can. Ent., vol. 56, no. 7, pp. 170-176, July; no. 8, pp. 182-189, Aug. Dragonflies found in stomachs of sucker, whitefish, sturgeon, and golden-eye ducks; a dragonfly nymph observed eating an adult of same species.

WILSON, CHARLES BRANCH.

1920. Dragonflies and damselflies in relation to pondfish culture, with a list of those found near Fairport, Iowa. Bull. 36, U. S. Bur. Fisheries, pp. 182-264, pls. 67-69, figs. 1-63, Aug. Notes on contents of alimentary canals of 250 nymphal and many adult Odonata; citation of previous studies; full bibliography. Odonate nymphs, diving beetles, water-scorpions, other aquatic Hemiptera, Hydra, nematodes, fungi, birds, fishes, reptiles and amphibians prey on nymphs; Diptera and Hymenoptera parasitize the eggs; and birds, other dragonflies, ants, spiders, robber flies, frogs, and fishes prey upon the adults, which also have both external and internal parasites.

AGNATHA

See various entries under Pisces; also Muttkowski and Smith under Miscellaneous Insects.

NEEDHAM, JAMES G.

1920. Burrowing mayflies of our larger lakes and streams. Bull. U. S. Bur. Fisheries, vol. 36 (1917-1918), pp. 269-292, pls. 70-92. Mayflies of prime importance as food of fishes; quotations from Forbes, Wagner, and Pearse, as to their value (pp. 270-271).

PLECOPTERA

See various entries under Pisces; also Muttkowski and Smith under Miscellaneous Insects.

ISOPTERA

[Hagen, H.]

1881. [Letter on birds vs. termites.] Proc. Boston Soc. Nat. Hist., vol. 20, 1878-1880, p. 118. Record of 15 species of birds following an emigration of white ants, robins, bluebirds, and sparrows being mentioned.

[Longstaff, G. B.]

1918. A flight of winged termites at Barrackpore. Trans. Ent. Soc. London, 1918, pp. lxiv-lxvi. Lizards, bullfrogs, rats, cats, dogs, jackals, mongoose, crows, Indian mynah, bats and cockroaches observed eating white ants.

Snyder, T. E.

1920. [Nearctic Termites.] Notes on biology and geographic distribution. U. S. Nat. Mus. Bull. 108, pp. 87-211. Termite checks include parasitic fungi, protozoans, nematodes, mites, and predacious ants, robber flies, beetle larvae, crickets, spiders, centipeds, lizards, and domestic and wild birds (pp. 116-118).

1924. New termites and hitherto unknown castes from the Canal Zone, Panama. Journ. Agr. Research, vol. 29, no. 4, p. 182, Aug. 15. Ants and anteaters as foes.

DERMAPTERA

Brindley, H. H.

1920. Notes on certain parasites, food, and capture by birds of the common earwig (*Forficula auricularia*). Proc. Cambridge Phil. Soc., vol. 19, (1916-1919) pp. 167-177. Fourteen species of British birds known to eat earwigs; also domestic fowls.

Morgan, W. P.

1924. Notes on the function of the forceps in earwigs. Proc. Indiana Acad. Sci., vol. 33, (1923), pp. 303-306, 7 figs. Earwigs are predatory and cannibalistic, use forceps in capturing and holding prey.

Sharp, David.

1910. Forficulidae—earwigs. Cambridge Nat. Hist., vol. 5, pp. 202-216. Eat larvae, snails, flowers, vegetables.

CHELEUTOPTERA

Badenoch, L. N.

1899. [Enemies of Phasmidae.] True tales of the insects, p. 48. Birds, lizards, mantids, bugs; eggs parasitized.

Sharp, David.

1910. Phasmidae—stick and leaf insects. Cambridge Nat. Hist., vol. 5, pp. 260-278. Vegetarian, but sometimes cannibalistic. Enemies include birds, Hemiptera, ichneumon flies.

SALTATORIA

Aughey, Samuel.

1878. Notes on the nature of the food of the birds of Nebraska. 1st Ann. Rep. U. S. Ent. Comm. (1877), Appendix II, pp. [13-62.] Records migratory locusts from the stomachs of 172 species of birds and field observations on 33 other species eating them.

BADENOCH, L. N.

1899. [Enemies of locusts.] True tales of the insects, pp. 127-128. Especially "locust birds"; but bears, skunks, squirrels, mice, frogs, and lizards are mentioned.

BRUNER, LAWRENCE.

1902. Grasshopper notes for 1901. Bull. 38, Div. Ent., pp. 39-49. Chickens, turkeys, blackbirds, sage grouse and sharp-tail grouse mentioned as natural enemies.

1905. Grasshopper conditions in Nebraska, Northeastern Colorado, Wyoming, Montana, and Western Kansas during the summer of 1904. Bull. 54, U. S. Bur. Ent., pp. 60-64. "Magnificent examples" of the usefulness of gulls as grasshopper destroyers; turkeys used to combat the insects.

BRYANT, H. C.

1912. Birds in relation to a grasshopper outbreak in California. Univ. California Publ. in Zool., vol. 11, no. 1, pp. 1-20, Nov. Los Banos; 15 species of land birds were found to eat the insects. Tame ducks also important. The native birds were calculated to be destroying daily 120,445 grasshoppers per square mile.

BURRILL, A. C.

1920. Meadowlarks control cricket pest. California Fish and Game, vol. 6, no. 1, p. 38, Jan. Meadowlarks recorded as important enemies of the coulee cricket.

CRIDDLE, NORMAN.

1920. Birds in relation to insect control. Can. Field-Nat., vol. 34, no. 8, pp. 152-153, Nov. Crows, gulls, black terns, blackbirds, and grouse recorded as destroying large numbers of grasshoppers.

1922. [Enemies of grasshoppers.] Can. Field-Nat., vol. 36, no. 4, pp. 66-68, Apr. Diptera, Hymenoptera, Coleoptera, birds, mammals (skunks, badgers, weasels, pocket mice, shrews, gophers), snakes, toads, and frogs.

GILLETTE, C. P.

1905. The western cricket. Colorado Agr. Exp. Sta., Bull. 101, 16 pp., Apr. *Anabrus simplex*. Bears and coyotes feed upon this pest but birds destroy them in greatest numbers; hawks, sage grouse and blackbirds noted (p. 7).

GRASSÉ, P.

1924. Les ennemis des Acridiens ravageurs francais. Rev. Zool. Agr. Appl., Bull. Soc. Zool. Agr., vol. 23, no. 1, pp. 1-14, pl. 1, figs. 1-4, Jan. Mammals, birds, reptiles, spiders, mites, wasps, beetles, flies, nematodes and Protozoa.

LUGGER, OTTO.

1889. Notes on the Rocky Mountain locust in Otter Tail County, Minnesota, in 1888. 5th Bienn. Rep. Dep. Agr. Minn., Suppl. 1, pp. 305-343, 22 figs. Nematodes, mites, tachina flies, bee flies, blister beetles, ground beetles, soldier beetles, robber flies, digger wasps, dragonflies, birds, skunks, shrews, toads, snakes, and turtles mentioned as enemies.

McAtee, W. L.

1913. Economic ornithology in California. The Auk, vol. 30, no. 1, pp. 132-136, Jan. H. C. Bryant records 22 species of water and shore birds and 40 species of land birds as enemies of grasshoppers.

1917. Economic ornithology in recent entomological publications. The Auk, vol. 34, no. 4, pp. 497-498, Oct. Grasshoppers are found on the bill-of-fare of practically all wild birds; freely eaten also by chickens and turkeys.

Merrill, D. E.

1916. [Enemies of grasshoppers.] Bull. 102, New Mexico Agr. Exp. Sta., pp. 15-16, Apr. Birds; fields near breeding grounds of the blackbirds are free from grasshopper damage; poultry; skunks; mites; parasitic flies; ground beetles; blister beetles; bee flies.

Morse, Albert P.

1920. [Enemies of Orthoptera.] Proc. Boston Soc. Nat. Hist., vol. 35, p. 271. Frogs, toads, salamanders, snakes, lizards, birds, mice, moles, shrews, skunk, and fox.

Sanderson, E. Dwight.

1906. The differential locust. Bull. 57, U. S. Bur. Ent., pp. 19-26, figs. 9-11. *Melanoplus differentialis.* Blackbirds and bobolinks suppressing an infestation; a conopid fly parasite also mentioned.

1906. Report on miscellaneous cotton insects in Texas. Bull. 57, U. S. Bur. Ent., p. 22. Blackbirds and bobolinks checking an outbreak of *Melanoplus differentialis.*

Sharp, David.

1910. [Enemies of Orthoptera.] Cambridge Nat. Hist., vol. 5, p. 291. Cantharidae, Bombyliidae, and mites destroy eggs; birds and mammals eat adults.

Smith, Harrison E.

1915. The grasshopper outbreak in New Mexico during the summer of 1913. Bull. 293, U. S. Dep. Agr., 12 pp. 2 figs. Six species of birds, several species of lizards, prairiedogs, a sarcophagid parasite, and a wasp observed doing notable execution.

Treherne, R. C. and Buckell, E. R.

1924. The grasshoppers of British Columbia. Bull. 39, Dominion of Canada Dep. Agr., pp. 29-35, Oct. Enemies include: nematodes, Diptera, Hymenoptera, Coleoptera, fungi and bacteria.

U. S. Entomological Commission.

1878. First annual report . . . . for the year 1877 relating to the Rocky Mountain locust, etc., pp. 477+[294], 111 figs., 5 pls. Invertebrate enemies (pp. 284-334) include larvae of anthomyiid and sarcophagid flies, ground beetles, blister beetles, click beetles, soldier beetles, robber flies, and mites all attacking the eggs; and the following preying upon the locusts after birth: mites, ground beetles, tiger beetles, robber flies, wasps, tachinid and sarcophagid flies, ichneumonids and nematodes. The vertebrate enemies (pp. 334-350) include birds, hogs, skunks, prairie squirrels, mice, and toads. Appendix II [pp. 13-62], is devoted to an account of the food of birds especially in relation to the locust.

PALEOPTERA

SHARP, DAVID.

1910. Blattidae—cockroaches. Cambridge Nat. Hist., vol. 5, pp. 220-241. Food chiefly dead animal matter, but a great variety of refuse also taken. Enemies include birds, rats, scorpions, spiders, and wasps (Ampulicides).

DICTYOPTERA

SHARP, DAVID.

1910. Mantidae—soothsayers or praying insects. Cambridge Nat. Hist., vol. 5, pp. 242-259. Voracious, eating insects of all kinds including their own, and even small birds.

CORRODENTIA

Food animal and vegetable refuse, and fungi.

MALLOPHAGA

Externally parasitic on birds and mammals.

SIPHONAPTERA

External parasites on birds and mammals.

RHYNCHOTA

CLARK, L. B.

1928. Seasonal distribution and life history of *Notonecta undulata* in the Winnipeg Region, Canada. Ecology, vol. 9, no. 4, pp. 383-403, pl. 20, 1 fig., Oct. Summary of literature as to food and enemies, pp. 395-399. Food: eggs of giant water bug, water-boatman, eggs and nymphs of dragonflies, ostracods, copepods, newly hatched fishes. Enemies: giant water bug, water-scorpion, waterstrider, dragonfly nymphs, fishes, and birds.

CURRAN, C. HOWARD.

1920. Observations on the more common aphidophagous syrphid flies (Dipt.). Can. Ent., vol. 52, no. 3, pp. 53-55, Mar. Larvae of five species consumed on the average from 15 to 47 plant lice daily.

DISTANT, W. L.

1892. A monograph of the Oriental Cicadidae, pp. vii-viii. "The Cicadidae appear to be one of the most non-protected families of insects and are the victims of most predacious creatures." Mentions birds, mantids, spiders, dragonflies, wasps, hymenopterous parasites and fungi.

FLUKE, C. L.

1929. The known predacious and parasitic enemies of the pea aphid in North America. Research Bull. 93, Wisconsin Agr. Exp. Sta., 47 pp., 3 pls., 32 figs. Mites, spiders, crickets, lacewing flies, Hemiptera, Coleoptera, Diptera, Hymenoptera, and birds. Lacewings, ladybirds, and Syrphidae appear to be most important.

FULLAWAY, DAVID T.

1920. Natural control of scale insects in Hawaii. Proc. Hawaiian Ent. Soc. (1919), vol. 4, no. 2, pp. 237-246, June. Forty-four species of scale insects, 87 parasites, 20 predators; varying up to 3 predators and 7 parasites to a species.

GARMAN, H.

1898. The chinch bug. Bull. 74, Kentucky Agr. Exp. Sta., pp. 45-70, figs. 1-10, May. Coccinellids, toads, quail, and meadowlarks prey upon it (p. 51); great fluctuations in abundance caused by disease.

GIBSON, EDMUND H.

1916. The clover leafhopper and its control in the central States. Farmers' Bull. 737, U. S. Dep. Agr., 8 pp., 5 figs., June. *Agallia sanguinolenta*. More than 100 species of birds, chickens, turkeys, and guinea fowl prey upon leafhoppers (p. 5).

HANFT, H.

1916. Beiträge zur Kenntniss der Cicadinenfeinde. Zeitschr. wiss. Insektenbiol., vol. 12, pp. 200-204, 217-223, 274-279, figs. Stresiptera, Dryinidae, Serphoidea, Pipunculidae, Neuroptera, Nematoda, mites, fungi. Bibliography.

HUNGERFORD, H. B.

1919. The biology and ecology of aquatic and semi-aquatic Hemiptera. Kansas Univ. Bull., vol. 11, 265 pp., 30 pls. Gelastocoridae—grasshoppers, lace bugs, beetle larvae, capsids. Ochteridae—tabanid larvae. Saldidae—drowned flies, etc. Hydrometra—Ostracoda, culicid larvae and pupae. *Mesovelia*—springtail, crambus, chalcid, Hydrometra, Ostracoda. *Gerris remigis*—midges, notonectid nymphs; jassids, etc., falling in water, snails. *Rheumatobates*—Ostracoda and fallen insects. *Microvelia*—Ostracoda and fallen insects, waterfleas. *Belostoma*—fish, snails. *Lethocerus*—frog, fish. *Nepa*—mayfly nymphs, Gyrinidae, Daphnia, Cyclops, fish eggs, fish, tadpoles. *Ranatra*—ostracod, fish, mayfly nymphs. *Plea*—Ostracoda and other small Crustacea. *Notonecta*—cannibalistic, Ostracoda and other small Crustacea, corixids. *Buenoa*—Entomostraca, corixids. Corixid nymphs cannibalistic.

JENSEN-HAARUP, A. C.

1924. Wasps preying on cicadas, Ent. Meddel, vol. 14, pp. 323-324. Also birds, spiders, mantids, and dragonflies noted as their enemies.

JOHNSON, ROSWELL H.

1907. Economic notes on aphids and coccinellids. Ent. News, vol. 18, no. 5, pp. 171-174, May. Coccinellids, syrphids, spiders, and fungi as aphid destroyers.

KIRKALDY, G. W.

1907. [Enemies of Aleyrodidae.] Bull. 2, Board Agr. and For. Terr. Hawaii, pp. 80-84. Three species of flies, 4 of beetles, 1 of hemiptera, 22 of hymenoptera, 1 neuropteron, 1 thysanopteron, 1 mite, and 2 fungi.

LORANDO, N. T.

1929. A biological method for destroying bedbugs. Sci. Monthly, pp. 265-268, Sept. Spiders, reduviid bugs, cockroaches, and ants as enemies.

LUGGER, OTTO.

1895. [Enemies of the chinch bug.] Bull. 37, Minnesota Agr. Exp. Sta., pp. 178-179. Birds, reptiles, frogs, toads; some specified.

MACANDREWS, A. H.

1923. Some notes on the natural control of the pine bark aphid (*Chermes pinicorticis* Fitch) in New Brunswick, 1922. Proc. Acadian Ent. Soc., vol. 8, 1922, pp. 52-56. A coccinellid exerted from 75 to 90 per cent of the natural control, and a syrphid fly and ant-lion the remainder.

MARLATT, C. L.

1907. The periodical cicada. Bull. 71, U. S. Bur. Ent., 181 pp., 6 pls., 68 figs. Natural enemies include dipterous, hymenopterous, and mite egg parasites, tachinid parasites of the adult, wasps, birds, squirrels, fishes; in some cases birds ate the insects as fast as they emerged.

MCATEE, W. L.

1907. Birds that eat scale insects. U. S. Dep. Agr. Yearbook, 1906, pp. 189-198. Fifty-seven species of birds are recorded as feeding upon scale insects.

1913. Relation of birds to [an outbreak of] grain aphides. U. S. Dep. Agr., Yearbook 1912, pp. 397-404. Spring migrant birds on about 100 acres of grainfields in North Carolina destroyed about 1,000,000 grain aphids daily.

1918. Bird enemies of tree hoppers (Membracidae). The Auk, vol. 35, no. 3, pp. 373-374, July. Treehoppers identified in the stomachs of more than 120 species of birds, as many as 26 individuals being found in a single stomach.

MCGREGOR, E. A.

1927. *Lygus elisus:* a pest of the cotton regions in Arizona and California. Techn. Bull. 4, U. S. Dep. Agr., 14 pp., 7 figs., July. Bugs of genus *Lygus* have been found in stomachs of 26 species of birds; Reduviidae and spiders also noted as enemies (p. 8).

MONTIZAMBERT, ERIC.

1908. Lampyrids and aphids. Can. Ent., vol. 40, no. 1, p. 36, Jan. *Telephorus carolinus* extirpating colonies of *Siphonophora rudbeckiae* (a red aphis).

MOZNETTE, GEO. F.

1915. Notes on the brown lace-wing (*Hemerobius pacificus* Bks.). Journ. Econ. Ent., vol. 8, no. 3, pp. 350-354, pl. 15, June. Number of aphids devoured daily by each of five larvae varied from 24 to 27. Captive.

MYERS, J. G.

1927. The natural enemies of *Dysdercus*. Ann. Ent. Soc. Amer., vol. 20, no. 3, pp. 290-294, Sept. In an article entitled " Ethnological Observations on some Pyrrhocoridae of Cuba," the author reports on observations, published records, and experiments with natural enemies of *Dysdercus*. The actually observed enemies are spiders, pseudoscorpions, thrips (the eggs), tachinid flies, reduviid and other bugs, lizards, and birds.

Reinhard, Edward G.

1925. The wasp *Hoplisus costalis,* a hunter of tree-hoppers. Journ. Washington Acad. Sci., vol. 15, no. 5, pp. 107-110, Mar. 4. An exclusive enemy of Membracidae; 12 species identified from nests.

Sherman, Franklin, Jr.

The harlequin cabbage bug. Bull. North Carolina Dep. Agr., vol. 32, no. 7, pp. 17-24, July. *Murgantia histrionica.* The English sparrow is quite an efficient aid in keeping this pest in check (p. 21).

Smith, Harry S.

1917. Insect parasites and predators as adjuncts in the control of mealybugs. Monthly Bull. California Comm. Hort., vol. 61, nos. 3-4, pp. 108-114, Mar.-Apr. One chrysopid, seven coccinellids, one agromyzid, and one syrphid as predators, and six Hymenoptera as parasites upon species of *Pseudococcus.*

Surface, H. A.

1907. [Enemies of plant lice.] Zool. Bull. Pennsylvania Dep. Agr., vol. 5, no. 3, pp. 81-82, July. Warblers, wrens, titmice, kinglets, chickadees.

1907. [Enemies of the periodical cicada.] Zool. Bull. Pennsylvania Dep. Agr., vol. 5, no. 3, p. 74, July. Skunks, squirrels, moles, chipmunks, pigs, poultry, most birds, snakes (four species mentioned) and turtles listed.

1907. Psyllidae. The jumping plant lice. Zool. Bull. Pennsylvania Dep. Agr., vol. 5, no. 3, pp. 78-79, July. White-breasted nuthatches practically freed an orchard from pear psyllids (*Psylla pyricola*).

Thompson, W. L.

1928. The seasonal and ecological distribution of the common aphid predators of central Florida. Florida Ent., vol. 11, no. 4, pp. 49-52, Feb. *Cycloneda* feeding on seven species of aphids; *Hippodamia* on 5, the larvae averaging 56 and the adults 87 bean aphids per day; *Scymnus* on 5; a few other species briefly mentioned, of which *Coccinella, Rodolia,* and *Chilocorus* are said to be primarily scale devourers.

Webster, F. M.

1897. [Enemies of the periodical cicada.] Bull. 87, Ohio Agr. Exp. Sta., pp. 61-63, Nov. Birds, especially the English sparrow, parasitic flies, dragonflies, soldier-bugs, ground beetles, hogs, and poultry.

1907. [Enemies of the chinch bug.] Bull. 69, U. S. Bur. Ent., pp. 58-59. Birds, frogs, nematodes, ants, ladybeetles, predacious Hemiptera, ground beetles, lacewing flies, spiders, and parasitic fungi.

1909. The Chinchbug (*Blissus leucopterus* Say.). Circ. 113, U. S. Bur. Ent., 27 pp., 8 figs., Nov. Natural enemies, bobwhite (100-400 eaten at a meal), 15 other birds, frogs, ants, ladybirds, anthocorids, carabids, chrysopids, spiders, and diseases.

Wildermuth, V. L.

1915. Three-cornered alfalfa hopper. Journ. Agr. Research, vol. 3, no. 4, pp. 343-362, pl. 43, fig. 1, Jan. *Stictocephala festina.* Spiders, ants, mites, egg parasites, birds, and toads recorded as enemies (pp. 359-360).

Williams, C. B.

1921. Report on the froghopper-blight of sugar-cane in Trinidad. Mem. 1, Dep. Agr. Trinidad and Tobago, Jan. *Tomaspis saccharina* Distant. Enemies listed are: 2 species of hymenopterous parasites and 2 species of thrips predatory upon the eggs; 3 kinds of birds, 1 syrphid larva, and 1 nematode upon the nymphs; and 17 species of birds, 2 of grasshoppers, 7 of ants, 1 of Lampyridae and 5 of Reduviidae predacious on the adults, besides sundry lizards, toads, frogs, spiders, mites, and two fungoid diseases.

NEUROPTEROIDEA

Insects chiefly predacious in the larval state and often also as imagos. For note on Trichoptera, see Muttkowski and Smith under Miscellaneous Insects.

McGregor, E. A.

1914. Some notes on parasitism of chrysopids in South Carolina. Can. Ent, vol. 46, pp. 306-308, fig 1. Forty-eight out of 99 cocoons were destroyed by hymenopterous parasites.

Smith, Roger C.

1922. The biology of the Chrysopidae. Mem. 58, Cornell Univ. Agr. Exp. Sta., pp. 1287-1372, pls. 75-88, figs. 154-163, June. Parasitized in all stages; ladybirds eat the eggs. Certain birds feed on adults. Robber flies noted catching adults and some Hemiptera prey on the larvae.

LEPIDOPTERA

Ainslie, C. N.

1910. The New Mexico range caterpillar. Bull. 85, U. S. Dep. Agr., pt. 5, pp. 59-96, figs. 1-53, June. *Hemileuca oliviae*—insect parasites, mites, robber flies, and robins recorded as enemies (pp. 88-93).

Allen, J. A.

1894. On the mammals of Aransas County, Texas, with descriptions of new forms of Lepus and Oryzomys. Bull. Amer. Mus. Nat. Hist., vol. 6, pp. 165-198. *Onychomys longipes*. Quotes a note from H. P. A[ttwater] to the effect that he found several hundred wings of *Danais archippus*, the bodies of which had been eaten by the *Onychomys*. Allen adds "This observation is of special interest from the fact that this butterfly is supposed to be 'protected' by a nauseous odor or taste that renders it unpalatable to animals" (p. 181).

Badenoch, L. N.

1899. [Enemies of the lictor moth.] True tales of the insects, p. 215. Notes on hymenopterous and dipterous parasites. The caterpillars of a species may be collected persistently for years for breeding and, because of parasites, none of them reach the perfect stage.

Ball, E. D.

1904. The codling moth. Bull. 87, Utah Exp. Sta., pp. 119-120. Birds, particularly the downy woodpecker and the chickadee, bats, ants, spiders, and predacious insects, recorded as enemies of this pest.

Barber, G. W.

1925. The efficiency of birds in destroying overwintering larvae of the European corn borer in New England. Psyche, vol. 32, no. 1, pp. 30-46. Birds credited with destroying an average of 61 per cent of the larvae in test cases.

Beebe, Wm.

1924. Notes on Galapagos Lepidoptera. Zoologica, vol. 5, no. 3, pp. 51-59, pl. A., Jan. 11. Birds feeding on butterflies (*Callidryas eubule* and *Agraulis vanillae*) and moths. "The relation between birds and butterflies is quite a negligible factor in any lepidopterous theory of evolution of pattern, color, form, or activity" (p. 57).

Bell, E. L.

1924. Notes on *Asilus sericeus* Say (Diptera, Asilidae). Journ. New York Ent. Soc., vol. 32, no. 4, p. 219, Dec. Capturing Hesperiidae, including *Epargyreus tityrus.*

Berger, E. W.

1920. The semitropical army worm. Quart. Bull. Florida State Plant Board, vol. 4, no. 2, pp. 17-34, figs. 4, Jan. *Xylomyges eridania.* Birds, the spined soldier bug, a wasp, tiger beetles, ground beetles, and parasitic insects recorded as enemies (pp. 26-28).

Bird, Henry.

1909. [Enemies of *Papaipema maritima.*] Can. Ent., vol. 41, no. 2, pp. 67-8, Feb. Field mice and skunks. "As very few pupae escape in any locality these animals go over, they become an important factor in the economy of the species."

Breakey, E. P.

1929. Notes on the natural enemies of the iris borer, *Macronoctua onusta* Grote (Lepidoptera). Ann. Ent. Soc. Amer., vol. 22, no. 3, pp. 459-464, Sept. Six species of Diptera, two of Hymenoptera, one beetle, one bird, and rodents.

Britton, W. E.

1906. The gypsy moth and the brown-tail moth. Bull. 153, Connecticut Exp. Sta., p. 7. Several species of parasitic Hymenoptera, Diptera, and predacious insects attack both the gipsy moth and brown-tail moths in Massachusetts; they are also devoured by birds, toads, and other insectivorous animals.

Brooks, Fred E.

1907. The grapevine root-borer. Bull. 110, West Virginia Agr. Exp. Sta., pp. 19-30, 5 pls., Nov. *Memythrus polistiformis* family Sesiidae. Great crested flycatcher feeding upon it (p. 28).

Bryant, Harold C.

1911. The relation of birds to an insect outbreak in northern California during the spring and summer of 1911. The Condor, vol. 13, pp. 195-208, Nov. Stomach examination revealed that four species of birds fed upon the butterflies (*Eugonia californica*), which formed an average of 32.8 per cent of their food. In addition a western flycatcher was observed feeding upon them. Chickens and ducks also reported as taking numbers of these insects.

Burgess, A. F., and Crossman, S. S.

1929. Imported insect enemies of the gipsy moth and the brown-tail moth. U. S. Dep. Agr. Techn. Bull. 86, 147 pp., 6 pls., 55 figs. More than 93 million parasites and predators liberated and a high degree of control was obtained by 1924; parasite population fluctuates. Heteroptera, dermestids, spiders, nematodes, mites, birds, and fungi contribute to the mortality, as do starvation and severe weather.

Chittenden, F. H.

1916. The common cabbage worm. Farmers' Bull. 766, U. S. Dep. Agr., p. 9, Nov. The English sparrow, chipping sparrow, and house wren are known to feed upon cabbageworms. It is certain that other species eat them—one instance noted where the pupae were reduced more than 90 per cent by birds.

1922. List of natural enemies of the celery leaf-tyer (*Phlyctaenia rubigalis* Guen.). Can. Ent., vol. 64, no. 8, p. 174, Aug. Twelve hymenopterous parasites.

Clark, A. H.

1926. Carnivorous butterflies. Smithsonian Rep. 1925, pp. 439-508, figs. 1-5. Lycaenidae feeding on ants or upon ant-tended insects, as aphids, coccids, jassids, and membracids.

Cockerell, T. D. A.

1898. Preliminary notes on the codling moth. Bull. 25, New Mexico Agr. Exp. Sta., pp. 55-58. Woodpeckers, and quite likely the kinglet, bats, toads, hymenopterous parasites, clerid beetle larvae, and parasitic fungi are recorded as enemies of the codling moth. Mention is also made of the house mouse.

Collins, C. W.

1926. Observations on a recurring outbreak of *Heterocampa guttivitta* Walker and natural enemies controlling it. Journ. Agr. Research, vol. 32, no. 7, pp. 689-699, Apr. 1. List of 15 hymenopterous, dipterous, and nematode parasites, and 8 coleopterous, hemipterous, and mammalian predators. Bibliography.

Comstock, J. H.

1879. Report upon cotton insects. U. S. Agr. Comm. 1879, 511 pp., 3 pls., 77 figs. Enemies of the cottonworm (pp. 138-214) include hogs, dogs, cats, raccoons, bats, wild birds, poultry, spiders, *Chrysopa*, dragonflies, mantis, Hemiptera, robber flies, tiger beetles, ground beetles, soldier beetles, ladybirds, boll worms, wasps, ants, chalcid, ichneumonid, and tachinid parasites, flesh flies and phorids.

Cooley, R. A.

1908. An army cutworm (*Chorizagrotis auxiliaris*). Bull. 71, Montana Exp. Sta., pp. 146-147. Several species of wild birds, domestic fowls, parasitic flies and wasps, besides beetles, are named as foes.

1930. The codling moth. Bull. 42, Montana Exp. Sta., p. 7. Birds considered to be great destroyers of this insect.

Criddle, Norman.

1920. Fragments in the life-habits of Manitoba insects—II. Can. Ent., vol. 52, no. 6, pp. 121-125, July. *Proteopteryx oregonana* checked by parasites, Calosoma, and birds.

Crumb, S. E.

1926. Tobacco cutworms and their control. Farmers' Bull. 1494, U. S. Dep. Agr., 13 pp., 11 figs., Aug. Among the agencies of natural control are mentioned spiders, ground beetles, birds, and toads. Birds play an important part.

[Davis, W. T.]

1914. [Dragonflies eating butterflies.] Ent. News, vol. 25, no. 4, p. 191, Apr. Mr. W. T. Davis said "That the dragonflies, especially on the west coast of Florida, were quite a nuisance to collectors on account of their catching many of the smaller butterflies that were disturbed."

Dustan, Alan G.

1923. The natural control of the white-marked tussock moth under city and forest conditions. Proc. Acadian Ent. Soc., vol. 8, 1922, pp. 109-126, pls. 15-16. In the city the principal enemies are parasites of the eggs and larvae, while in the forest, birds, ants, and spiders assume that rôle.

Felt, E. P.

1912. [Green maple worm (*Xylina antennata* Walk.)]. 27th Rep. State Entomologist, 1911, New York State Mus. Bull. 155, pp. 50-51, Jan. Nine species of birds actually observed eating or carrying away caterpillars, and nine others apparently associated in the work.

Floersheim, C.

1906. On some enemies of the diurnal Lepidoptera. Ent. Rec. vol. 18, no. 2, pp. 36-39, Feb. Two cases of birds; predacious beetles very abundant and get many sleeping butterflies. Spiders and coccinellid larvae eat butterfly larvae; eggs destroyed by Hemiptera.

Forbes, S. A.

1883. The regulative action of birds upon insect oscillations. Bull. Illinois State Lab. Nat. Hist., vol. 1, no. 6, pp. 1-32, May. Chiefly on birds in relation to an outbreak of cankerworms which made up 35 per cent of food of all birds in the affected orchard. Schedule of all food items identified.

Forbush, E. H.

1899. The destruction of hairy caterpillars by birds. Bull. 20, Div. Ent., U. S. Dep. Agr., pp. 85-93. List of 46 species with detailed notes on feeding habits of some of them, especially in relation to gipsy moth and brown-tail moth larvae, and tent caterpillars.

Garman, H.

1895. [Cutworm enemies]. Bull. 58, Kentucky Exp. Sta., p. 106, Nov. Birds, chickens, turkeys, and pigs, besides insect parasites.

Gibson, Arthur.

1915. The army-worm. Dominion of Canada Dep. Agr., Ent. Branch, Bull. 9, 34 pp., 19 figs. *Cirphis unipuncta.* Many species of wild birds, large numbers of parasitic and predacious insects, domestic poultry, toads, and skunks recorded as enemies. Bacterial and fungous diseases also recorded attacking this worm (pp. 13-17).

Gill, John B.

1913. The fruit-tree leaf roller. U. S. Dep. Agr. Bull. 116, pt. 5, pp. 91-110, pls. 12-16, Mar. *Archips argyrospila*—eight species of birds, parasitic Hymenoptera and Diptera and predacious beetles and ants recorded as enemies; a small mite also noted feeding upon the eggs of the leaf-roller (p. 102).

Gillette, Clarence P.

1905. The beet webworm. Colorado Agr. Exp. Sta., Bull. 98, pp. 3-12, 2 pls., Mar. *Loxostege sticticalis.* Records of insect-eating birds devouring these in quantities, mention being made of large flocks of blackbirds. Parasitic Hymenoptera also noted (pp. 10-11).

Hardenberg, C. B.

1912. The willow tree caterpillar (*Angelica tyrrhea*, Cramer). Agr. Journ. South Africa, vol. 4, no. 3, pp. 397-418, Sept. Parasitic flies and wasps attack the caterpillar and eggs. The larvae are reported to be distasteful to birds although they are said to be eaten by some tribes of Kaffirs. Guinea fowls and meerkats feed upon the pupae, and moles probably do so. They are also attacked by a fungus (pp. 412-416).

Haskin, J. R.

1916. Butterflies as food for squirrels. Ent. News, vol. 27, no. 8, p. 370, Oct. *Melitaea chalcedon*, evidence of destruction of 25 or more by gray squirrels; California.

Herrick, Glenn W.

1910. The snow-white linden moth. Bull. 286, Cornell Agr. Exp. Sta., pp. 51-64, figs. 54-58, Nov. English sparrow freed cities of this pest—*Ennomos subsignarius* (p. 62).

Horton, J. R.

1922. A swallow-tail butterfly injurious to California orange trees (*Papilio zolicaon* Boisd.). Monthly Bull. Dep. Agr. California, vol. 11, no. 4, pp. 377-387, Apr. Larvae of *Chrysopa californica* sometimes destroy 80-90 per cent of the eggs. Young caterpillars eaten by same foe, also by *Zelus renardi*, and a hymenopterous parasite; the pupa by *Chalcis ovata* (p. 385).

Howard, L. O.

1904. The insect book. The Nature Library, vol. 8, pp. 56-57. Parasitic Hymenoptera attacking the cotton caterpillar; an instance of destruction of 95 per cent of the eggs.

Howard, L. O. and Chittenden, F. H.

1907. The catalpa sphinx (*Ceratomia catalpae* Bdv.). Circ. 96, U. S. Bur. Ent., p. 6. Cuckoos, the catbird and the Baltimore oriole recorded as enemies.

1909. The green-striped maple worm (*Anisota rubicunda* Fab.). Circ. 110, U. S. Bur. Ent., p. 5. Domestic fowls and nine species of wild birds recorded as enemies.

Johnson, E. E.

1926. Birds eating butterflies. The Field, London, vol. 147, p. 658, Apr. 15. Observations made of a stonechat taking butterflies.

KERSHAW, JOHN C. W.

1905. Butterfly-destroyers in Southern China. Trans. Ent. Soc. London, 1905, pp. 5-8. Has seen only a dozen attacks by birds in five years; lizards destroy most adults. Notches in wings made by striking twigs, etc., a cuckoo the worst enemy of larvae, taking even the hairy and most conspicuous kinds. Also ants fastening on butterfly tongues.

KIRKLAND, A. H.

1896. The army worm. Massachusetts Crop Rep. 1896, pp. 34-36. Birds are recognized as being the most important enemies of the army worm. Toads, parasitic flies, and beetles also are recorded as being enemies of this pest.

LAMBORN, W. A.

1912. Butterflies a natural food of monkeys. Trans. Ent. Soc. London, 1912, p. iv. Mangabeys eating butterflies at mudholes.

LAWSON, G.

1888. Insect injuries to field and orchard crops. Provincial Crop Rep. Nova Scotia, 1888, p. 29. American and forest tent caterpillars are eaten by the crow and cuckoo and to a lesser extent by the linnet and swallow; cankerworms by the linnet (purple finch?).

LINTNER, J. A.

1888. Cutworms. Bull. 6, New York State Mus., 36 pp., 28 figs. Natural enemies include wild birds, poultry, toads, ground beetles, predacious bugs, mites, spiders, parasitic Diptera and Hymenoptera (pp. 23-28).

LOUNSBURY, C. P.

1895. Canker worms, army worms. etc. Bull. 28, Hatch Exp. Sta., p. 15. Poultry, birds, frogs, toads, beetles, and parasitic flies listed as foes.

LUGGER, OTTO.

1892. Tent-caterpillars. Ann. Rep. Minnesota Hort. Soc., p. 372. Cuckoos, skunks, and Calosoma are enemies.

MALLONEE, A. M.

1916. Frogs catching butterflies. Science, n. s., vol. 43, pp. 386-387, Mar. 17. *Rana catesbiana* eating a number of *Papilio turnus*.

MALLY, F. W.

1893. Report on the boll worm of cotton (*Heliothis armiger* Hubn.). Bull. 29, U. S. Div. Ent., p. 26. Woodpeckers and sparrows reported as enemies.

MANDERS, N.

1912. [Enemies of *Danais chrysippus*.] Trans. Ent. Soc. London, p. 446. *Trichogramma evanescens* parasitizes large numbers of eggs; ants eat the eggs; larvae are commonly parasitized; spiders and ants eat them; they are cannibalistic; adults eaten by lizards, and sometimes by birds.

MARLATT, C. L. AND ORTON, W. A.

1906. The control of the codling moth and apple scab. Farmers' Bull. 247, U. S. Dep. Agr., p. 9. Woodpeckers noted as preying upon the codling moth.

McAtee, W. L.

1912. Bird enemies of the codling moth. Yearbook U. S. Dep. Agr. 1911, pp. 237-246. Birds recognized as most effective natural enemies—from 66 to 85 per cent of the hibernating larvae recorded as being destroyed. 36 species of birds known to prey upon this moth.

1923. Another insect birds should not eat. The Auk, vol. 40, no. 3, p. 560, July. Red-humped apple caterpillar (*Schizura concinna*)—recorded as preyed upon by six species of birds.

1924. Birds as factors in the control of the fall webworm. The Auk, vol. 41, no. 2, p. 372, Apr. Results of eight years' study in Canada, red-eyed vireo destroys 11.4 to 89.5 per cent of the broods, averaging more than 68 per cent; birds "tremendously important" in control of the insect.

1925. Economic ornithology. The Auk, vol. 42, no. 3, pp. 464-465, July. European corn borer—This pest is recorded as preyed upon by four species of birds.

1926. Birds feeding on the European corn borer. The Auk, vol. 43, no. 3, p. 395, July. Red-wing blackbirds and downy woodpeckers recorded as feeding on the larvae.

1927. Economic ornithology in recent entomological publications. The Auk, vol. 44, no. 3, pp. 458-459, July. European corn borer recorded as taken by six species of birds.

Neal, H. V.

1912. Monkeys eating butterflies. Trans. Ent. Soc. London, 1912, pp. xvii-xviii. Commonly do so in Lagos.

Otanes, F. O.

1925. The rice stem borer (*Schoenobius incertellus* Walker). Philippine Agr. Rev., vol. 18, no. 1, pp. 81-82. "The adult moths are said to be preyed upon by birds, mudfish (dalag), spiders, frogs, and mantids" (p. 82).

Pack, H. J.

1922. Toads in regulating insect outbreaks. Copeia, no. 107, pp. 46-47, June 20. Feeding exclusively on sugar-beet webworms and taking from 20 to 40 each.

Patch, Edith M.

1908. The saddled prominent, *Heterocampa guttivitta* (Walker). Maine Agr. Exp. Sta., Bull. 161, pp. 311-350, figs. 14-40, Nov. Predacious bugs and beetles, hymenopterous parasites, a fungus, skunks, domestic fowls, and wild birds recorded as enemies. (Pp. 340-348.)

1921. A meadow caterpillar. Bull. 302, Maine Agr. Exp. Sta., pp. 309-320, 2 pls., Dec. *Ctenucha virginica.* One dipterous and 5 hymenopterous parasites. "Though covered with stiff hairs, the over-worked theory that such caterpillars are thereby immune from birds' attacks cannot stand up against the testimony of my pet thrush which whips these caterpillars vigorously against the floor of the cage until, in a surprisingly short time, their bodies are beaten limp and naked, whereupon they are swallowed in one gulp."

Pettit, R. H.

1904. The codling moth in Michigan. Bull. 222, Michigan Agr. Exp. Sta., pp. 78 and 89-90. Birds most important; shrews, parasitic Hymenoptera and fungi also mentioned.

PHILLIPS, W. J. and KING, KENNETH M.

1923. The corn earworm. Farmers' Bull. 1310, U. S. Dep. Agr., 17 pp., 18 figs., Jan. *Heliothis obsoleta.* Seventeen species of birds, egg parasites, and other parasitic insects, certain ants, and spiders recorded as foes. The earworms' cannibalistic habit is the most important factor in reducing its attacks on corn (pp. 10-12).

PHIPPS, C. R.

1927. The black army cutworm. Maine Agr. Exp. Sta., Bull. 340, pp. 201-216, figs. 29-30, May. *Agrotis fennica.* Three kinds of flies and one of wasp parasites, predators including bugs, beetles, wasps, and birds recorded as enemies (pp. 212-213).

PLANK, H. K.

1929. Natural enemies of the sugar cane moth stalkborer in Cuba. Ann. Ent. Soc. Amer., vol. 22, pp. 621-640, 7 figs. Its burrowing habit is "an admirable protection against direct, or artificial, but does not seem to afford any great amount of protection against the attack of a rather formidable array of natural enemies." Tachinids, sarcophagids, and Hymenoptera recorded as parasites, and earwigs, beetles, and ants as predators. Bibliography.

POOS, F. W.

1928. An annotated list of some parasitic insects. Proc. Ent. Soc. Washington, vol. 30, no. 8, pp. 145-150, Nov. Parasites varying from 1 to 14 in number bred from each of 19 hosts, mostly Lepidoptera.

POULTON, E. B.

1911. The attacks of tachinid flies upon the African Danaine genus *Amauris.* Trans. Ent. Soc. London, 1911, p. xcix. Twenty out of 25 pupae of *Amauris psyttalea* parasitized; another lot all parasitized. This a good indication enemies of adults are scarce; otherwise species would be rare.

QUAINTANCE, A. L.

1908. The apple-tree tent caterpillar (*Malacosoma americana*). Circ. 98, U. S. Bur. Ent., p. 6. Black-billed and yellow-billed cuckoos, blue-jay, crow, chickadee, Baltimore oriole, red-eyed vireo, chipping sparrow, and yellow warbler mentioned as enemies; also the common toad.

SANDERSON, E. D.

1903. The codling moth. Bull. 59, Delaware Agr. Exp. Sta., pp. 7-8. Parasitic worms and insects, soldier beetles, named as enemies as well as 10 or more species of birds which are the most efficient.

1905. The gipsy moth in New Hampshire. Bull. 121, New Hampshire Agr. Exp. Sta., p. 99. Ground beetles, parasitic insects, and several species of birds are recorded as preying upon the gipsy moth.

1906. The brown-tailed moth in New Hampshire. Second report. Bull. 122, New Hampshire Agr. Exp. Sta., p. 127. Parasitic insects, predacious bugs, toads, bats, and several species of birds, particularly the English sparrow, recorded as enemies.

1909. The codling moth and how to control it by spraying. Bull. 143, New Hampshire Agr. Exp. Sta., pp. 64-82. Downy woodpeckers and nuthatches are recorded as being the most important enemies of the codling moth.

Sanderson, E. D., Headlee, T. J., and Brooks, Charles.

1907. Spraying the apple orchard. Bull. 131, New Hampshire Agr. Exp. Sta., pp. 18-19 and 35. Woodpeckers and nuthatches are recorded as feeding extensively on the codling moth.

Saunders, Aretas A.

1916. A note on the food of the western robin. The Condor, vol. 18, no. 9, p. 81, Mar.-Apr. Robin feeding on *Papilio rutulus*, and a chipmunk feeding upon the same species and also on *P. eurymedon*.

Sharp, D.

1910. [Parasites of winter moth.] Cambridge Nat. Hist., vol. 5, p. 521. "The destructive winter moth—*Cheimatobia brumata*—is known to be subject to the attacks of 63 species of Hymenopterous parasites. So abundant are these latter that late in the autumn it is not infrequently the case that the majority of caterpillars contain these destroyers."

Sherman, F.

1921. Observations of natural enemies of the fall cankerworm (*Alsophila pometaria* Peck) in forests of southern Alleghany Mountains in 1920. Journ. Econ. Ent., vol. 14, no. 6, pp. 478-481, Dec. Names 15 species of birds presumably of material help, five predacious insects, and 3 parasites of which one destroyed from 25 to 40 per cent of the eggs.

Shiras, Geo., 3rd.

1921. Frogs eating butterflies. Nat. Geogr. Mag., vol. 40, no. 2, p. 174, Aug. Leopard frogs catching about 500 "blues" in a week; also eating many *Argynnis aphrodite*.

Skaife, S. H.

1921. Some factors in the natural control of the wattle bagworm. South African Journ. Sci., vol. 17, nos. 3-4, pp. 291-301, July. *Acanthopsyche junodi* Heylaerts. Out of a total of 59,687 examined, just over one per cent were destroyed by birds and rats, 19 per cent by insect parasites, 16 per cent by fungous disease, and 17 per cent by other diseases. Only one-quarter of one per cent survive the early perils of their life.

Smith, J. B.

1895. [*Zeuzera pyrina*.] 15th Ann. Rep. New Jersey Exp. Sta. 1894, pp. 531-532. Almost all insectivorous birds, especially woodpeckers and the sparrow, in addition to bats, and predacious insects, are recorded as enemies of this insect.

Spencer, G. J. and H. G. Crawford.

1923. The European corn borer in Ontario. Ontario Dep. Agr. Bull. 295, 11 pp., 10 figs., Mar. Ants, aphis-lions, ladybird beetles, ground beetles, crickets, a parasitic fly, and several species of birds noted as foes. One instance recorded of downy and hairy woodpeckers destroying 60 per cent of the borers (pp. 7-8).

Tothill, John D.

1922. The natural control of the fall webworm [*Hyphantria cunea* Drury] in Canada together with an account of its several parasites. Dep. Agr. Dominion of Canada, Bull. 3, n. s. (techn.), 107 pp., 6 pls., 99 figs. Tabulations of the destruction by various enemies in different localities and years; birds average most important, parasites sometimes important, sometimes not.

1923. Notes on the outbreaks of spruce budworm, forest tent caterpillar, and larch sawfly in New Brunswick. Proc. Acadian Ent. Soc., vol. 8, 1922, pp. 172-182. Spruce budworm. Natural checks effective in New Brunswick were eggs, larvae, and pupal parasites, spiders, and birds; and in British Columbia, parasites and birds. Nothing of importance on enemies of the other forms.

Trouvelot, Leopold.

1868. The American silkworm. Amer. Nat., vol. 1, pp. 30-38, 85-94, 145-149. *Telea polyphemus*. Thrushes, catbirds, orioles; 95 out of a hundred worms become the prey of these feathered insect hunters.

U. S. Entomological Commission.

1883. 3rd Rep. U. S. Ent. Comm., p. 125. All insectivorous birds, hogs, chickens, turkeys, toads, and frogs prey upon the armyworm. " The worms themselves, when hard pushed, will even devour each other."

1883. 3rd Rep. U. S. Ent. Comm., pp. 175-178. Forty or more species of wild birds, notable mention being made of bluebirds, cedarbirds and butcherbirds, and parasitic and predacious insects, also hogs, are recorded as enemies of the cankerworm.

1885. 4th Rep. U. S. Ent. Comm., pp. 87-90. More than 20 species of wild birds, poultry, hogs, raccoons, skunks, opossums, bats, tree frogs, lizards, spiders, and numerous kinds of predacious insects are recorded as preying upon the cottonworm.

Vickery, R. A.

1929. Studies on the fall army worm in the Gulf Coast District of Texas. Techn. Bull. 138, U. S. Dep. Agr., 63 pp. Numerous hymenopterous parasites sometimes destroy 40-50 per cent of the caterpillars.

Warren, B. H.

1897. The army worm. Ann. Rep. Pennsylvania State Coll. 1896, pp. 164-220, 16 pls. Much on natural enemies including tachinids and ichneumonids, ground beetles, birds, mammals, and toads.

Webster, R. L.

1909. The lesser apple leaf-folder. Iowa State Coll. Exp. Sta. Bull. 102, pp. 181-212, figs. 1-13, Mar. *Peronea minuta*—tachinid and hymenopterous parasites recorded as the most important natural enemies although birds and diseases are also important factors (pp. 206-211).

Weed, C. M.

1899. The forest tent caterpillar. Bull. 64, New Hampshire Agr. Exp. Sta., pp. 77-98, figs. 20-33, Apr. *Clisiocampa disstria*—preyed upon by insects, spiders, toads, and birds. Ten kinds of birds feeding on larvae, one on the cocoons and four on the adults.

1899. The spiny elm caterpillar. Bull. 67, New Hampshire Agr. Exp. Sta., pp. 125-141, figs. 40-51, Oct. *Vanessa antiopa*—egg parasites chalcid, ichneumonid and tachinid flies on caterpillars; *Calosoma,* wasps, cuckoos, and toads named as enemies (pp. 138-140).

1900. Insect record for 1899. Bull. 72, New Hampshire Exp. Sta., pp. 64-65. The Baltimore oriole and the cuckoos are especially noted as enemies of tent caterpillars.

1900. The forest tent caterpillar. Second report. Bull. 75, New Hampshire Exp. Sta., pp. 120-121. Eighteen or more species of birds are recorded as preying upon these caterpillars.

1902. [Enemies of cankerworms.] Bull. 90, New Hampshire Agr. Exp. Sta., 1902, p. 35, Mar. Robins, bluebirds, cedarbirds, and many others feed freely upon the pests.

West, L. S.

1923. Immunity to parasitism in *Samia cecropia* Linn. (Lep.: Saturniidae; Dip.: Tachinidae.) Ent. News, vol. 34, no. 1, pp. 23-25, Jan. Ineffectiveness of attack of 35-40 tachinid larvae; nevertheless lists two Tachinidae and eight species of Hymenoptera that do successfully parasitize this host.

Yothers, M. A.

1913. *Eugonia californica* Bdv. in the Pacific Northwest. Can. Ent., vol. 45, no. 12, pp. 421-422, Dec. "I think that the total disappearance of these caterpillars and chrysalids was no doubt due to birds" (p. 422).

Young, R. A.

1907. Insects affecting the poplar. Proc. Columbus Hort. Soc. 1906, pp. 68-82. Birds constitute an important agency in keeping the *Hemerocampa leucostigma* in check (p. 74).

COLEOPTERA

Agassiz, L., and Cabot, J. Elliot.

1850. Lake Superior, etc., p. 72. *Monochamus scutellaris* preyed upon by Canada jay and two species of *Picoides.*

Blackman, M. W.

1915. Observations on the life history and habits of *Pityogenes hopkinsi* Swaine. Techn. Publ. no. 2, New York State Coll. Forestry, pp. 11-66, 6 pls., Nov. Natural enemies include beetles, mites, and parasitic Hymenoptera (pp. 53-56).

Britten, H.

1926. A pentatomid bug preying on beetle larvae. North Western Nat., vol. 1, p. 38. *Rhacognathus punctatus* found sucking larvae of beetle (*Hydrothassa marginella*).

1927. Red ants and beetles. North Western Nat., vol. 2, p. 256. *Myrmica ruginodis* killing beetles (*Melandrya caraboides*).

Brooks, F. E.

1919. The flat-headed apple-tree borer. Farmers' Bull. 1065, U. S. Dep. Agr., 12 pp., 13 figs. *Chrysobothris femorata.* Woodpeckers, and other birds, ants, and six species of hymenopterous parasites recorded as enemies (p. 9).

Burgess, A. F. and Collins, C. W.

1917. The genus *Calosoma,* including studies of seasonal histories, habits, and economic importance of American species north of Mexico and of several introduced species. Bull. 417, U. S. Dep. Agr., 124 pp., 19 pls., 5 figs. Caterpillars the principal food of these beetles; cannibalism, and attacks of toads, skunks, and birds the chief organic checks; predatory bugs, and parasitic flies also noted (pp. 10-13).

Cartwright, Oscar L.

1929. The maize billbug in South Carolina. Bull. 257, South Carolina Agr. Exp. Sta., 35 pp., 13 figs., May. Natural enemies (p. 31) include egg parasite, predacious beetles, ants, and wasps.

Chamberlin, F. S., and Tenhet, J. N.

1923. The tobacco flea-beetle in the southern cigar-wrapper district. Farmers' Bull. 1352, U. S. Dep. Agr., 9 pp., 8 figs. *Epitrix parvula.* A spider, lygaeid bug, and birds noted as enemies (p. 5).

Chittenden, F. H.

1911. Notes on various truck-crop insects. Bull. 82, pt. 7, U. S. Bur. Ent., pp. 85-93, fig. 24. Natural enemies of *Leptinotarsa decemlineata,* pp. 85-88; 1 beetle, 3 hemiptera, 16 wild birds, and guinea fowls.

1926. Notes on the behavior of *Cotinis nitida* L. and its bird enemies. Proc. Biol. Soc. Washington, vol. 39, pp. 15-17, Feb. Starling and cardinal eat it.

Chittenden, F. H., and Fink, D. E.

1922. The green June beetle. Bull. 891, U. S. Dep. Agr., 52 pp., 10 pls., 7 figs. *Cotinis nitida.* Natural enemies (pp. 31-37) include parasitic flies, digger wasps, ground beetles, mites, various mammals, and birds; fungal and bacterial diseases also noted.

Chittenden, F. H., and Marsh, H. O.

1920. The western cabbage flea-beetle. U. S. Dep. Agr. Bull. 902, 21 pp., 4 figs., 1 pl., Oct. *Phyllotreta pusilla.* Hymenopterous and worm parasites recorded as well as 12 species of birds feeding on beetles of this genus.

Davis, John J.

1913. Common white grubs. U. S. Farmers' Bull. 543, 20 pp., 12 figs., July. More than 60 species of birds, domestic fowls, skunks, a number of predacious and parasitic insects recorded preying upon white grubs at one stage or another (pp. 13-15).

Fenton, F. A., and Dunham, E. W.

1929. Biology of the cotton boll weevil at Florence, S. C. Techn. Bull. 112, U. S. Dep. Agr., 75 pp., 35 figs. Considerable variation exists in mortality rate from parasitism (by three species of Hymenoptera) from as low as 2.37 to as high as 51.52 per cent; predators, heat, proliferation by the plant, disease and unknown causes take their toll, the average total from all these causes being about 40 per cent; then from the number that go into hibernation only an average of 3.27 per cent survive.

FEYTAUD, JEAN.

1922. Le Doryphore, Chrysomèle nuisible à la pomme de terre (*Leptinotarsa decemlineata* Say). Rev. Zool. Agr. Appl., vol. 21, Numero special, 48 pp., 13 figs., Aug. Natural checks include skunks, birds, snakes, frogs, spiders, phalangids, mites, beetles, bugs, wasps, robber flies, and parasitic flies (pp. 14-17).

FORBES, S. A.

1880. Notes upon the food of predacious beetles. Bull. Illinois State Lab. Nat. Hist., vol. 1, no. 3, pp. 149-152, Nov. Both vegetable and animal, the latter including beetles, larvae, and plant lice.

1880. Notes on insectivorous Coleoptera. Bull. Illinois State Lab. Nat. Hist., vol. 1, no. 3, pp. 153-160, Nov. Carabidae, Lampyridae, Coccinellidae, from stomach examination. Animal food, mites and their eggs, ants, caterpillars, beetles and their larvae, plant lice, and centipeds.

1883. The food relations of the Carabidae and Coccinellidae. Bull. Illinois State Lab. Nat. Hist., vol. 1, no. 6, pp. 33-64, May. Report on dissections of 175 Carabidae and 39 Coccinellidae. Animal food included Hymenoptera, Lepidoptera, Diptera, Neuroptera, and Coleoptera, spiders, mites, myriapods, mollusks. Notes on birds as enemies of Cicindelidae and Carabidae.

1907. On the life history, habits, and economic relations of the white-grubs and may beetles. Bull. 116, Illinois Agr. Exp. Sta., pp. 447-480, Aug. Principal enemies, swine, crows, blackbirds, and *Tiphia;* other parasites *Macrophthalma, Sparnopolius, Pyrgota,* and *Ophion* (pp. 468-475).

FORBUSH, E. H.

1912. 4th Ann. Rep. State Ornithologist Mass., 1911, 32 pp., 4 pls., 9 figs. *Galerucella luteola.* Cedar waxwing clearing trees of infestations of the elm leaf beetle (pp. 19-20).

HESS, WALTER N.

1920. The ribbed pine borer. Mem. 33, Cornell Agr. Exp. Sta., pp. 367-381, pl. 8, figs. 61-66. *Rhagium lineatum.* Woodpeckers, most important; a parasite reared (pp. 378-379).

HOPKINS, A. D.

1896. The relation of insects and birds to present forest conditions. Proc. Amer. Forestry Assoc., vol. 11, pp. 175-176. Woodpeckers recorded as enemies of bark and clerid beetles.

HYSLOP, JAMES A.

1912. The false wireworms of the Pacific Northwest. Bull. 95, pt. 5, U. S. Bur. Ent., pp. 73-87, figs. 22-27. Numerous species of birds, horned-toads, garden toads, skunks, parasites, and disease recorded as enemies (pp. 84-86).

1915. Wireworms attacking cereal and forage crops. Bull. 156, U. S. Dep. Agr., 34 pp., 8 figs. Elateridae—a long list of bird enemies given; horned-toads, mites, predacious flies, hymenopterous parasites, nematodes, fungi (pp. 25-29).

INGRAM, J. W.

1927. The striped blister beetle on soy beans. U. S. Dep. Agr. Leafl. 12, 5 pp., 3 figs. *Epicauta lemniscata*—three species of birds and a robber fly named as enemies.

Kalmbach, E. R.

1914. Birds in relation to the alfalfa weevil. Bull. 107, U. S. Dep. Agr., 64 pp., 5 pls. Forty-five species of birds found to feed on this comparatively recently introduced pest; also domestic fowls, toads, frogs, salamanders, horned-toads, snakes, and shrews.

McAtee, W. L.

1914. Bird enemies of Diabroticas. The Auk, vol. 31, no. 1, p. 120, Jan. Southern corn root worm (*Diabrotica duodecim-punctata*) recorded as preyed upon by 24 species of birds; western corn root worm (*Diabrotica longicornis*) taken by the nighthawk and the wood pewee.

1915. Bird enemies of two beetle pests. The Auk, vol. 32, no. 3, pp. 377-378, July. *Oncideres putator*—it is believed that the southern downy woodpecker and the Texas woodpecker attack the larvae of this pest. *Monocrepidius vespertinus*—the records show that these beetles are devoured by eight species of birds.

Mail, G. Allen.

1930. Winter soil temperatures and their relation to subterranean insect survival. Journ. Agr. Research, vol. 41, no. 8, pp. 572-592, Oct. 15. Few parasites; mites, birds, fungal and bacterial diseases reduce them, but climate a control factor of much importance.

Muir, F.

1917. The introduction of *Scolia manilae* Ashm. into the Hawaiian Islands. Ann. Ent. Soc. Amer., vol. 10, no. 2, pp. 207-210, June. A parasite of the beetles *Anomala orientalis* and *Adoretus tenuimaculatus.*

[Nelson, E. W.]

1921. Report of chief of Bureau of Biological Survey, 34 pp. Bird enemies of the Japanese beetle (*Popillia japonica*) mentioned (p. 14); five species of birds and the toad listed.

Quaintance, A. L., and Jenne, E. L.

1912. The plum curculio. Bull. 103, U. S. Bur. Ent., 250 pp., 20 pls., 33 figs. Natural enemies (pp. 139-154) include an egg parasite, hymenopterous and dipterous parasites of later stages, ants, chrysopids, carabids, lampyrids, fowls and wild birds; also the toad.

Satterthwait, A. F.

1919. How to control billbugs destructive to cereal and forage crops. Farmers' Bull. 1003, U. S. Dep. Agr., 23 pp., 24 figs. Insect, worm, and fungus parasites, toad and bird predators mentioned, the birds apparently most important (pp. 19-20).

Schuster, W.

1909. [Beetles and their enemies in the bird world.] Ent. Blätt. Nürnberg, vol. 5, no. 7, pp. 142-144, July 15. Birds the principal enemies of beetles; notes on European bird foes of various families of beetles; similar notes for Lepidoptera.

Slingerland, M. V.

1906. The bronze birch borer: an insect destroying the white birch. Bull. 234, Cornell Agr. Exp. Sta., pp. 65-78, figs. 31-38. *Agrilus anxius.* Woodpeckers and chalcid parasites mentioned as foes.

THOMAS, C. A.

1931. The predatory enemies of Elateridae (Coleoptera). Ent. News, vol. 42, no. 5, pp. 137-140, May; no. 6, pp. 158-167, June. Mites, pseudoscorpions, spiders, hemiptera, beetles, flies, hymenoptera, amphibians, reptiles, birds, and mammals; birds most important; predators more effective than parasites. Bibliography.

WEBB, J. L.

1906. The western pine-destroying bark beetle. Bull. 58, pt. 2, U. S. Bur. Ent., pp. 17-30, pls. 2-3, figs. 7-12. *Dendroctonus brevicornis.* Woodpeckers destroyed large percentage in some trees (p. 27).

WEBSTER, F. M.

1880. Notes upon the food of predacious beetles. Bull. Illinois State Lab. Nat. Hist., vol. 1, no. 3, pp. 149-152, Nov. Chiefly on vegetarian Carabidae but notes on carnivorous species of Carabidae, Staphylinidae, and Lampyridae; the prey mentioned includes plant lice, cricket, grasshopper, and beetles.

1892. Underground insect destroyers of the wheat plant. Bull. Ohio Agr. Exp. Sta., vol. 5, no. 9, pp. 221-247, 8 figs., Dec. Wireworms—crows, thrushes, robins, blackbirds (p. 228). Whitegrubs—poultry, crows, jays, nighthawks, robin, catbird, brown thrasher, wood thrush, red-headed woodpecker; swine, bats, badger, weasel, martin, rat, skunk, raccoon, fox, mole, frogs, digger wasps, robber flies, and fungi (pp. 236-237).

1913. The southern corn rootworm, or budworm. U. S. Dep. Agr. Bull. 5, 11 pp., 2 figs., Sept. *Diabrotica 12-punctata*—12 species of birds and parasitic flies (pp. 9-10).

1913. The western corn rootworm. Bull. 8, U. S. Dep. Agr., 8 pp., 5 figs., Sept. *Diabrotica longicornis* preyed upon by nighthawks, wood pewees, a parasitic fly, and chinch bug fungus (p. 6).

WILDERMUTH, V. L.

1910. The clover-root curculio. Bull. 85, pt. 3, U. S. Bur. Ent., pp. 29-38, figs. 15-19. *Sitones hispidulus*—14 species of birds recorded as enemies (p. 37).

WILSON, C. B.

1923-1924. Life history of the scavenger water beetle *Hydrous* (*Hydrophilus*) *triangularis*, and its economic relations to fish breeding. Bull. Bur. Fisheries, vol. 39, pp. 9-38, 22 figs. Food of larvae, snails, midge larvae, fishes, other water beetle larvae, tadpoles, and several groups of insects and crustaceans in smaller quantity. Food of adults, vegetable matter, fishes. Enemies of *Hydrophilus* include cannibalistic larvae, dragonfly nymphs, frogs, fishes, birds. Bibliography.

1923-1924. Water beetles in relation to pondfish culture, with life histories of those found in fishponds at Fairport, Iowa. Bull. U. S. Bur. Fisheries, vol. 39, pp. 231-345, figs. 1-143. Larvae highly cannibalistic, dragonfly nymphs are enemies, as are also, mites, hydra, ants, fishes, turtles, frogs, and snails; foes of pupae include hymenopterous parasites, horse fly larvae, and ants; of adults, turtles, fishes, birds, toads, and frogs. Notes are given on the feeding

habits of the larvae and adults of a number of water beetles; fish destruction not so apparent as would have been inferred from previous literature. Bibliography.

MECAPTERA

Predacious.

DIPTERA

Alexander, Charles P.

1920. The crane-flies of New York. Mem. 38, Cornell Univ. Agr. Exp. Sta., pp. 699-1132, pls. 12-97, June. Ninety-one species of birds, besides foxes, mice, shrews, moles, amphibians, fishes, mites, spiders, dragonflies, Diptera, Coleoptera, Hymenoptera, Protozoa recorded as enemies of crane flies in one stage or another (pp. 721-734).

Bromley, S. W.

1923. Observations on the feeding habits of robber flies. Part I. Psyche, vol. 30, no. 2, pp. 41-45, Apr. Tabulation of the prey of 26 *Proctacanthus rufus,* all Hymenoptera and in 14 cases honey bees. Six records for *P. brevipennis* include three of beetles, one ant, one blow fly, and one assassin bug.

1930. Bee-killing robber flies. Journ. New York Ent. Soc., vol. 38, no. 2, pp. 159-176, pl. 10, June. Especially the honey bee; review of records from various countries; discussion of the U. S. species, with notes on other kinds of prey taken by some of them. The Dasypogoninae tend to favor Hymenoptera, the Laphriinae beetles, while the Asilinae are more general feeders.

Burrill, A. C.

1913. Economic and biologic notes on the giant midge: *Chironomus* (*Tendipes*) *plumosus* Meigen. Bull. Wisconsin Nat. Hist. Soc., vol. 10, nos. 3-4, pp. 124-163, Apr. Swallows, red-winged blackbirds as enemies (p. 146); other notes in annotated bibliography refer to fishes, birds, Utricularia, and fungi as natural checks.

1913. Notes on Lake Michigan swarms of chironomids; quantitative notes on spring insects. Bull. Wisconsin Nat. Hist. Soc., vol. 11, nos. 1-2, pp. 52-69, June. Enemies of adults include mites, spiders, ants, and birds (pp. 66-67).

Cockerell, T. D. A.

1894. On the habits of some Asilidae. Ent. News, vol. 5, no. 6, pp. 173-174, June. *Mallophora fautrix* eating *Odynerus* sp.; *Mallophora* sp. eating honey bee; *Proctacanthus philadelphicus* preying upon *Erax dubius,* and butterfly, *Synchloe lacinia* var. *crocale*; *Proctacanthus milberti* preying upon *Bembex* sp. and honey bee; *Promachus princeps* preying upon *Odynerus annulatus.*

Cuthbertson, Alexander.

1926. The trout as a natural enemy of crane-flies. Scottish Nat., 1926, pp. 85-88. *Salmo fario* an important consumer of crane flies in all stages; earthworms, phalangids, and click beetles also in the stomachs.

1926. Spiders as enemies of crane-flies. Scottish Nat., 1926, pp. 127-129. List of species that eat crane flies, of which the names are given. Special study of the prey found in webs of the wood spiders *Zilla atrica* and *Z. x-notata.*

HARSHBARGER, W. A.

1894. The bold robber-fly and the mantis. Ent. News, vol. 5, no. 6, p. 169, June. Asilid attacked mantis (*Stagmomantis carolina*) but was itself captured and partly eaten.

HILDEBRAND, S. F.

1919. Fishes in relation to mosquito control in ponds. Rep. U. S. Comm. Fisheries 1918, App. 9, 15 pp., 18 figs.

HINE, JAMES S.

1906. Habits and life histories of some flies of the family Tabanidae. Bur. Ent., U. S. Dep. Agr., Techn. Bull., no. 12, pt. 2, pp. 19-38, 12 figs., Aug. Birds, hornets, and spiders noted as enemies.

HOWARD, L. O.

1904. The insect book. The Nature Library, vol. 8, pp. 158-159. Outbreaks of the armyworm sometimes completely controlled by tachina flies. They also attack grasshoppers, bugs, and beetles, sawflies and sawfly larvae and bumble bees and wasps.

1910. Preventive and remedial work against mosquitoes. Bull. 88, U. S. Bur. Ent., 126 pp., June 20. Use of natural enemies, salamanders, dragonflies, predacious mosquitoes and fish (pp. 62-72).

HYSLOP, J. A.

1910. The smoky crane-fly. Bull. 85, pt. 7, U. S. Bur. Ent., pp. 119-132, figs. 60-66. *Tipula infuscata*. Natural enemies include a tachinid parasite, ground beetles, ants, mites, and birds; a long list is given of birds that feed on crane flies; fungi also kill the insects.

LEATHERS, A. L.

1922. Ecological study of aquatic midges and some related insects with special reference to feeding habits. Bull. U. S. Bur. Fisheries, 38, Doc. no. 915, 61 pp., 44 figs., May. Food includes Protozóa, small Crustacea, diatoms, algae, and other vegetation.

MATHESON, ROBERT.

1929. A handbook of the mosquitoes of North America. 268 pp., 25 pls. Food; suck blood of mammals, birds, amphibians, and snakes (pp. 39-41); enemies, birds, bats, fishes, tadpoles, salamanders, and insects (pp. 71-72).

SMITH, K. M.

1927. A study of *Hylemyia* (*Chortophila*) *brassicae* Bouche, the cabbage root fly, and its parasites. With notes on some other dipterous pests of cruciferous plants. Ann. Appl. Biol., vol. 14, pp. 312-330. Description of life-history, enemies, and parasites. The larvae of a small beetle (*Aleochara bilineata*) destroy the pupae of the fly; while a cynipid and a braconid parasitize the larvae, which are also eaten by the carnivorous larva of an anthomyid fly. The larva of the beetle is itself parasitized by a proctotrupid.

TWINN, C. R.

1931. Observations on some aquatic animal and plant enemies of mosquitoes. Can. Ent. 63, no. 3, pp. 51-61, Mar. Other mosquito larvae, water beetle larvae, dragonfly and damselfly nymphs, backswimmers, water-scorpions, caddis larvae, salamanders, fishes, hydras, and bladderworts. Bibliography.

Van Dine, D. L.

1907. The introduction of top-minnows (natural enemies of mosquitos) into the Hawaiian Islands. Press Bull. 20, Hawaiian Agr. Exp. Sta., 10 pp., 3 figs., July 25.

Weed, C. M.

1902. [Enemies of *Bibio albipennis*.] Bull. 90, New Hampshire Agr. Exp. Sta., pp. 32-33, Mar. Fishes eating those falling in lake; chief food of robin in early spring.

HYMENOPTERA

Beilawsky, A. G.

1927. [Enemies of bees.] Vragi Pchet, Leningrad, 204 pp., 2 pls., 148 figs. Mammals, birds, reptiles, amphibians, insects, arachnids, worms, and protozoans.

Bequaert, J.

1922. The predacious enemies of ants. Bull. Amer. Mus. Nat. Hist., vol. 45, pp. 271-331, pls. 24-25, Oct. Spiders, beetles, ant-lions, Diptera, Hymenoptera, amphibians, lizards, birds and mammals, including man, discussed at length. "There is certainly little or no evidence to show that, as the theory is often expressed, ants are unpalatable to most insectivorous animals" (p. 271).

Bigelow, N. K.

1922. Insect food of the black bear (*Ursus americanus*.) Can. Ent., vol. 54, no. 3, pp. 49-50, Mar. *Vespula diabolica, V. consobrina,* and ants; notes on observations of others.

Davis, Wm. T.

1919. A remarkable nest of *Vespa maculata,* with notes on some other wasps' nests. Bull. Brooklyn Ent. Soc., vol. 14, nos. 4-5, pp. 119-123, Oct.-Dec. Notes on food habits of *Vespa* spp., cannibalistic, eat flies and damselflies; robber flies are their enemies.

1924. Oak apple galls destroyed by gray squirrels. Bull. Brooklyn Ent. Soc., vol. 19, no. 3, pp. 91-93, 1 fig., June. *Amphibolips confluens* freely eaten.

Graham, S. A.

1928. The influence of small mammals and other factors upon the larch sawfly survival. Journ. Econ. Ent., vol. 21, no. 2, pp. 301-310, Apr. *Lygaeonematus erichsoni.* Small mammals, probably *Microtus* chiefly, destroy from 50 to 80 per cent of the hibernating cocoons; parasites and fungi about 10 per cent.

Groneman, Carl F.

1923. Birds as destroyers of gall insects. Audubon Bull. (Illinois Audubon Soc.), pp. 13-15, 6 figs., Fall issue. Birds and squirrels recorded as enemies.

Heikertinger, Franz.

1919. Die metöke Myrmekodie. Tatsachenmaterial zur Lösung des Mimikryproblems. Biol. Zentralbl., vol. 39, no. 2, pp. 65-102, Feb. Enemies of ants (pp. 81-100), insects, spiders, amphibians, reptiles, mammals, birds.

Hersey, J. L.

1873. Bees and kingbirds. Can. Ent., vol. 5, pp. 159-160. Kingbirds and purple martins feed on honey bees, mostly drones; kingbirds feed freely on dragonflies also.

Howard, L. O.

1904. [Prey of Proctotrypoidea.] The insect book, p. 51. Gall flies, gall gnats, butterflies, moths, beetles, and the eggs of spiders, bugs, butterflies, and moths.

Hunter, W. D.

1912. Two destructive Texas ants. U. S. Dep. Agr., Bur. Ent. Circ. 148, 6 pp., Apr. *Pogonomyrmex barbatus molefaciens.* Eight species of birds and the horned lizard recorded as enemies.

Isely, Dwight.

1913. The biology of some Kansas Eumenidae. Kansas Univ. Sci. Bull., vol. 8, no. 7, pp. 235-309, pls. 34-37, July. Prey includes larvae of several families of Lepidoptera, of two of beetles, and of sawflies. Bibliography.

Phillips, E. F.

1917. Beekeeping. Chap. 22, Bee diseases and enemies, pp. 397-416. Three diseases of the brood, two of adults; enemies include two wax moths, toads, birds, mice, rats, and other small mammals, certain spiders and mites, dragonflies, various Hemiptera, the death's head moth, Mediterranean flour moth, a dipterous parasite (*Braula caeca*), blister beetle (*Meloe*) and other beetles, wasps, hornets, and ants. "Dragonflies are so destructive to queens as to make queen-rearing unprofitable in some places."

Sharp, D.

1910. [Summary of the prey of Fossores.] Cambridge Nat. Hist., vol. 6, pp. 92-93. General notes on prey of 16 families of wasps.

1910. [Prey of Ichneumonidae.] Cambridge Nat. Hist., vol. 5, p. 551. "Most of the species, in the larval state, live inside the larvae of Lepidoptera, and they thus keep the myriads of caterpillars within bounds, the number of these destroyed by ichneumons being prodigious. Some of the family are, however, external parasites, and some are known to attack spiders and insects of other Orders than Lepidoptera."

Swenk, M. H.

1910. A new sawfly enemy of the bull pine in Nebraska. Rep. Nebraska Agr. Exp. Sta., pp. 3-33, 18 figs. *Diprion* n. sp.—natural checks include ichneumonids, tachinids, chipmunks, birds, and a bacterial disease.

Williams, F. X.

1913. Monograph of the Larridae of Kansas. Kansas Univ. Sci. Bull., vol. 8, no. 4, pp. 121-213, pls. 22-30, July. Prey includes Orthoptera chiefly, but also Hemiptera, and spiders. Bibliography.

1913. Notes on the habits of some wasps that occur in Kansas. Kansas Univ. Sci. Bull., vol. 8, no. 6, pp. 223-230, pl. 33, fig. 1, July. *Harpactus* preying upon *Gypona cinerea*, *Mimesa* upon *Athysanus exitiosus* and other jassids; *Prionyx* upon locusts.

ARACHNIDA

Bilsing, S. W.

1920. Quantitative studies in the food of spiders. Ohio Journ. Sci., vol. 20, no. 7, pp. 215-260, May. Summarizes a large number of observations on prey actually seen eaten by spiders, and upon insects found in their webs; gives also some experimental results.

Calvert, Philip P.

1923. Studies on Costa Rican Odonata. *X. Megaloprepus,* its distribution, variation, habits, and food. Ent. News, vol. 34, no. 6, (Food), pp. 171-174, June. Feeds on spiders.

Lincecum, G.

1867. The tarantula killers of Texas. Amer. Nat., vol. 1, no. 3, pp. 137-141, May. *Pompilus formosus* Say feeds on *Mygale hentzii* and other large spiders.

Lovell, J. H.

1915. Insects captured by the Thomisidae. Can. Ent., vol. 47, no. 4, pp. 115-116, pl. 2, Apr. Crab spiders prey upon butterflies, dragonflies, wasps, bumble bees, honey bees, and large flies.

McAtee, W. L.

1911. Bird enemies of the Texas-fever tick and other ticks. The Auk, vol. 28, no. 1, pp. 136-138, Jan. A résumé of seven publications on the subject; of the birds mentioned, 12 species are inhabitants of the United States.

Savory, Theo. H.

1928. The biology of spiders. 376 pp., 16 pls., 121 figs., London. Food (pp. 116-125), flies, wasps, bees, ants, beetles, earwigs, butterflies, moths, harvestmen, woodlice, and other spiders; more rarely caterpillars, worms, fish, birds. "They show no trace of discrimination." Enemies (pp. 176-179) include birds, toads, lizards, mammals, harvestmen, spiders, wasps, and ichneumon flies, and other parasites.

MOLLUSCA

Baker, F. C.

1916. The relations of mollusks to fish in Oneida Lake. Techn. Publ. no. 4, New York State Coll. Forestry, 366 pp., 50 figs., one table, one map, July. On pp. 154-218 is summarized information on food of 54 species of fresh-water fishes, especially in relation to mollusks.

1918. The relation of shellfish to fish in Oneida Lake, New York. Circ. 21, New York State Coll. Forestry, pp. 11-33, figs. 1-16, Aug. Some snails carnivorous, eating other snails, leeches, and small fish; shellfish form a large part of the food of many species of fishes; other enemies of shellfish include flukes, dragonfly nymphs, horse fly larvae, water bugs, water beetle larvae, leeches, crawfishes, frogs, salamanders, turtles, ducks, other water birds, muskrats, mink and otter.

Bequaert, J.

1925. The arthropod enemies of mollusks, with description of a new dipterous parasite from Brazil. Journ. Parasitol., vol. 11, pp. 201-212, fig. 1. Carnivorous snails probably the most important predatory

enemies; predacious beetles, mites, and dipterous parasites also numbered among their foes. Bibliography which is abstracted in the paper.

Bishop, Sherman C.

1921. The map turtle, *Graptemys geographica* (Le Sueur) in New York. Copeia, no. 100, pp. 80-81, Nov. 15. Feeding on *Unio complanatus*.

Churchill, E. P., and Lewis, Sara I.

1924. Food and feeding in fresh-water mussels. Bull. U. S. Bur. Fisheries, vol. 39, 1923-1924, pp. 439-471, figs. 1-26. Protozoa, diatoms, other algae, organic detritus. Bibliography on the food of fresh-water mussels, and upon that of lamellibranchs in general.

Cooke, A. H.

1895. [Enemies of mollusca.] Cambridge Nat. Hist., vol. 3, pp. 56-62. Birds, rats, frogs, toads, beetles, mongooses, monkeys, walruses, whales, fishes, other mollusks, trematodes, nematodes, and mites.

Dyche, L. L.

1903. Notes on the food habits of California sea-lions (*Zalophus californianus* Lesson.) Trans. Acad. Sci. Kansas, 1901-1902, pp. 179-182. Food found in numerous stomachs, chiefly squids.

Federighi, Henry.

1930. Control of the common oyster drill. Econ. Circ. 70, U. S. Bur. Fisheries, 7 pp., 5 figs. *Urosalpinx cinerea* "destroys oysters to the value of several million dollars annually in the United States" (p. 1).

Field, Irving A.

1911. The food value of sea mussels. Bull. U. S. Bur. Fisheries, vol. 29, 1909, pp. 85-128, pls. 18-25. Food (pp. 92-95), mostly diatoms and Protozoa. Enemies (pp. 95-97), are numerous, fishes, mollusks, sea-stars, crows, rats, parasitic crabs.

Forrest, H. E.

1927. Fishes, Caradoc and Severn Valley Field Club, record of bare facts for the year 1926, p. 19. Stomach of an eel (*Anguilla vulgaris*) from the Severn was full of small bivalves (*Sphaerium corneum*).

Herrington, Wm. C.

1930. The Pismo clam. Fish. Bull. 18, California Div. Fish and Game, 69 pp., 16 figs. *Tivela stultorum*—birds, rays, starfish, and marine snails are enemies (pp. 52-54).

Moore, H. F.

1908. Volumetric studies of the food and feeding of oysters. Bull. U. S. Bur. Fisheries, 28, pp. 1297-1308, pl. 125, 6 figs. Ninety-five per cent diatoms; remainder of equally minute plants and animals.

Ritchie, J.

1927. A remarkable whale invasion. Scottish Nat. 1927, pp. 161-163. A school of false killers (*Pseudorca crassidens*) visited the Dornoch Firth in October, 1927, and some of them ran aground there. This whale is very rare, and had hardly been seen anywhere for 80 years (a few appeared off Western Europe in 1861 and 1862, and it was also seen in Tasmania). Examination of these whales showed they feed mainly on large cuttlefish.

STEVENSON, CHARLES H.

1892. A bibliography of publications in the English language relative to oysters and the oyster industries. Extract from Rep. U. S. Comm. Fish and Fisheries for 1892, art. 3, pp. 305-359. Some of the papers referred to deal with the food and enemies of oysters.

STILES, CH. WARDELL.

1902. Frogs, toads, and carp (*Cyprinus carpio*) as eradicators of fluke disease. Ann. Rep. U. S. Bur. Animal Industry 1901, pp. 220-222, figs. 197-203. By feeding on snails the intermediate hosts.

PISCES

ADAMS, CHAS. C., AND HANKINSON, T. L.

1928. The ecology and economics of Oneida Lake fish. Roosevelt Wild Life Ann., vol. 1, nos. 3-4, pp. 242-548, 1 pl., figs. 179-244, Nov. Notes on food and enemies of most of the species; full bibliography.

ALLIN, A. E.

1929. Seining records and food of the intermediate stages of Lake Erie fishes. Suppl. 18th Ann. Rep. New York Conserv. Dep. 1928, pp. 95-106. Cyprinidae and Catostomidae feed on algae and diatoms; the smaller Percidae on crustaceans and insect larvae, and the larger Percidae, Esocidae, and Catostomidae (fish eggs) on smaller fishes and fish eggs.

ANNIN, J.

1902. In Rhead, Louis, The speckled brook trout, pp. 129-140. Winged enemies include night heron, kingfisher, ducks, loons, grebes, fish hawk, bald eagle and barred owl.

BAKER, F. C.

1918. The productivity of invertebrate fish food on the bottom of Oneida Lake, with special reference to mollusks. Techn. Publ. no. 9, New York State Coll. Forestry, 264 pp. Notes on food of five species of fishes (pp. 214-216). Bibliography.

BARBOUR, T.

1921. Spiders feeding on small cyprinodonts. Psyche, vol. 28, no. 4, pp. 131-132, Aug. *Dolomedes tenebrosus.*

BIGELOW, N. K.

1924. The food of young suckers (*Catostomus commersonii*) in Lake Nipigon. Univ. Toronto Studies, no. 24, Publ. Ontario Fish Res. Lab., no. 21, pp. 81-115. Rotifers, Cladocera, insects.

BREDER, C. M., JR.

1921. The food of *Mustelus canis* (Mitchill) in mid-summer. Copeia, no. 101, pp. 85-86, Dec. 20. Notes on contents of 102 stomachs. (Fish in 10, crabs 44, *Nereis* sp. 1, univalves and vegetable matter 3.)

1922. Observations on young bluefish. Copeia, no. 106, pp. 34-36, May 20. Contents of 15 stomachs listed; 86 per cent fishes.

BREDER, C. M., JR., AND CRAWFORD, D. R.

1922. The food of certain minnows. A study of the seasonal dietary cycle of six cyprinoids with especial reference to fish culture. Zoologica, vol. 2, no. 14, pp. 287-327, figs. 101-128, Aug. *Semotilus bullaris,* 87 per cent insects, including larvae and adults of several orders plus some worms, millipeds, crayfish; *Leuciscus vandoisulus,* 98 per cent insects together with worms, spiders, crayfish and slug; *Notropis procne,* 36 per cent insects and in addition some worms and water mites; *Notropis cornutus* and *Rhinichthys atronasus,* 57 per cent insects plus same additional items as in last; *Exoglossum maxillingua,* 35 per cent insects, plus worms and fish eggs. Most of the insects were terrestrial species.

Carr, A. M.

1908. Food of fishes. Rep. Sci. Invest. Northumberland Sea Fisheries Comm. 1907, pp. 68-71. Reports on stomach examinations of 10 species.

1909. The food and condition of fish obtained from the North-east coast. Rep. Sci. Invest. Northumberland Sea Fisheries Comm. 1908-1909, pp. 41-50. Stomach analyses of seven species of fishes (pp. 43-46).

Chamberlain, F. M.

1907. Some observations on salmon and trout in Alaska. U. S. Bur. Fisheries, Doc. 627, 112 pp., 5 pls. Enemies (pp. 107-109) include trout, sculpins, mergansers, golden-eyes, mallards. The trout feed on other fishes, insects and their larvae, snails, and bivalves.

Cole, Leon J.

1905. The German carp in the United States. Rep. U. S. Comm. Fisheries 1904, pp. 523-641, pls. 1-3. Considerable on food and economic relations. Bibliography.

DeRyke, Willis.

1922. The food of the fishes of Winona Lake. Indiana Dep. Conserv., 47 pp., 1 pl., 1 map. Notes on 17 species, 6 of which are treated in some detail; yellow perch: young, midge larvae, Entomostraca, amphipods; adults, chiefly fish; bluegill: young, chiefly midge larvae and Entomostraca; older, the same plus caddis larvae, insects, snails; large-mouth black bass: young, amphipods, Cladocera, mayfly and midge larvae; larger, chiefly fish; log perch: amphipods, Cladocera, midge, caddis, and mayfly larvae, snails; skipjack: chiefly nonaquatic insects; sunfish: snails, midge larvae, insects; hogmolly: midge, and mayfly larvae, oligochaetes. Bibliography.

Eaton, E. H.

1928. The Finger Lakes fish problem. Suppl. 17th Ann. Rep. New York Conserv. Dep. 1927, pp. 40-46. Tabulation of food of some 30 species, 3 of which are almost exclusive fish-eaters, 7 others largely so, 8 feed chiefly on larval, and 5 on flying insects. Six species eat many scuds, and 4 even as adults, subsist more or less on plankton Crustacea. Enemies of fish, besides their own kind, include lampreys, turtles, snakes, loons, grebes, and mergansers.

Elmhirst, Richard.

1926. Notes on fishes from the Firth of Clyde. Scottish Nat., pp. 151-158, and 179-186. Full notes on food of cod and briefer reference to that of some other species. Nine kinds of fishes (including itself) listed as predatory on herring.

ELROD, M. J.

1929. The fishes of Flathead Lake. Montana Wild Life, vol. 2, no. 1, pp. 6-9, June. Notes on food of: *Catostomus* spp.: Insects, Entomostraca; *Ptychocheilus oregonensis:* Mainly insects such as mayfly and caddisfly larvae, grasshoppers, some fish and shrimps; *Mylocheilus caurinus:* Entomostraca and insects; *Leuciscus gillu:* Entomostraca and insects; *Salmo clarkii:* Beetles, mayflies, grasshoppers; *Salvelinus malma:* Fishes including *Coregonus* and *Ptychocheilus; Coregonus williamsoni:* Larvae of Tipulidae, Simuliidae, *Planorbis, Physa; Micropterus salmoides:* Fish, insects.

FIELD, IRVING A.

1907. Unutilized fishes and their relation to the fishing industry. U. S. Bur. Fisheries Doc. no. 622, 50 pp. Notes on the food of eight species.

FORBES, S. A.

1880. The food of fishes. Bull. Illinois State Lab. Nat. Hist., vol. 1, no. 3, pp. 18-65, Nov. Notes on stomach examinations for numerous species.

1883. The food of the smaller fresh-water fishes. Bull. Illinois State Lab. Nat. Hist., vol. 1, no. 6, pp. 65-94, May. Examination of 319 stomachs representing 25 species; food chiefly neuropteroid and chironomid larvae, and Entomostraca; other animal items, fishes, mollusks, Hymenoptera, Diptera, Coleoptera, Hemiptera, Thysanura, Arachnida, amphipods, isopods, worms, and protozoans.

1890. Studies of the food of fresh-water fishes. Bull. Illinois State Lab. Nat. Hist. vol. 2, pp. 433-473. Many stomach examinations of 28 species; tabulation of items and percentages.

1890. On the food relations of fresh-water fishes. Bull. Illinois State Lab. Nat. Hist., vol. 2, pp. 475-538. Summary of the preceding papers, discussion of fishes as predators on other fishes, on mollusks, insects, crustaceans, worms, fresh-water sponges, and protozoans. Schedule of food items and the species taking them.

FULTON, T. WEMYSS.

1903. The distribution, growth, and food of the angler (*Lophius piscatorius.*) 21st Ann. Rep. Fishery Board Scotland 1902, pp. 186-217. Analyses of 280 stomach contents; 269 containing fishes, 10 squids, and 1 a crab.

GUDGER, E. W.

1927. Hydras as enemies of young fishes. Nat. Hist., vol. 27, pp. 270-274, 3 figs.

1929. Wide-Gab, the angler fish. Nat. Hist., vol. 29, no. 2, pp. 155-159, illus., Mar.-Apr. Case of attempt to swallow a gull; review of literature, showing that birds up to the size of the loon are eaten; seven wild ducks from one stomach; the principal food, however, is fishes.

HANKINSON, THOMAS L.

1908. A biological survey of Walnut Lake, Michigan. Rep. Biol. Surv. Michigan Geol. Surv. 1907, pp. 158-288, pls. 13-75. Food of several species of fishes noted from examination of stomachs (pp. 200-216).

Harnell, J., and Nayudo, M. R.

1924. A contribution to the life history of the Indian sardine, with notes on the plankton of the Malabar Coast. Madras Fisheries Bull. 17, pp. 129-197, 10 pls. Food extensively treated; consists of diatoms, peridineans, infusorians, Heliozoa, larval bivalves, and copepods.

Hildebrand, S. F., and Towers, I. L.

1927. Food of trout in Fish Lake, Utah. Ecology, vol. 8, no. 4, pp. 389-397, Oct. Contents of 181 stomachs tabulated, the more important items being *Daphnia, Gammarus,* midges and vegetation; leeches, snails, dragonfly nymphs, and fishes and their eggs are other items of the food.

Johansen, Frits.

1912. The fishes of the Danmark Expedition. Danmark-Ekspeditionen Gronl. Nordostkyst 1906-1908, vol. 5, no. 12, pp. 633-675, 5 figs., pls. 44-46. Notes on the food of *Gadus* and *Salmo.*

Johnson, Robert S., and Stapleton, M. F.

1917. Fish ponds on farms. App. 2, Rep. U. S. Comm. Fisheries 1915, 29 pp. Cannibalistic and other predacious fishes, turtles, snakes, birds, and minks are the principal foes.

Juday, Chancey.

1906. A study of Twin Lakes, Colorado, with especial consideration of the food of the trouts. Bull. U. S. Bur. Fisheries, vol. 26, pp. 147-178, pl. 3. In addition to notes on contents of 370 trout stomachs of six species this publication contains a good bibliography and a digest of papers relating to Entomostraca as food of fishes.

Kendall, William C.

1897. Notes on the food of four species of the cod family. Rep. U. S. Fish Comm. 1896, App. 3, pp. 177-186. A long list of food items. "Protective mimicry seems of little avail against these fishes."

Kendall, William C., and Dence, W. A.

1927. A trout survey of the Allegany State Park in 1922. Roosevelt Wild Life Bull., vol. 4, no. 3. pp. 291-482, figs. 54-86, tables, July. Notes on 112 stomach contents (pp. 472-474, table 27): Midges, caddisflies, beetles, ants and other Hymenoptera, Diptera, grasshoppers, plant lice, lacewing flies, stoneflies, mayflies, spiders, crustaceans, and fish. Bibliography.

Knight, A. P.

1927. Losses in speckled trout fry after distribution. Science, n. s., vol. 65, pp. 525-526, Aug. Losses 71-98 per cent, mostly to natural enemies, birds, trout and other fishes.

Kraatz, Walter C.

1923. A study of the food of the minnow *Campostoma anomalum.* Ohio Journ. Sci., vol. 33, pp. 265-283. Diatoms, algae, etc.

Lebour, Marie V.

1924. The food of young herring. Journ. Marine Biol. Assoc. United Kingdom, n. s., vol. 13, pp. 325-330. Among animal items, Infusoria, larval mollusks, copepods.

LEWIS, RALPH C.

1929. The food habits of the California sardine in relation to the seasonal distribution of microplankton. Bull. Scripps Inst. Oceanography, Techn. Ser. 2, pp. 155-180, 2 figs. Items of animal food are schizopods and copepods.

LINTON, EDWIN.

1901. Fish parasites collected at Woods Hole in 1898. Bull. U. S. Fish Comm., vol. 19, 1899, pp. 267-304, pls. 33-43. Notes on fish food, pp. 270-284.

1901. Parasites of fishes of the Woods Hole region. Bull. U. S. Fish Comm., vol. 19, 1899, pp. 405-492, pls. 1-34. Summary of parasites, pp. 425-488, contains many references to food of fishes.

1921. Food of young winter flounders. Rep. U. S. Comm. Fisheries, App. 4, 14 pp. *Pseudopleuronectes americanus,* food of young principally amphipods, other small Crustacea, and annelids; food of adults, annelids, Crustacea, ascidians, fish, mollusks. Almost as much on parasites (Sporozoa, trematodes, nematodes, and Acanthocephala) as on food.

MACCOY, CLINTON V.

1929. The mackerel in New England. Bull. Boston Soc. Nat. Hist., vol. 53, pp. 3-7, Oct. Food, small fish, squids, pteropods, amphipods, copepods. Enemies, whales, porpoises, sharks, dogfish, bluefish, gannets, parasitic worms.

MARSHALL, W. S., AND GILBER, N. C.

1905. Notes on the food and parasites of some fresh-water fishes from the lakes at Madison, Wis. Rep. U. S. Comm. Fisheries 1904, App., pp. 513-522. Incidental notes on food.

MOORE, J. PERCY.

1922. Use of fishes for control of mosquitoes in northern fresh waters of the United States. Rep. U. S. Comm. Fisheries, App. 4, 60 pp., 7 pls. Food of roach: Entomostraca, insects, mites, Protozoa; mudminnow: Insects, Crustacea, mollusks, Protozoa; killifish: Oligochaetes, mollusks, Entomostraca; top minnow: cannibalistic; blue-spotted sunfish: Midge larvae, Entomostraca, amphipods; long-eared sunfish: Midge larvae, Entomostraca, oligochaetes; common sunfish: Midge larvae, Entomostraca, snails, mites, tadpoles. All eat mosquito larvae. Bibliography.

MUTTKOWSKI, RICHARD A.

1925. The food of trout in Yellowstone National Park. Roosevelt Wild Life Bull., vol. 2, no. 4, pp. 471-497, figs. 114-133, Feb. Stoneflies, 90 per cent; mayflies, caddisflies, adults and young of all; and water-trapped land insects.

1929. The ecology of trout streams in Yellowstone National Park. Roosevelt Wild Life Ann., vol. 2, no. 2, pp. 155-240, figs. 53-116, Oct. Food of trout, pp. 222-230, conclusions as in his 1925 paper on the subject. Food of insects, pp. 230-233; see under Muttkowski and Smith.

NEEDHAM, JAMES G.

1903. Food of brook trout in Bone Pond. Bull. 68, New York State Mus., pp. 204-217. Contents of 25 stomachs tabulated.

NEEDHAM, JAMES G.; JUDAY, CHANCEY; MOORE, EMMELINE; SIBLEY, CHAS. K.; AND TITCOMB, JOHN W.

1922. A biological survey of Lake George, N. Y. N. Y. State Conserv. Comm., 78 pp., 27 figs. Much on the food of fishes; the staples of the diet of carnivorous fry are waterfleas, midges (all stages), other insects, scuds (amphipods), and crayfishes; cannibalism prevalent (p. 63); food of adults of eight species outlined on pp. 65-68. Lake trout: Principal food, lake smelt, other items yellow perch, and caddisflies; black bass: Perch, crawfish, grasshoppers, scuds; pike: Other fishes; yellow perch: Staples, midge larvae, mayfly nymphs, scuds, snails, secondary, caddisworms and waterfleas; bullhead: Scuds, midge larvae, mayfly nymphs, snails; long-eared sunfish: Mayfly nymphs, midge larvae, ants, scuds, waterfleas, miscellaneous insects, and crayfishes; common sunfish: Snails, mayfly nymphs, caddisworms, beetles, midge larvae, various insects; rock bass: Crayfish, fishes, insects.

NEEDHAM, P. R.

1929. Quantitative studies of the fish food supply in selected areas. Suppl. 18th Ann. Rep. New York Conserv. Dep. 1928, pp. 220-232. Ithaca, N. Y., Erie-Niagara watershed. Foods consumed by trout in comparison with available foods; in the case of aquatic foods the relation of consumption to availability is very clear. This is a reworking of a similar paper in the 17th Ann. Rep. (1927) 1928, pp. 192-206.

NEW YORK CONSERVATION DEPARTMENT.

1928. A biological survey of the Oswego River System. Suppl. 17th Ann. Rep. New York Conserv. Dep. 1927, 248 pp., 12 col. pls., text figs., maps. Much on fish food; in a tabulation of food items of adults of 31 species, midges, mayflies, and minnows seem to be most commonly used; and of young of eight species, copepods, Cladocera, and midges.

PAGE, WM. F.

1895. Feeding and rearing fishes, particularly trout, under domestication. Bull. U. S. Fish Comm., 1894, pp. 289-314. Some notes on natural food, and an indexed bibliography.

PATTERSON, A. H.

1926-1927. Food of the Sturgeon. Trans. Norfolk and Norwich Nat. Soc., vol. 12, pp. 380-381. Stomach of one contained about 729 small fish (lesser sandlaunces).

PEARSE, A. S.

1915. On the food of the small shore fishes in the waters near Madison, Wisconsin. Bull. Wisconsin Nat. Hist. Soc., vol. 13, no. 1, pp. 7-22, 1 fig., Mar. Sixteen species, of which nine lived largely on insects and their larvae, two on ostracods, two on copepods, and one on Cladocera.

1918. The food of the shore fishes of certain Wisconsin lakes. Bull. U. S. Bur. Fisheries, vol. 35 (1915-16), pp. 249-292. Report on more than 1,600 specimens of 32 species, with bibliography.

1919. Habits of the black crappie in inland lakes of Wisconsin. Rep. U. S. Comm. Fisheries 1918, app. 3, pp. 5-16. Tabulation of contents of 276 stomachs.

1921. Distribution and food of the fishes of Green Lake, Wis., in summer. Bull. U. S. Bur. Fisheries, vol. 37, 1919-1920, pp. 255-272, 1 map. Notes on 16 species; the food of all combined comprised insect larvae 21.7 per cent, amphipods 16.5 per cent, fish 9.6 per cent, crayfishes 7.8 per cent, cladocerans 7.6 per cent, insect pupae 6.7 per cent, snails 4.4 per cent, bivalves 4.1 per cent, and the following items in smaller proportions, adult insects, ostracods, oligochaetes, leeches, mites, *Mysis*, and copepods. Sixty-seven per cent is arthropods, composed of 31.7 insects and 35.6 crustaceans. Comparison is made with the fishes of Lake Mendota. Bibliography.

1924. Amount of food eaten by four species of fresh-water fishes. Ecology, vol. 5, no. 3, pp. 254-258, July. Order of choice, minnows, earthworms, amphipods, dragonfly nymphs, crayfishes, grasshoppers, snails, and caddis larvae.

PEARSE, A. S., AND ACHTENBERG, HENRIETTA.

1917-1918. Habits of yellow perch in Wisconsin Lakes. Bull. U. S. Bur. Fisheries, vol. 36, 1917-1918, pp. 297-366, pl. 83, figs. 1-35. Report on 1,147 stomach examinations of which the food as a whole was made up of 38.3 per cent insect larvae, 21.4 Entomostraca, 9.5 insect pupae and adults, 5.5 macroscopic crustaceans, 4.5 fishes, 2.4 mollusks, 1.4 oligochaetes, leeches and arachnids. Enemies of the perch include pickerel, black bass, a number of birds, and a variety of parasites. Bibliography.

PEARSON, JOHN C.

1928. Natural history and conservation of the redfish and other commercial sciaenids of the Texas coast. Bull. U. S. Bur. Fisheries, vol. 44, pp. 129-214, 44 figs. *Sciaenops ocellatus:* Shrimps, crabs, mollusks, fish; *Pogonias cromis:* Clams, mussels, oysters, crabs, shrimps, fish, annelids; *Cynoscion nebulosus:* Shrimps, crabs, fish; *Micropogon undulatus:* Shrimps, crabs, annelids, fish.

PECK, JAMES I.

1894. On the food of the menhaden. Bull. U. S. Fish Comm., vol. 13, 1893, pp. 113-126, pls. 1-8. Food filtered from water by gill-raker mechanism, consists chiefly of unicellular organisms, both animal and vegetable. They also take ostracods, copepods, amphipods and other small Crustacea, and young *Nereis*. Composition of food the same as material filtered from water by mechanical contrivances: Diatoms, rotifers, dinoflagellates, etc. The supply of such food illimitable.

1896. The sources of marine food. Bull. U. S. Fish Comm., 1895, pp. 351-368, pls. 64-71. Plankton, largely diatoms, the basis; notes on the food of the squeteague, the bluefish, sea bass, scup, and tautog.

PETERSEN, C. G. J.

1894. On the biology of our flat-fishes. Rep. Danish Biol. Sta., vol. 4, 1893, pp. v+146,2 pls., 1 map, 18 tables. Notes on food of young and adults.

SCOTT, ANDREW.

1899. Observations on the habits and food of young fishes. Proc. & Trans. Liverpool Biol. Soc., vol. 13, 1898-99, pp. 90-93.

SCOTT, THOMAS.

1902. Observations on the food of fishes. 20th Ann. Rep. Fishery Board Scotland 1901, pt. 3, pp. 486-538. Notes on 56 species.

1903. Some further observations on the food of fishes, with a note on the food observed in the stomach of a common porpoise. 21st Ann. Rep. Fishery Board Scotland 1902, pp. 218-227, 2 figs.

SIBLEY, C. K.

1929. The food of certain fishes of the Lake Erie Drainage Basin. Suppl. 18th Ann. Rep., New York Conserv. Dep. 1928, pp. 180-188. Thirty-four species feed mainly on immature aquatic insects, especially midge larvae, and Crustacea; eight species are pronounced spawn-eaters; small fish are important food of the larger species; food of young chiefly copepods and Cladocera.

SMALLWOOD, W. M., AND STRUTHERS, P. H.

1927. Carp control studies in Oneida Lake. Suppl. 17th Ann. Rep., New York Conserv. Dep., pp. 67-83. Much on food; animal matter taken by adults includes fish, ostracods, phyllopods, copepods, crayfish, midge and caddis larvae and other insects; by young, ostracods, copepods, Cladocera, insect larvae, snails, worms, mites, eggs of snails, insects and copepods, rotifers, and bivalves.

SMITH, HUGH M.

1896. A review of the history and results of the attempts to acclimatize fish and other water animals in the Pacific States. Bull. U. S. Fish Comm., vol. 15, 1895, pp. 379-472, pls. 73-83. Notes on food of a few species. Catfish, fish eggs and fry; carp, spawn; shad, shrimps; striped bass, carp, catfish, crabs.

SMITH, W. RAMSAY.

1889. On the food of fishes. 7th Ann. Rep. Fishery Board Scotland 1888, pp. 222-258.

1890. On the food of fishes. 8th Ann. Rep. Fishery Board Scotland 1889, pp. 230-256.

1891. On the food of fishes. 9th Ann. Rep., Fishery Board Scotland 1890, pp. 222-242.

1892. On the food of fishes. 10th Ann. Rep. Fishery Board Scotland 1891, pp. 211-231. This and similar papers in three previous reports are based on investigations of Thomas Scott.

STEWART, N. H.

1926. Development, growth, and food habits of the white sucker, *Catostomus commersonii* Lesueur. Bull. U. S. Bur. Fisheries, vol. 42, pp. 147-184, 55 figs. Among animal food midge larvae are most important at all ages; some rotifers, Entomostraca, and Protozoa are taken at all stages also, but dragonfly, caddisfly, mayfly larvae, and Mollusca are taken only by adults. Bibliography.

STRUTHERS, P. H.

1929. Carp control studies in the Erie Canal. Suppl. 18th Ann. Rep. New York Conserv. Dep. 1928, pp. 208-219. Animal food (p. 214) includes insect larvae, snails, midge larvae, bivalves, ostracods, Malacostraca, copepods, Cladocera, and decapods.

SUMNER, FRANCIS B.; OSBURN, RAYMOND C.; AND COLE, LEON J.

1911. A biological survey of the waters of Woods Hole and vicinity. Bull. U. S. Bur. Fisheries, vol. 31, pt. 2. The catalogue of the marine fauna, fishes, pp. 734-744, contains notes on the food mainly quoted from Verrill, Goode, Linton, and Field.

TAVERNER, P. A.

1915. The double-crested cormorant (*Phalacrocorax auritus*) and its relation to the salmon industries on the Gulf of St. Lawrence. Can. Geol. Surv., Bull. 13, 24 pp., 1 pl. Food sculpins, herring, capelin, eel, etc., no salmon; the salmon feeds on other fishes, and crustaceans, and is cannibalistic.

TIFFANY, LEWIS H.

1921. Algal food of the young gizzard shad. Ohio. Journ. Sci., vol. 21, no. 4, pp. 113-122, Feb. Mentions several game fishes that prey on this wholly vegetarian species.

TURNER, CLARENCE L.

1920. Distribution, food and fish associates of young perch in the Bass Island region of Lake Erie. Ohio Journ. Sci., vol. 20, no. 5, pp. 137-152, Mar. Details of analyses of 138 stomach contents.

1921. Food of the common Ohio darters. Ohio Journ. Sci., vol. 22, pp. 41-62. Usually the food changes with age from Entomostraca to midge larvae and similar organisms, and then with maturity, to a varied diet in which ephemerid and other large insect larvae predominate.

1922. Notes on the food habits of young *Cottus ictalops* (miller's thumb). Ohio Journ. Sci., vol. 22, pp. 95-96. Midge and other insect larvae.

VERRILL, A. E.

1873. Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. Report on Sea Fisheries of New England, pt. 1, pp. 295-778. Lists of species found in the stomach of fishes (pp. 514-521).

WARREN, B. H.

1897. Fish-eating birds and mammals. Ann. Rep. Pennsylvania Dep. Agr., 1896, pp. 297-303, 1 pl. Seventeen or more kinds of birds, wild cats, raccoons, muskrats, mink, and the otter.

WELSH, WM., AND BREDER, C. M., JR.

1923-1924. Contributions to life histories of *Sciaenidae* of the eastern United States coast. Bull. U. S. Bur. Fisheries, vol. 39, pp. 141-201, 60 figs. Notes on food of eight species; it is chiefly crustaceans, next in order coming worms and fishes. Bibliography. *Cynoscion regalis:* Shrimps, schizopods, isopods, amphipods, worms when small, fish when mature, but including shrimps and squids; *Bairdiella chrysura:* Schizopods, isopods, amphipods, worms, fish; *Stellifer lanceolatus:* Schizopods, copepods, decapods, ostracods, amphipods, worms; *Leiostomus xanthurus:* Ostracods, copepods, amphipods, worms, mollusks; *Micropogon undulatus:* Shrimps, echinoderms, worms, mollusks, copepods, ostracods, amphipods; *Menticirrhus americanus:* Crabs, shrimps, worms, fish; *Menticirrhus saxatilis:* Shrimps, amphipods, schizopods, worms, fish; *Pogonias cromis:* Mollusks including oysters; *Eques pulcher:* Small crustaceans.

WICKLIFF, EDWARD L.

1920. Food of young small-mouth black bass in Lake Erie. Proc. Amer. Fisheries Soc., pp. 364-371. Report on 313 specimens, the most important items being copepods found in 61 per cent of the stomachs and Cladocera in 39 per cent. Other commonly taken foods were midge larvae and pupae, adult insects, fish, and mayfly nymphs.

AMPHIBIA

DRAKE, CARL J.

1914. The food of *Rana pipiens* Schreber. Ohio Naturalist, vol. 14, no. 5, pp. 257-269, Mar. Detailed account of the contents of 209 stomachs collected at Cedar Point, Ohio.

FROST, S. W.

1924. Frogs as insect collectors. Journ. New York Ent. Soc., vol. 32, no. 4, pp. 174-185, pl. 14, Dec. Eat worms, snails, crayfishes, spiders, mites, insects and frogs; insects most important. Larvae: Lepidoptera 9; Coleoptera 24; Diptera 13; Neuroptera 1. Adults: Orthoptera 1; Hemiptera 25; Neuroptera 3; Mecaptera 1; Diptera 33; Coleoptera 242; spiders 37; pseudoscorpions 1.

GARMAN, H.

1901. The food of the toad. Bull. 91, Kentucky Agr. Exp. Sta., pp. 60-68, fig. 16. Report on 20 stomach contents.

HAMILTON, W. J., JR.

1930. Notes on the food of the American toad. Copeia, 1930, no. 2, June 30, p. 45. *Bufo americanus.* Report on food of 400 young toads: Diptera 22 per cent, mostly larvae; mites 15.5 per cent; ants 12.8; beetles and their larvae 11.8, the most abundant group being Staphylinidae; thrips 10.1; Collembola 6.2; Lepidoptera, Hymenoptera, aphids, sowbugs, spiders, worms, and snails, the remainder.

KIRKLAND, A. H.

1904. Usefulness of the American toad. Farmers' Bull. no. 196, U. S. Dep. Agr., 16 pp. Contents of 149 stomachs discussed.

KLUGH, A. Brooker.

1922. The economic value of the leopard frog. Copeia, no. 103, pp. 14-15, Feb. 15. Contents of 25 stomachs; chiefly *Melanoplus femur-rubrum* and *Leptinotarsa 10-lineata.*

MUNZ, PHILIP A.

1920. A study of the food habits of the Ithacan species of *Anura* during transformation. Pomona Coll. Journ. Ent. Zool., vol. 12, no. 2, pp. 33-56, June. Report on 586 stomachs of eight species; summaries of results of previous investigators.

SMALLWOOD, W. M.

1928. Notes on the food of some Onondaga Urodela. Copeia, no. 169, pp. 89-98, Oct. 25. *Ambystoma maculatum:* Centipeds, earthworms, snails, sowbugs, crickets, grasshoppers, beetles; *Plethodon cinereus:* Centipeds, earthworms, snails, sowbugs, ants, beetles, mites, spiders, phalangids, caterpillars, grasshoppers, flies springtails; *Eurycea bislineata:* Earthworms, caterpillars, and beetle, fly, and caddisfly larvae; *Triturus viridescens:* Snails, waterboatmen, fish, earthworms, beetle larvae; bivalves, daphnia, caterpillars, amphibian eggs (including its own), water bugs, mosquito and other fly larvae, slugs, snails, leeches, spiders, springtails, beetles, mites.

Surface, H. A., [Ed.]

1913. First report on the economic features of the amphibians of Pennsylvania. Zool. Bull. Div. Zool. Pennsylvania Dep. Agr., vol. 3, nos. 3-4, pp. 67-152, figs. 1-25, pls. 1-11, May-July. General discussion of the subject, including report on examination of stomachs of 14 species of salamanders, two of toads, and nine of frogs.

Wright, A. H.

1920. Frogs: Their natural history and utilization. App. 6, Rep. U. S. Comm. Fisheries 1919, 44 pp. Notes on the food of various species, pp. 38-42. Enemies, pp. 42-44; invertebrates, fishes, amphibians, reptiles, birds, and mammals discussed.

Wright, A. H., and Haber, Julia M.

1922. The carnivorous habits of the purple salamander. Copeia, no. 105, pp. 31-32, April 15. Feed on aquatic insects; in captivity take frogs and salamanders.

REPTILIA

Burt, Chas. E.

1928. Insect food of Kansas lizards with notes on feeding habits. Journ. Kansas Ent. Soc., vol. 1, no. 3, pp. 50-68, July. Notes on stomach contents of seven species with compiled information on others. Of the total food in all lizard stomachs examined 51.92 per cent was Orthoptera, 11.65 Lepidoptera, 9.35 Arachnida, 8.90 Hymenoptera, and 6.00 Coleoptera; Diptera, Hemiptera, Trichoptera, and Mollusca in smaller amounts.

Kellogg, Remington.

1929. The habits and economic importance of alligators. Techn. Bull. 147, U. S. Dep. Agr., 36 pp., 2 pls., Dec. Food (pp. 21-32), nearly half is crabs, crawfishes, and shrimps; spiders, insects of various orders, toads, smaller alligators, lizards, turtles, snakes, birds and mammals also eaten.

Lydekker, R.; Cunningham, J. T.; Boulenger, G. A.; and Thomson, J. A.

1912. Food and growth [of reptiles], reptiles, Amphibia, fishes, and lower Chordata, pp. 47-61, London. "The food of reptiles is very various," a dictum which shows distribution of predation is as characteristic of this phylum as of others. Details in many cases.

Pack, H. J.

1921. Food habits of *Sceloporus graciosus graciosus* (Baird and Girard). Proc. Biol. Soc. Washington, vol. 34, pp. 63-66, Mar. Report on the contents of 71 stomachs.

1922. Food habits of *Crotaphytus wislizenii* Baird and Girard. Proc. Biol. Soc. Washington, vol. 35, pp. 1-3, Mar. 20. Report on the contents of 18 stomachs.

1923. Food habits of *Callisaurus ventralis ventralis* (Hallowell). Proc. Biol. Soc. Washington, vol. 36, pp. 79-81, Mar. Twenty stomachs: disclosing caterpillars, coccinellids, meloids, erotylids, chrysomelids, weevils, grasshoppers, mantids, Hemiptera, ant-lions, Diptera, and spiders.

1923. Food habits of *Crotaphytus collaris baileyi* (Stejneger). Proc. Biol. Soc. Washington vol. 36, pp. 83-84, Mar. Report on 16 stomach examinations; Orthoptera the principal animal food, caterpillars, wasps, bugs, leaf-hoppers, and ant-lions also being taken.

1923. The food habits of *Cnemidophorus tessellatus tessellatus* (Say). Proc. Biol. Soc. Washington, vol. 36, pp. 85-89, Mar. Sixty-three stomachs containing caterpillars, 37.7 per cent of the food, grasshoppers 14.4; beetles 14.2; other insects 14.27; and arachnids 8.2.

SURFACE, H. A. [ED.]

1906. The serpents of Pennsylvania. Monthly Bull. Div. Zool. Pennsylvania Dep. Agr., vol. 4, nos. 4-5, pp. 115-202, pls. 14-52, figs. 5-23, Aug.-Sept. Includes data on contents of stomachs of snakes of 14 species.

1907. The lizards of Pennsylvania. Bull. Div. Zool. Pennsylvania Dep. Agr., vol. 5, no. 8, pp. 235-258, pls. 30-33, figs. 26-28, Dec. 1. Notes on food of five species, in the case of two of them based on examinations of stomachs.

1908. First report on the economic features of turtles of Pennsylvania. Bull. Div. Zool. Pennsylvania Dep. Agr., vol. 6, nos. 4-5, pp. 107-195, pls. 4-12, 16 figs., Aug.-Sept. Includes report on stomach contents of representatives of nine species.

WINTON, W. M.

1915. A preliminary note on the food habits and distribution of the Texas horned lizards. Science, n. s., vol. 41, pp. 797-8, May 28. Brief summary of the results of examination of 485 stomachs; agricultural ants found in 80 per cent and stink bugs in 60 per cent of the stomachs.

WRIGHT, A. H.; FUNKHOUSER, W. D.; AND BISHOP, S. C.

1915. A biological reconnaissance of the Okefinokee Swamp in Georgia. Turtles, lizards, and alligators, by Wright and Funkhouser, pp. 108-139; snakes by Wright and Bishop, pp. 139-192. Proc. Acad. Nat. Sci. Philadelphia, pp. 107-192, pls. I-III, figs. 1-14, Mar. (Apr.). Notes on food of many of the species.

AVES

The entries under food of birds are chiefly general papers in which bibliographies introductory to the very extensive literature of the subject can be found.

CLELAND, J. B.

1922. The parasites of Australian birds. Trans. and Proc. Roy. Soc. South Australia, vol. 46, pp. 85-118. Cestodes in 86 species, adult nematodes in 28, Microfilaria in 34, Acanthocephala in 25, trematodes in 38, fleas on 3, Hippoboscidae on 4, Mallophaga on 107, ticks on 4, mites on 38, Haemosporidia in 47, and haemoflagellates in 12.

CRAM, ELOISE B.

1927. Bird parasites of the nematode suborders Strongylata, Ascaridata, and Spirurata. U. S. Nat. Mus. Bull. 140, 465 pp., 444 figs. About 500 species.

Forbush, E. H.

1904. Special report on the decrease of certain birds, and its causes with suggestions for bird protection. 52nd Ann. Rep. Massachusetts State Board Agr., pp. 429-543, 2 pls. Chief causes, gunners, trappers, egg collectors, destruction of environment, natural enemies, and the elements.

1907. Useful birds and their protection. Massachusetts State Board Agr., 437 pp., 56 pls., 171 figs. Capacity of birds for destroying pests, birds as enemies of insects, and mammals, hairy caterpillars, plant lice, also on natural checks upon bird life.

1916. The natural enemies of birds. Econ. Biol. Bull. 3, Massachusetts State Board Agr., 58 pp., 7 pls., figs. A thorough review of the subject, treating enemies among domesticated animals and among wild mammals, birds, reptiles, amphibians, fishes, and insects.

Gross, A. O.

1928. The heath hen, pp. 525-526. Marsh hawk, Cooper's hawk, sharp-shinned hawk, and goshawk, the snowy owl, and crows enemies of this species. Domestic cat the worst.

Henderson, Junius.

1927. The practical value of birds, 342 pp. An exhaustive review of literature on the economics of American birds, with a long bibliography. Chapters on birds as enemies of injurious insects, mammals, and plants; birds as scavengers, and on the destruction of birds.

Hersey, L. J.

1907. A naturalist's notes on birds and snakes. Outdoor Life, pp. 481-483, Nov. Snakes eating birds and their eggs.

Lewis, Elisha J.

1857. [Enemies of the partridge]. The American sportsman, 3rd ed., Enemies of the partridge (pp. 102-4): fox raccoon, weasel, polecat, serpent, hawk, crow (p. 102); sparrow hawk, pigeon hawk, goshawk (p. 103).

1857. [Enemies of the wild turkey]. The American sportsman, 3rd ed. Wolf, fox, lynx, cougar, opossum, and wild cat. Also the larger hawks and owls (p. 141).

1857. [Enemies of the ruffed grouse]. The American sportsman, 3rd ed. Polecats, weasels, raccoons, opossums, foxes, crows, larger hawks (p. 150).

Linton, E.

1927. Notes on cestode parasites of birds. Proc. U. S. Nat. Mus., vol. 70, art. 7, 73 pp. 15 pls. Thirty-four species.

1928. Notes on trematode parasites of birds. Proc. U. S. Nat. Mus., vol. 73, 36 pp., 11 pls. Twenty-two species.

Longstaff, T. G.

1927. Bird's-nesting mice and insects. British birds, vol. 20, pp. 198-199. Notes certain insects (*e. g.* ants) attacking nestlings, and mice destroying eggs.

McAtee, W. L.

1913. Index to papers relating to the food of birds by members of the Biological Survey in publications of the United States Department of Agriculture, 1885-1911. U. S. Biol. Surv. Bull. 43, 1913, 69 pp. Bibliography with subject index.

PLATH, O. E.

1919. Parasitism of nestling birds by fly larvae. The Condor, vol. 21, pp. 30-38. *Protocalliphora azurea* in 39 out of 63 nests; parasites and scavengers on this dipteron.

RANSOM, B. H.

1909. The taenioid cestodes of North American birds. U. S. Nat. Mus. Bull. 69, 141 pp., 42 figs. About 140 species; bibliography.

RUSSEL, J. F.

1926. Predatory bass. Outdoor Life, vol. 57, no. 2, pp. 146-147, Feb. Black bass with swallow in its stomach. San Diego Co., Calif.

TUCKER, B. W.

1926. Bird's-nesting bank voles. British birds, vol. 20, pp. 158-160. Evidence was given that bank voles destroy birds' eggs. This note was followed by a number of other communications by various authors, in the same journal (vol. 20, pp. 180-181, 198-199, 207, 230, 255), which showed that various species of mice commonly attack birds' eggs.

WEED, C. M., AND DEARBORN, NED.

1903. Birds in their relations to man, 380 pp., illus. Extensive chronological bibliography; chapters on birds as regulators of outbreaks of injurious animals, relations of birds to predacious and parasitic insects.

WILD, O. H.

1927. Wasps destroying young birds. British birds, vol. 20, pp. 254-255.

MAMMALIA

BABCOCK, H. L.

1914. Some observations on the food habits of the short-tailed shrew (*Blarina brevicauda*). Science, n. s., vol. 40, pp. 526-530, Oct. 9. Review of literature, chiefly about observations on captive animals.

BAILEY, VERNON, AND SPERRY, CHAS. C.

1929. Life history and habits of grasshopper mice, genus *Onychomys*. Techn. Bull. 145, U. S. Dep. Agr., 19 pp., 4 pls., Nov. Animal food (pp. 10-19), nearly 90 per cent of the whole, largely grasshoppers, crickets, caterpillars, moths, and beetles; insects of other orders, spiders, and mice also taken.

BROOKS, FRED E.

1908. Notes on the habits of mice, moles, and shrews. Bull. 113, West Virginia Agr. Exp. Sta., pp. 89-133, 10 pls., 2 figs., Jan. Considerable on food; review of previous writings.

BRUCE, JAY.

1925. The problem of mountain lion control in California. California Fish and Game, vol. 2, no. 1, pp. 1-17, figs. 1-5, Jan. Each mountain-lion costs the State $1,000 a year in deer meat, or about $15,000 to maintain the animal during its natural existence.

CRIDDLE, NORMAN.

1917. Varying hares of the prairie provinces. Agr. Gaz. Canada, vol. 4, no. 4, p. 262, Apr. Goshawk, golden and bald eagles, and great horned owls serious enemies.

DIXON, JOSEPH.

1925. Food predilections of predatory and fur-bearing mammals. Journ. Mamm., vol. 6, no. 1, pp. 34-46, pl. 4, Feb. Wild cat: Mammals, birds, fish; coyote: Game, stock, rodents, insects, mammals, birds; mountain-lion: Deer, stock, small wild mammals; skunks: Insects, rodents, birds, mammals.

DYCHE, L. L.

1903. Food habits of the common garden mole (*Scalops aquaticus machrinus* Rafinesque). Trans. Acad. Sci. Kansas 1901-1902, pp. 183-186. Report on the stomach contents of 50 specimens.

FORBUSH, E. H.

1916. The domestic cat. Bird killer, mouser, and destroyer of wild life. Means of utilizing and controlling it. Econ. Biol. Bull. 2, Massachusetts State Board Agr., 112 pp., 20 pls., figs. The most comprehensive review of the subject; cats kill millions of birds annually; destructive also to moles, shrews, toads, field mice, wood mice, insects.

GARMAN, H.

1895. The food of the common mole. 7th Ann. Rep. Kentucky Agr. Exp. Sta. 1894, pp. xli-xlv. Notes on contents of 14 stomachs.

HAMILTON, W. J., JR.

1930. The food of the Soricidae. Journ. Mamm., vol. 11, no. 1, pp. 26-39, Feb. Over 300 stomachs representing four species; food is insects, annelids, Crustacea, snails, mice, salamanders, arachnids, centipeds, and millipeds. Bibliography.

JOHANSEN, FRITS.

1910. Observations on seals (Pinnipedia) and whales (Cetaceae) made on the "Danmark Expedition" 1906-1908. Danmark Eksp. Grönl. Nordöstkyst, 1906-1908, vol. 5, no. 2, pp. 203-224, 9 figs. Includes some notes on food.

JOHNSON, CHAS. E.

1925. The muskrat in New York; its natural history and economics. Roosevelt Wild Life Bull., vol. 3, no. 2, pp. 205-320, pl. 5, figs. 48-87, Mar. Animal food includes bivalves, snails, crayfish, insects, fishes, turtles, and birds; enemies include minks, foxes, weasels, otters, hawks, and owls.

LANTZ, D. E.

1905. Kansas mammals in their relations to agriculture. Bull. 129, Kansas Agr. Exp. Sta., Dec., 1904, pp. 331-404, 1 pl., 1 fig. Notes on the food habits of most of the groups.

1906. Meadow mice in relation to agriculture and horticulture. U. S. Dep. Agr. Yearbook 1905, pp. 363-376, pls. 38-41, fig. 89. Natural enemies (pp. 370-373) include wolves, lynxes, foxes, badgers, raccoons, opossums, skunks, minks, weasels, shrews, hawks, owls, crows, shrikes, cranes, herons, bitterns, snakes, and domestic cats and dogs.

1918. The house rat the most destructive animal in the world. U. S. Dep. Agr. Yearbook 1917, pp. 235-251, pls. 41-44. Natural enemies (pp. 248-249) include domestic dog, cat, and ferret, as well as snakes, storks, herons, owls, hawks, skunks, weasels.

1923. Economic value of North American skunks. Farmers' Bull. 587, U. S. Dep. Agr., 24 pp., 10 figs. Food (pp. 9-14), poultry, game, mice, and armyworms, tobacco worms, whitegrubs, hop grubs, grasshoppers, potato beetles and other insects.

L.[ucas], F. A.

1905. The Newfoundland whale fisheries. Science, n. s., vol. 21, p. 713, May 5. Large whales feed almost exclusively on *Euphausia;* finbacks upon caplin.

Piper, S. E.

1909. Mouse plagues, their control and prevention. U. S. Dep. Agr. Yearbook 1908, pp. 301-310, pls. 21-25. During a plague near Humboldt Lake, Nevada, 2,000 predatory birds and 1,000 mammals put in their appearance and together consumed about 1,350,000 mice per month.

1928. The mouse infestation of Buena Vista Lake Basin, Kern County, California, September, 1926, to February, 1927. Monthly Bull. California Dep. Agr., vol. 17, no. 10, pp. 538-560, figs. 91-102, Oct. Ring-billed gulls, short-eared owls, barn owls, various hawks, ravens, great blue herons, road-runners, shrikes, coyotes, skunks, and house cats noted as predators (pp. 550-552).

Rainbow, W. J.

1913. Food, medicines, and charms of savage man. Abstract in Rep. Trustees Australian Mus. 1913, p. 9. Humans feeding on spiders, beetle larvae, caterpillars, grasshoppers, ants, bees, wasps, termites, and scorpions.

Scheffer, Theo. H.

1910. The common mole. Bull. 168, Kansas Agr. Exp. Sta., 36 pp., figs. Natural enemies (pp. 20-21) include hawks, owls, coyotes, domestic dogs. On the whole has few foes.

1927. American moles as agricultural pests and as fur producers. Farmers' Bull. 1247, U. S. Dep. Agr., 20 pp., 18 figs. Animal food (pp. 7-8), earthworms, beetles and their larvae, spiders, centipeds, ants, caterpillars.

West, James A.

1910. A study of the food of moles in Illinois. Bull. Illinois State Lab. Nat. Hist., vol. 9, pp. 14-22, Oct. Details of contents of 56 stomachs; references to previous literature.

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MODERN SQUARE GROUNDS OF THE CREEK INDIANS

(WITH FIVE PLATES)

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MODERN SQUARE GROUNDS OF THE CREEK INDIANS

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(With Five Plates)

The writer has already published descriptions of many of the square grounds of the Creek Indians, the sacred areas where their busks and other annual ceremonies took place.[1] In collecting this material, however, my endeavor was to learn the most ancient arrangement of the several grounds and the arrangement of those grounds no longer in use. During the summer of 1929 I visited the Creek country again to secure information regarding the organization of the extant grounds. This work duplicates and supplements the earlier to a considerable extent, but the main purpose was somewhat different.

Besides the three Yuchi grounds, now in the vicinity of Kellyville, Bixby, and Depew, respectively, with which I did not concern myself, there are, or were in 1929, 17 square grounds, as follows: Abihka and Otciapofa near Henryetta; Nuyaka north of Okemah; Łáłogálga[2] or Fish Pond and Åsilanabi west of Okemah; two Tulsa grounds near Holdenville; Tukabahchee at Yeager; Łapłáko near Wetumka; Alabama east of Alabama Station on the Frisco Railroad; Eufaula west of Eufaula; Kasihta east of Okmulgee; and Hilibi, Kealedji, Okchai, Pakan Tallahassee, and Wiogufki about Hanna. Abihka, Otciapofa, Nuyaka, Łáłogálga, Kasihta, Hilibi, Pakan Tallahassee, and Wiogufki were visited, and new information obtained regarding all of the others except Eufaula, of which I secured very good descriptions 17 years before. The Eufaula ground, that of Åsilanabi, one of the Tulsa grounds, Tukabahchee, Alabama, and Okchai were visited in the winter of 1911-1912. Kasihta is the only square ground representing the Lower Creeks now maintained. It was not in existence during my earlier work in the Creek Nation, nor were Łapłáko or Kealedji.[3] These two last and the Yuchi grounds are the only ones that I have not seen. I was present at part of the busks at Otciapofa, Nuyaka, and Pakan Tallahassee. Not much attention was devoted

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[1] 42d Ann. Rep., Bur. Amer. Ethnol., 1924-25, pp. 204-296, 1928.

[2] In the present paper, á indicates the obscure a in such a word as ability, and ł or Ł is a surd l approximating thl in English.

[3] But see p. 35 regarding the former.

to the Seminole grounds, but information was obtained regarding one of these, Ochesee Seminole, which had been discontinued in 1912, when I visited the Seminole squares, but was afterwards revived.

In order to make the material obtained in 1929 intelligible, it will be necessary to give a brief outline of the Creek political, social, and ceremonial organization.

The name Creek is a shortened form of Ochesee Creek Indians, a name which English traders from South Carolina came to apply to that part of the Indians of the Creek Confederation who were living upon Ocmulgee River in the closing decades of the seventeenth century and the opening years of the eighteenth. The word Ochesee signifies "people of a different speech" in the language of the Hitchiti, one of the minor constituents of the Creek Confederacy, being equivalent to the word Tciloki in the Creek or Muskogee language. It was applied to the Creeks proper or Muskogee by the Hitchiti along with many other tribes, but came in some way to be particularly associated with the Muskogee and the river upon which they were then living.

Anciently there seems not to have been a single term applicable to all of the Muskogee, the latter name having been unknown to the Spaniards who first entered this section. It does not make its appearance until the English had settled in the Carolinas. The origin of the word is uncertain, but there are indications that it was derived from Shawnee, since a band of Shawnee lived for a time near what is now Augusta, Ga., and from a very early period occupied an intermediate position between South Carolina and Georgia on the one hand and the Creek Nation on the other. It is probable that there were originally several tribes speaking the same language but having separate names and that the necessity for a distinguishing term for all did not present itself until the number of non-Muskogee tribes in the Confederation came to be considerable. As to the names of these Muskogee tribes, we seem to have indications of the following: Abihka, Coosa, Okchai, Pakana, Tukabahchee, Hilibi, Eufaula, Kasihta and Coweta (or perhaps an original tribe of which the Kasihta and Coweta were sections). There were some other groups on the lower course of Tallapoosa River, such as the Atasi, Kealedji, and Kolomi, which cannot be definitely placed and may have been independent of these or early subdivisions of them. Of course some may represent people of wholly different connections who had become assimilated to the Muskogee and had lost their own language and customs. This is rendered probable from the fact that we have several actual cases of such assimilation in later times. However, so far as the tribes enumerated are concerned, this must always remain in doubt.

When the tribes of the Confederation first became known to white people, they were distributed geographically into two main sections to which the names Upper Creeks and Lower Creeks have become attached. The former were on the Coosa and Tallapoosa rivers and the upper course of Alabama River in the present state of Alabama, the latter on the lower and middle courses of the Chattahoochee, which now forms part of the boundary between Alabama and Georgia. It was this latter division principally which lived upon Ocmulgee River for a time and thus gave rise accidentally to the popular English name for the entire people. A minor division also existed between those Creeks living on the middle course of Coosa River and those centering about the lower Tallapoosa, the two being sometimes designated as Upper and Middle Creeks, respectively. In the distribution of the original Muskogee tribes, the Abihka and Coosa constituted the greater part of the Upper Creeks, while the Kasihta and Coweta were the dominating element among the Lower Creeks. The Okchai, Pakana, Tukabahchee, Atasi, Kealedji, Łiwahali, Łapłäko, Kolomi, and a number of towns descended from the Coosa, including Otciapofa, the Tulsa towns, and the Okfuskee towns, besides several minor groups, formed the bulk of the Middle Creeks. The Eufaula had the distinction of being connected with all three. Their oldest seat seems to have been in the Upper Creek country; later they established themselves among the Middle Creeks and about the period of first white contact they formed a colony well down Chattahoochee River, among the Lower Creeks. To complete the story of their migrant habits, we may add that they seem to have furnished the first true Muskogee contingent to the Florida Seminole in the Red House or Tcuko Tcati Indians north of Tampa Bay.

Tradition seems to be borne out by circumstantial evidence in pointing to the Lower Creek country as that region in which the tribes in question began their federation. According to the story this had to do on the one hand with the division of the Muskogee into the Kasihta and Coweta and on the other with the relations between them and the non-Muskogee elements, particularly the Apalachicola. The relations of the Kasihta and Coweta to each other are somewhat uncertain, for while it is at times implied that they resulted from the fission of a single body of people, the most popular traditions speak of them as having come from the west as two distinct tribes and it is possible that the one-tribe idea may be the result of later rationalizing. The story goes that, having defeated all of their enemies, the Kasihta and Coweta instituted periodical ball games as a kind of "moral equivalent for war," and afterwards, when either of them established relations of friendship with other Indians, whether Muskogee or not, these Indians entered on the same side as their friends so that this dual system soon became general.

One of these sides, that of Kasihta, came to be known as the White or Peace side, though it did not receive that specific name; while the side of Coweta was the Red or War side.

At the same early period the Muskogee entered into intimate relations with the Apalachicola Indians, who spoke a dialect related to Hitchiti. This was the outgrowth of a treaty of peace following upon hostilities, or to avert threatened hostilities. The Apalachicola were then taken into the Confederation on the same side as Kasihta. In some particulars, however, they are held to have been more representative of the White towns than Kasihta and for that reason their settlement came to be called Tȧlwa Łȧko, " Big Town." Indeed, the migration legend related to Oglethorpe by Tchikilli implies that Kasihta was at least partly Red, their hearts being " red on one side and white on the other." However, in all later times Kasihta assumes the leadership of the White towns among the Lower Creeks, as does Coweta the leadership of the Red towns. Four having been the sacred number—the sacred formulae being gone through four times, four arbors or beds constituting the ceremonial buildings in the square ground and four sticks the number employed in the ceremonial fires—it is not surprising that the Creeks should select two towns from the Upper Creeks, taken collectively, to add to these two leading Lower Creek towns. The White towns of the Upper Creeks were represented by Abihka, the Red towns by Tukabahchee, the second being from that group I have called Middle Creeks, the other from the northernmost bounds of the Nation. These four towns were the " back sticks " of the Confederation, and each had a special ceremonial name, viz., Kasihta Łȧko (" Big Kasihta "), Coweta Mahmayi (" Tall Coweta "), Tukabahchee Ispokogi, and Abihka Nȧgi. Ispokogi was the name of the culture heroes of the Tukabahchee and it may be a Shawnee term. It bears a suspicious resemblance to that of the Kispokotha band of Shawnee. I do not know the meaning of Nȧgi. The Abihka were also called specifically " the door-shutters " because they protected the northern frontier of the Confederation.

In course of time the non-Muskogee element represented by the Apalachicola Indians was increased, first by other groups related to the last mentioned—such as the Hitchiti, Okmulgee, Sawokli, and Tamałi—who spoke closely related languages and called themselves Atcik-hata, a term said to have some reference to the ashes of the ceremonial fire in the square grounds. These Indians formed the greater part of the first Creek invaders of Florida who presently constituted the Seminole nation. The leading town in this southward movement was Oconee, almost certainly affiliated with the Atcik-hata, and the titular leadership among the Seminole remained with them until after the Seminole War. However, the complexion of the Seminole as a whole was changed from Atcik-hata or Hitchiti, to Muskogee by the multitudes of refugees which fled to Florida after the Creek War of 1813-14. The later removal to Oklahoma seems to have reversed the situation since more than two-thirds of the Indians now in Florida speak a language of the Hitchiti group.

There is strong evidence that the Chiaha Indians originally spoke Hitchiti and that the Mikasuki of Florida branched off from them, but some early event in their history separated them from the other Atcik-hata and made them allies of the Coweta. This friendship they shared with the Osotci who seem originally to have belonged to the Timucua linguistic group of Florida. To the Upper Creeks were added the distinct but dialectically related Alabama, Koasati, and Tuskegee, while bands of Yamasi and Apalachee were temporarily connected with both Upper and Lower Creeks. The Alabama town of Tawasa seems to have had an origin similar to that of the Osotci. At a very late date the wholly alien Yuchi population was admitted into the Confederation, most of them making their home among the Lower Creeks though there was a small body also among the Upper Creeks. And more divergent still were the Shawnee, from among whom two towns made their homes in Creek territory for several decades during the eighteenth century. One of these probably continued on into the early years of the nineteenth century.

It may be added that towns are known to have changed from one side to the other. Alabama was once a White town closely associated with the Okchai, but later they were affiliated with the Tukabahchee and came to be reckoned as Red. Wiogufki, Hilibi, and Wiwohka are also said to have shifted from one side to the other. In the case of the two last this may be partially explained by the fact that, if we may trust native tradition, they were built up of refugees from other settlements.

In former times a certain aloofness was maintained by the towns of one moiety toward those of the other. They did not encourage intermarriage and did not attend each other's annual ceremonies. This latter inhibition is now breaking down and it is claimed that men of all towns attend the busk of Otciapofa. Otciapofa, however, has long occupied an exceptional position. A chief belonging to the Bird clan of this town always delivered the principal speech when a new chief of the Confederation was installed. This town was also the residence of the Creek dictator Alexander McGillivray, and it was here that Crazy Snake, leader of the Creek conservatives, called his important councils. Evidently the functions of the White and Red sides in maintaining peace or bringing on hostilities were formerly of great importance and some White towns, certainly Apalachicola and Coosa, were places of refuge for murderers. The "regular" ball games, as distinguished from practice games, always took place between towns of different sides and the supporters of each town marched to the encounter in much the same spirit as if they were going to war.

The principal White towns were: Kasihta, Ȧpalachicola, Hitchiti, Okmulgee, Sawokli, Yuchi, Abihka, Coosa, Otciapofa, Tulsa, Okfuskee, Okchai (including Łȧłogȧlga and Ȧsilanabi), Pakana, Koasati, Tuskegee, and Wiogufki.

The principal Red towns were: Coweta (including Łikatcka), Eufaula, Chiaha, Osochi, Tukabahchee, Łiwahali, Łapłȧko, Atasi, Kealedji, and Hilibi. Alabama changed from White to Red in the manner described.

The people of each town were subdivided into clans which were usually named after animals and were invariably perpetuated in the female line. The only clan of importance not named for an animal was the Wind clan and with this the Skunk was closely associated, the Skunk clan having always been linked with it. I obtained the names of over 50 clans but some of these were known to only one or two informants, and a number of others were small and bound into phratral associations with clans of greater prominence. Some clans were considered as equivalents throughout the entire nation. The Skunk, Fish, Rabbit, Otter, and Turtle seem always to have been united in one phratry with the Wind; the Wolf and Salt with the Bear; the Pahosa with the Deer; the Wildcat with the Panther; and the Turkey and Tȧmi with the Alligator. In the same way the Snake, Kapitca, and Woksi were almost invariably counted in with the Aktayatci; the Mole, Toad, and Tcikote always went together and were generally allied with the Deer and Pahosa; and the

Łidjàmi, Eagle, Hickory nut, Fox, Cane, and Muskrat[1] were usually placed with the Raccoon.

Some phratral associations, however, were confined to one or a few towns and did not extend throughout the nation. Thus the Potato was commonly placed in one phratry with the Raccoon but in Tukabahchee it was separated. The Beaver was usually placed with the Bird, but in Alabama it was quite distinct. On the other hand it was sometimes classed with the Alligator. Occasionally the Aktayatci formed one phratry with the Raccoon, and much more rarely the Deer and Panther were found together. Differences of this kind were due in some measure to the council system. Every important clan in a given town, or every group of related clans, held meetings during the annual ceremony known as the busk and each listened to an address by its oldest capable male member or "uncle." If an individual came to live in a town in which his own clan or his phratral group was not represented, he would elect to affiliate with one of those already in existence. It was usual for all of the children of each group of this kind to consider themselves brothers and sisters between whom marriage was ordinarily prohibited. However, the information I received shows plainly that sexual intimacy between individuals of linked clans was not considered as serious as between members of the same clan. It is specifically stated regarding some of these clans that "they were kin" up to noon, or up to midnight, and separate the rest of the time, *i. e.*, a limited taboo was maintained against them. It is also said that a man would sometimes pretend that a woman whom he wished to marry was of a certain clan, for which he would manufacture a name, although she was in fact of his own, and that, if he were a man of influence, he often "put over" this new creation of his. On the other hand, I have been told that, even though children of certain of the primary clans were brought up together, they would never be regarded as brothers and sisters. It is quite plain that all sorts of variations had grown up in response to unpredictable situations.

When one eliminates the obscure and the constantly linked clans, about nine are left of something like major importance. These are the Wind, Bear, Bird, Beaver, Alligator, Raccoon, Aktayatci, Deer, and Panther. We should perhaps add the Potato. The Beaver, however, has importance mainly in one group of towns, and the Aktayatci appear to have been rather closely associated with the Hitchiti and the Seminole, but also with Hilibi, Wiogufki, and Eufaula.

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[1] In the 42d Ann. Rep., Bur. Amer. Ethnol. (p. 116) I erroneously called this the Mink.

The question naturally arises whether some of these clans may not have been brought in with formerly independent tribes. All we can say is that certain clans are more prominent in some of these tribes than among the true Muskogee but whether they were brought in by them we do not know. Thus, as just mentioned, the Aktayatci was particularly prominent among the Hitchiti, as were the Snake, Kapitca and Woksi, and in a more pronounced manner the Toad, Mole, and Tcikote. The Daddy-long-legs and Salt were similarly associated with the Alabama, the former, indeed, being hardly known outside of that tribe.

Besides this division into phratral groups all of the clans were ranged in two moieties called respectively, Hathagàlgi, "White People," and Tcilokogàlgi, "People of a different speech." The Wind and Bear with their phratral associates were almost invariably White, and the Raccoon and Aktayatci and their allies almost invariably Tciloki. The Bird is usually White but among the Alabama and Koasati it is Tciloki. The Beaver is also White usually, but when it is associated with the Alligator and when the Alligator is not a White clan, the Beaver often becomes Tciloki. The Alligator is most often Tciloki but in a number of towns it is White. The Deer is usually Tciloki but it is White in a few towns. Today the Panther is almost always Tciloki but some of the oldest myths and some of my best informants assert that it was anciently White.

When I first went among the Creeks, I was told that in one or two towns the clan moieties were exogamous, but the greater number of my informants held the contrary opinion. I was much surprised, therefore, during my last visit to have most of my informants maintain that they were exogamous. This much is certain, that there were striking exceptions to this law in comparatively early times, for instance, in the case of the famous Creek speaker Hobohīł Yàhola. Probably it will never be possible to say whether this phratral exogamy was breaking down or growing in times known to us. In recent years the principal function performed by these moieties has been to determine the line-up of the players in practice games within the town. The important bearing the mere character of a name may have in social evolution is shown by the fact that, on account of the name, persons of European blood were usually reckoned as "friends" of the Hathagas, and in consequence the latter acquired a reputation as "progressives," while the Tcilokis were considered, and acted like, "conservatives."

Besides the clans, phratries, and moieties there were certain groups in each town which had official functions. Some of these were determined by the individual ability—usually military—of those who belonged to them. Thus a man might start his public career as a common warrior or tásikaia, a word now often translated "citizen," be promoted to the position of an imała lábotski, or "Little Imała," then to that of an imała łáko, or "Big Imała," and finally become a tástanági, or "war leader." If sufficiently prominent he might be made a tástánági łáko or hołibonaia, "war speaker," though of these there was never more than one in a town at any one time. There were "beds" or seats in the square grounds for each of these classes, but not all were promoted into them. Men who belonged to the clan of the chief (miko) would be given seats in his section and form the mikálgi, "chiefs," who acted as a kind of special executive council. If they belonged to a certain clan known as henīhálgi, they would be given seats in another place. The functions of the henīhálgi are somewhat uncertain but they were concerned largely with the maintenance of peace and charged themselves with the internal prosperity of the tribe. The henīhálgi were almost always formed of the Wind clan, and if, for any reason, the Wind clan could not be used, the Bird or Beaver, or at least some clan considered White, would take their place. There was also a class of men called istatcagagi, the old, experienced men from all tribes, retired from active service but keepers of the tribal lore. It seems fairly evident that a correlation existed anciently between White towns, White clans, and the henīhálgi, and that the miko of a White town was generally chosen from a White clan. It is even possible that the miko of a Red town was formerly chosen from a White clan. Certainly there is a marked tendency to choose chiefs from the Bear clan, even in Red towns, though many of them are also from the Raccoon and the Aktayatci.

A word must now be said regarding the ceremonial grounds. Originally every Creek town had such a ground which at a still earlier period was probably the ceremonial ground of a small tribe. As a tribe increased in numbers, however, the ground often became too small to accommodate all of its members comfortably and so it split into two or more. Undoubtedly, before the organization of the Creek Confederation, there was great diversity among these grounds and a certain element of diversity has persisted until the present day, but on the other hand considerable standardization has undoubtedly taken place. Creek legend asserts that the first ceremonial ground was given to the Coweta, the Kasihta, or the Tukabahchee by the Breath Controller or by other supernatural beings, and copied by the remaining towns from them. While this represents a modern rationalization, there can be no doubt that the earlier ceremonial grounds of the constituent members were altered in many particulars in conformity with the prevailing pattern.

All the grounds known to us originally consisted of three elements, a tcokofa or community hot house used in bad weather or for secret ceremonies, a " square ground," and a " chunkey yard," or ball ground. The name " chunkey yard " is derived from an old pastime which consisted in rolling a stone disk along a level plot of land and throwing certain long poles after it, the game turning on the relative nearness of the poles to the roller after all had come to rest. There was a single pole in the middle of this yard surmounted by a cow or horse skull or by a wooden figure, and about this men and women played against each other in a kind of ball game. This game was mainly confined to people of the town and was social in character while the great ball game, similar to our game of lacrosse, was played by men only and was highly ceremonial. The fact that the " chunkey yard " was a part of the ceremonial ground may indicate that the single pole game formerly had more religious significance than was the case in later times.

The tcokofa has long been out of use, though at Tukabahchee fire was until recently lighted in the middle of a circular offset of the ceremonial ground where this structure would stand if it were still in existence, and one such building was put up at Pakan Tallahassee after the Civil War.

The most important part of the ceremonial area today is the " square ground," so called because in the largest towns there were on it four long cabins or arbors, in native parlance " beds," forming four sides of a square. Partly from tribal idiosyncrasy and still more on account of failing numbers, several of these grounds now lack one cabin, and the Alabama ground lacks two. Today the cabins consist merely of two or three rows of split logs to serve as seats and an arbor of boughs to shield their occupants from the direct rays of the sun, but anciently the seats consisted of mats woven out of cane raised upon short posts and the cabins were provided with a back and roof of wattle or split shingles plastered with clay. The arbors in the largest modern towns are supported on eight posts, four in front and four behind, but some have only six, and most of the Seminole towns only four. On the other hand, a sketch of one of these cabins made by a Frenchman early in the eighteenth century shows ten posts, five in front and five at the back. Today, however, the eight post arrangement seems to be considered orthodox, and the three sections marked off by these posts are used for the seating of as many clans, groups of clans or related officials.

Considerable variation in the ancient and intended plan has been brought about by the attrition which the tribe and its several divisions have undergone, loss of the keepers of the sacred lore, and other factors, but it is plain that normally one of the four cabins was mainly devoted to the miko and his clan. Hence it was called mikålgi (or mikâgi) intupa, the " Chiefs' bed." Another was devoted mainly to the henīhålgi and was named from them, another to the higher class of warriors, the tåstånågålgi, and so received their name, and still another to the novitiate warriors or youths from whom it was called tåsikaiålgi intupa or tcibånågålgi intupa. The positions of these in the square ground varies considerably. It should be stated in the first place that the cabins are placed normally toward the four points of the compass, but that for some unexplained reason in the square of Tukabahchee the entrances are toward the cardinal points. In the old Kasihta square, which seems to have set the fashion for many other towns, the mikos' cabin lay west, the henihas' south, the tåstånågis' north, and the tåsikaias' east. In the Okfuskee towns, of which Nuyaka is an example, the mikos' cabin lay north, the henihas' east, the tåstånågis' west, and the tåsikaias' south. In Pakan Tallahassee the mikos' cabin is north, the henihas' south, the tåstånågis' west, and there is no east cabin. In Eufaula the mikos' cabin is north, the henihas' east and the tåstånågis' south, the west cabin being missing. In Alabama, where there are but two cabins, the mikos' cabin is east.

The other variations in the arrangement of the squares will come out in the subjoined material, but before presenting it something must be said regarding town officials.

The miko, as already stated, was chief of the town, its head presiding officer and responsible executive. Like many of the other officers he had a special companion or henīha taken from the Wind clan or whatever clan occupied the position of henīhålgi. This henīha is sometimes called miko apokta, " second chief," but the latter name is also given to still another functionary who shares the burdens of state with his superior. The chief had one or more yatikas or interpreters who also bore the name asimbonaia, " speakers." Unless wanted to make an announcement or to send upon an errand, they sat with their clan or other group to which they normally belonged. The tåstånågi łåko and hołibonaia have been mentioned. The position of hołibonaia, " war speaker " was the most exalted military position, and it is possible that there was only one such official at a time in the entire Creek Nation. It was the position occupied by Hobohīł Yȧhola, famous leader of the Creeks during their removal west and all of their subsequent troubled history until the Civil War. He was not a miko even of one town, but his influence was actually greater than that of any miko, or any number of them. There were two ta'pala, whose chief function was to act as messengers before and during the women's dance, and there were two singers for the women (inyahaikȧlgi, " singers for them "), who sat at the end of one of the cabins just in front of the spot where the women began dancing. They were usually selected for their knowledge of songs rather than on account of their clan affiliations. The hilis haya was the head priestly functionary. He supervised the preparation of the medicines and gave them their final potency and he ordered everything in any way touching upon the supernatural. He was assisted by one or more men called hilis tcȧlaba or " medicine mixers," whose functions are defined by the name, and by two or more young men called hilis hoboia, " medicine gatherers," who collected the red root, pasa, and other plants that went into the sacred medicine. Some towns seem to have had a separate official called tutka dīdja, " fire builder," to start the fire, but in others the hilis haya did that, and there was instead a tutka oktidīdja, " gatherer of wood " for the fire. A number of boys known as oidjawȧlgi brought water for the medicines. In one town we learn of ahaga haiyȧlgi, " law makers," who are said to carry out the instructions of the tȧstȧnȧgis and may be identical with the imałas elsewhere mentioned. There were also officers called simiabaia, or " leaders." The hoktȧgi immiko, " chief of the women," and his henīha, may have been identical with the ta'palas. Anciently the tȧstȧnȧgis and their assistants acted as town police, but nowadays three or four light horsemen are selected at random to police the square ground during ceremonies, and there are boys called " dog whippers " with long whips stationed at each opening into the square during the women's dance to drive away dogs. Many of these officers were chosen for four years only. If one died before the expiration of his term, a substitute was selected from the same clan, which seems to indicate that the position was something of a clan prerogative.

Of the ceremonies which took place on these grounds, only two have survived. One, called by the popular local name of " stomp dance," was confined to the people of the town and was simple in character, the miko hoyanīdja (red willow) being ordinarily the only medicine used during it. There were no dances other than the common and relatively secular ones, no ceremonial lighting of the fires, no ceremonial complications of any sort. It seems to have been usual to hold three of these dances in the spring and early summer, a month apart, the series paving the way for, and leading up to, the second ceremonial, the "busk," which was the great annual ritual. This last is usually considered as lasting four days, though in that four are included the days of assembling and departure. The principal event on the second day is the women's dance. On the third day the men fast, take medicine four times, and near its close march down to the creek and bathe. After they return, they are dismissed to their camps and break their fast. Later they are summoned to the square again where they dance four times, and then the dance becomes "common," visitors from friendly towns being admitted to it. A fire is kept up all night in the center of the square and dancing continues about it until it is nearly day. In former times many, perhaps all, of the towns extended their busks over eight days, but from what can be learned of these longer ceremonials they seem to have been in the main a simple doubling of the shorter ceremony, except for a few features like the kindling of the new fire which took place but once annually.

Let us now turn to the new material regarding the square grounds and the ceremonies conducted there. Under each heading I give the notes obtained from native informants belonging to the square or town in question.

ABIHKA

Figure 1 gives the general arrangement of the square of Abihka, or Talladega, and Plate 1, Figure 1, gives a view of the ground itself near Henryetta, Okla., as it appeared in 1912. The exposure was made from the southwest.

The medicines were taken first by those in the Bears' bed, then in succession by those in the beds of the Raccoon on the west side, the Raccoon on the east side, the Deer, and those in the south bed. The asimbonaia in the northern section of the east cabin acted more particularly as the chief's messenger; the one in the western compartment of the south cabin called first the women and then the children to come to take their medicine from the vessel at the north end of the east cabin. The ta'palas were changed every four years. The women gathered preparatory to their dance at a tree on the edge of the tádjo (the ridge of sweepings that makes the edge of the ceremonial ground) and entered the section about the fire at its northwestern corner. Five pots of medicine were prepared at the north end of the west cabin (fig. 1, 11). Afterward one pot was placed a little farther north and west for the boys (12) and another was carried around to the north end of the east cabin for the women and children (13). The ingredients of this medicine were miko hoyanīdja ("red root"), pasa ("buttonsnake-root"), wīlana ("wormseed"), and hobȧga ("maypop"); tcato hȧtki ("white stones") were added. After the ceremony was about over and the fasters were ready to go down to bathe in the creek, what was left

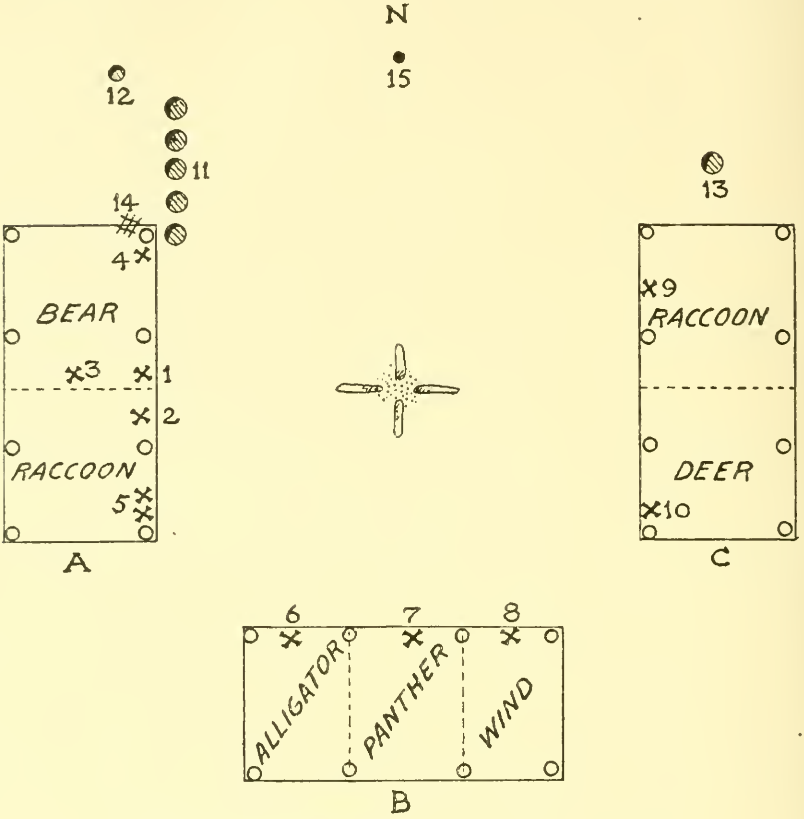


FIG. 1.—General arrangement of the square of Abihka.

A. Chiefs' Bed (mikȧlgi or mikȧgi intupa); 1, miko (Bear); 2, henīha (Raccoon); 3, hilis haya (Raccoon); 4, hilis tcȧlaba; 5, yȧhaikas (any clan).
B. Henihas' Bed (henihȧlgi intupa): 6, asimbonaia (Alligator); 7, ta'pala (Panther); 8, ta'pala (Wind).
C. Warriors' Bed (tȧstȧnȧgȧlgi intupa): 9, asimbonaia (Raccoon); 10, tutka dīdja (Deer).

11, medicine pots (1st position); 12, medicine pot for boys (2d position); 13, medicine pot for women (2d position); 14, place where medicines were piled immediately after they were brought in; 15, ball post (pokȧbi).
It is to be noted that, in all of these diagrams, the ball post was actually much farther from the center of the square than is indicated.

of the medicine was poured on the fire. It is said that one gallon of spring water was brought for all five pots. This must mean a gallon for each. Following are the busk names of the present officers:

miko	Tcûktcàt Henīha
henīha	Itchas Hadjo
hilis tcàlaba	Konip Yàhola
ta‘pala	Katca Tàstànàgi
“	Kona Yàhola
tutka dīdja	Tàstànàkutci
asimbonaia	Wotko Fiksiko
“	Kapitca Hadjo

The Hathagàlgi of this town are Wind and Bear; the Tcilokogàlgi are Panther, Raccoon, Deer, Beaver, Alligator, and Bird.

My information regarding this ground was obtained mainly from Jim Star who described the Talladega ground to me in 1912, the plan of which is in the Forty-second Annual Report of the Bureau of American Ethnology, page 205. The different aspect of the east cabin is mainly due to the fact that the earlier account gives a more ancient arrangement, when the warriors were graded into tàstànàgis, and big and little imałas. The position assigned to the hilis haya in the earlier plan is probably erroneous. The other differences are due mainly to the more extensive information obtained on my last trip. My new information disagrees with the older, however, in assigning the Bird, Beaver, and Alligator clans to the Tciloki side as was said to be the case at Abihka-in-the-West instead of to the White side as was given me for Talladega and the old Abihka town near Eufaula. It is probable that the new information is correct since the last mentioned square was given up when the man from whom I obtained data regarding it was a boy. However, it must be remembered that these allocations are not invariable and probably changed at times even within the same town.

OTCIAPOFA, OR HICKORY GROUND

Figure 2 shows the square ground of Otciapofa, popularly known as Hickory Ground.

The hilis tcàlaba was changed every four years and was not taken invariably from the same clan.

At the southernmost front post of the east cabin were fastened two poles with black feathers tied to the ends and at every other front post were three similar poles but with white feathers. These were carried by the men in the “feather dance.”

In the women's dance there is but one leader who carries a notched stick called atȧsa, the old name of the war club, from the middle of which depends an eagle feather.

Besides the invariable miko hoyanīdja or "red root," the busk medicine contained tutka hiliswa ("fire medicine"), wīlana ("wormseed"), tutka-tcok-hissi (a place on the ground where wood has been burned and moss has sprung up), and hobȧga ("maypop").

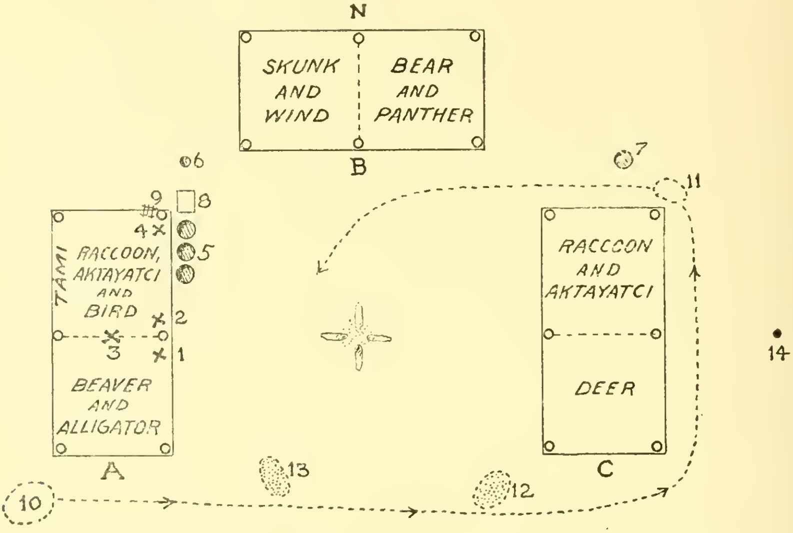


FIG. 2.—The square ground of Otciapofa, or Hickory Ground.

A. Chiefs' Bed: 1, miko (Beaver); 2, miko apokta (Beaver); 3, hilis haya (any clan; at present Wind); 4, hilis tcȧlaba (changed every 4 years; now Beaver).
B. Henihas' Bed.
C. Warriors' Bed.

5, medicine pots (1st position); 6, medicine pot for boys (2d position); 7, medicine pot for woman (2d position); 8, log on which medicines were laid and macerated with a small wooden pounder; 9, place where medicines were kept; 10, point where women gathered preparatory to their dance; 11, point where women made a final stop before entering to dance; 12, where the ashes from the central fire were deposited every year; 13, sweepings from the square ground (tȧdjo); 14, ball post.

As usual, the doctor perfected this medicine by blowing into it through a hollow reed. Two men took medicine at the same time, using gourd dippers. After all were through a dipperful was poured on the fire.

For a drum they use a stout jar and there are two coconut-shell rattles.

There is a line of tȧdjo (sweepings) around the four cabins but it does not include the ball post. In playing the single pole game a hit on the skull at the top counts five and a hit on the pole above a certain mark counts two when it is struck twice in succession.

The Hathagas consisted of the Beaver, Alligator, Bird, Bear, Skunk, Wind, and Rabbit; the Tcilokis of the Raccoon, Deer, Panther, and Aktayatci. The Rabbit, Wind, and Skunk formed one phratry.

The information regarding this ground which I obtained in 1912 was particularly incomplete. It is therefore gratifying to find that there are no serious discrepancies between the plan based on that (42d Ann. Rep., Bur. Amer. Ethnol., p. 211) and the present information. Some clans are given in one and omitted from the other, but where the same ones appear in both they have practically the same positions except for the Bear, which, according to the earlier description, sat in the west cabin and according to the later at the east end of the north cabin; and the Tȧmi, which the former places at the west end of the north cabin and the latter at the back of the northern section of the west cabin. The location of the miko, miko apokta or henīha, and hilis haya is probably more exact in the later plan which also adds many more details. The informants differed somewhat regarding the Hathagas and Tcilokis, the earlier authority placing the Beaver among the Tciloki and the Panther among the Whites, allocations exactly reversed by my later informant.

LITTLE TULSA

Next we come to one of the two divisions into which the Tulsa have recently split, this being known as Little Tulsa (fig. 3). Plate 1, Figure 2, shows the old Tulsa ground in 1911 from the southeast, before the fission had occurred.

It is said that all of the offices are filled from particular clans. The following is a list of the present officers; exclusive of the miko and his henīha:

tȧstȧnági lako	Ispani Tȧstȧnági
tȧstȧnági	Kapitca Tȧstȧnági
"	Lata Miko (controls the two above)
ahaga haiyȧlgi ("law makers")...... (messengers for the tȧstȧnágis)	Kapitca Tȧstȧnági (Aktayatci), and Tȧmi Tȧstȧnági (Tȧmi)
simiabaia	Kȧntcati Miko (busk name) or Nokos Hadjo (common name)
hilis haya	Miko Tcȧpko (Beaver)
hilis tcȧlaba	Tȧmi Yȧhola (Tȧmi)
tutka oktidīdja	Tȧmȧłȧkutci (Tȧmi)

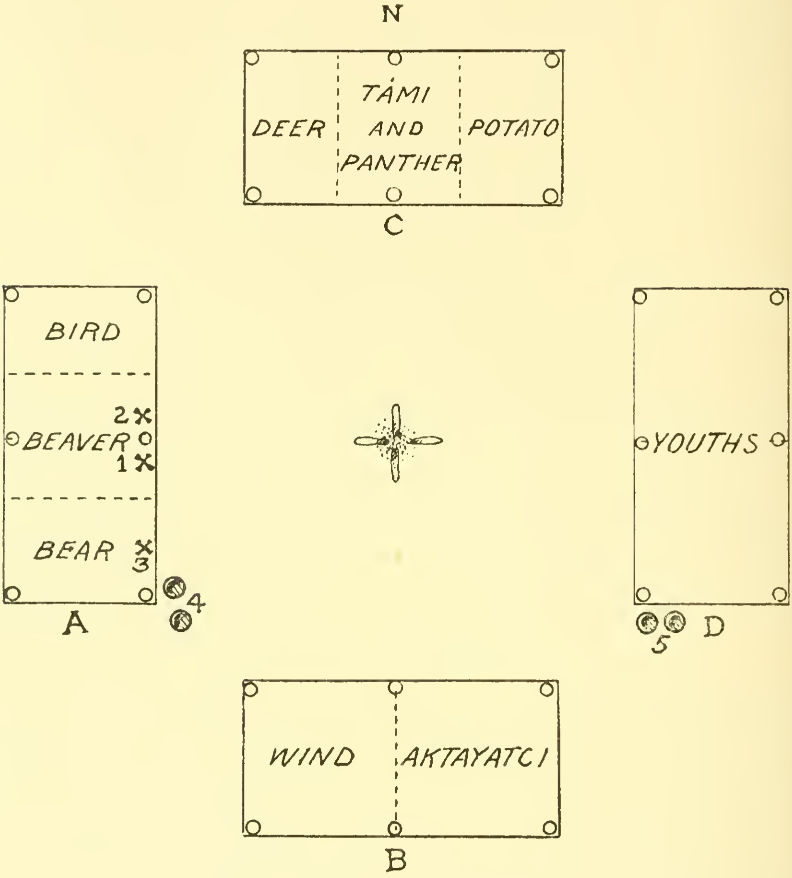


Fig. 3.—Little Tulsa square ground.

A. Chiefs' Bed: 1, miko; 2, henīha; 3, simiabaia.
B. Henihas' Bed.
C. Warriors' Bed.
D. Youths' Bed.

4, old location of medicine pots; 5, modern location of medicine pots.

ta'pala	Nokos Fiksiko (Bear)
"	Tâmi Hâtkutci (Tâmi)
yâhaikas	Kapitca Fiksiko (Aktayatci), and Pin Hadjo (Tâmi)
Captain of the Light Horsemen	Yâhola Tcâpko (Tâmi)
Light Horsemen	Oktcân Hadjo (Bear) Fûs Yâholutc (Beaver) Kapitcutci (Aktayatci)

The ta'palas functioned at the women's dance, the yâhaikas sang at the women's dance and at the feather dance.

My original Tulsa data, published in the Forty-second Annual Report of the Bureau of American Ethnology (p. 213), was obtained from an old man and was intended to reflect the most ancient arrangement he could remember. Since that time the Tulsa Indians who used to meet at the Little River ground have divided and maintain two distinct squares. The general agreement between the older and the later plan is therefore surprisingly close. The principal difference seems to be in the position given the Aktayatci who appear in the north bed in the earlier plan and in the south bed in the later one. The earlier plan may also be in error in the position given the medicine pots but this was subject to change from town to town and during the ceremony itself. The Eagle clan, which appears on the older plan, died out so long ago that it can barely be remembered by any living Creeks.

NUYAKA

The plan of this ground is given in Figure 4 and a view of it as it appeared some years ago in Plate 2, Figure 1.

The positions of hilis haya, hilis tcâlaba, and tutka dīdja were held for four years when the man and clan were changed so as to teach others the duties of these offices. The tâstânâgis and imałas had become confined to one or two clans. The hoktâgi immiko and his henīha controlled the women's dance and were called istatcagas. The term hola'ta was applied to a certain class at the square ground in some towns, sometimes to the Tcilokis, but its application here is not explained. The first ta'pala acted under the women's chief. He was taken from the Bear clan, or, failing that, from the following in order of preference: Wind, Raccoon, Tâmi.

In taking the medicines they drank of the miko hoyanīdja first and pasa second.

A rock was placed under the miko's seat " to make the seat heavy." Anciently there was a tcokofa northeast of the square. Nowadays the ground is hoed off only once a year.

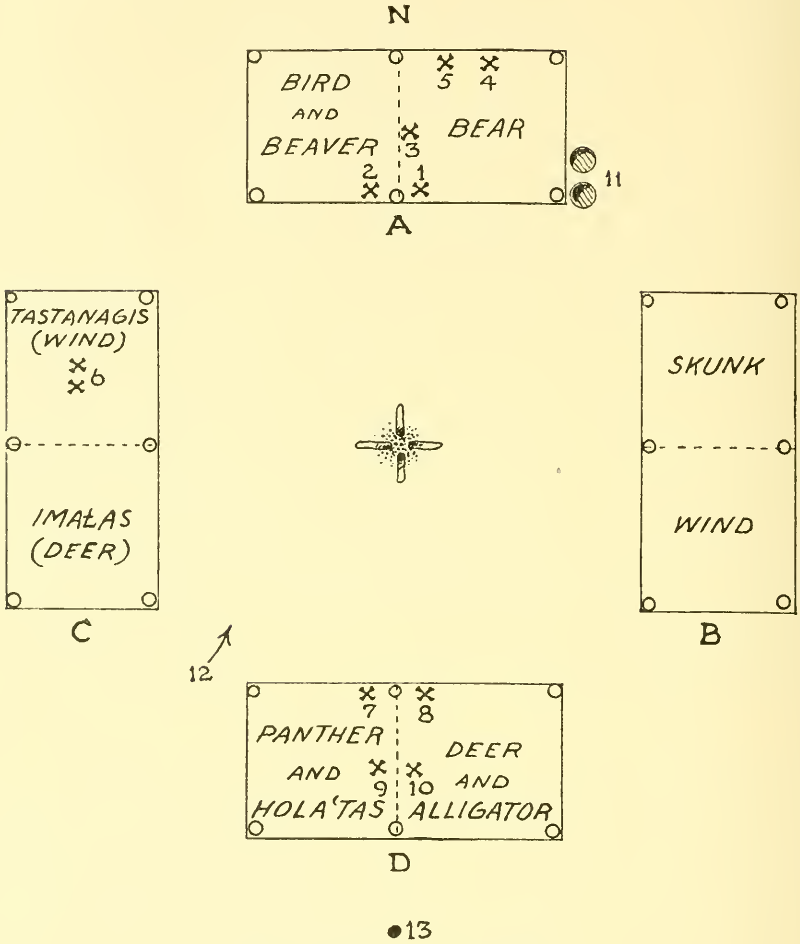


FIG. 4.—Nuyaka square ground.

A. Chiefs' Bed: 1, miko (Bear); 2, henīha (usually Wind; Deer in 1929); 3, hilis haya (changed every 4 years; Turkey in 1929); 4, hilis tcålaba (Alligator); 5, tutka dīdja (Raccoon).
B. Henihas' Bed.
C. Warriors' Bed; 6, two tåstånågis (or law makers).
D. Tciłokis' Bed (Tciłokogålgi intupa), or Tåsikaias' Bed (Tåsikaiålgi intupa): 7, hoktågi immiko (Aktayatci); 8, henīha for hoktågi immiko (Alligator); 9, 1st ta‘pala (Bear preferentially); 10, 2d ta‘pala (Alligator).

11, medicine pots; 12, point at which women enter; 13, ball post.

In this town the Turkey and Alligator clans belong in one phratry and so do the Wind and Skunk.

The present officers are as follows:

miko	Nokos Miko
henīha	Miko Tcàpko
hilis haya	Tástánákutci
tutka oktidīdja	Hotàlgi Hadjudji
hilis tcálaba	Lōdja Yàhola
hoktági immiko	Wotko Yàhola

When the present Nuyaka data are compared with that which I obtained in 1912 for Nuyaka and the related towns Okfuskee, Abihkutci, Talmutcási, and Tcatoksofa, the agreement is found to be close except in the cases of the two last where the square grounds had long been given up and were described by individuals from memories of their early years. The main correction is in locating the miko, henīha, and hilis haya and the difference here is not great.

PAKAN TALLAHASSEE

Figure 5 gives the plan and Plate 2, Figure 2, and Plate 3, Figure 1, views of the ground, one showing the three cabins, or arbors, and the other the chunk yard and ball post.

The tutka oktidīdja, hilis tcálaba, hilis haya, and oīdjawas, were appointed every four years from any clan. The ta'palas and hilis hoboia were appointed every four years from the same clan. The miko and asimbonaias held their positions for life.

Here we seem to meet some strange innovations. The Bears' section of the south cabin receives one name connected with war, tásikaiálgi intupa, and the section of the Birds, Beavers, and Alligators another, tástánágálgi intupa, while, at the same time, they are White or Hathaga clans and their cabin is called hathagálgi intupa. Yet one section of the west cabin is called tástánágálgi intupa also, and the whole cabin receives the unusual name of láksáfáskálgi intupa, "bed of the Blacks," the Blacks being evidently the clans elsewhere called tcilokogálgi.

The tcokofa was to the northwest and this was the last town to put up such a structure.

The Birds' section was called istatcagági intupa. The Deer and Pahosálgi were formerly called the imałágálgi.

Three poles with white feathers attached were fastened to each of the front posts for use in the feather dance.

Back of the tástánágis' section of the west cabin was a little structure in which to inclose the medicine pots when they were not in use.

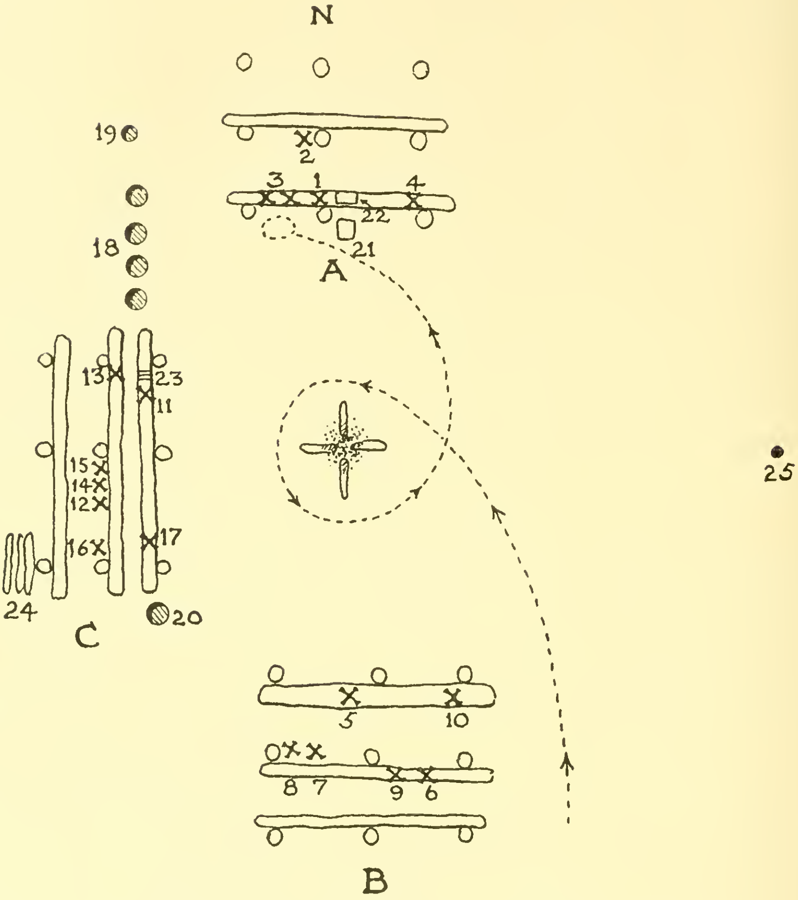


FIG. 5.—Square ground of Pakan Tallahassee.

A. Chiefs' Bed (mikàlgi intupa): 1, miko (Bear); 2, hilis haya (Panther in 1929); 3, yàhaikas (singers for women); 4, dog whipper.

B. Whites' Bed (hathagàlgi intupa): 5, asimbonaia (Bird); 6, ta'pala (Bear); 7, hilis hoboia (Bird); 8, oīdjawa (Bird); 9, oīdjawa (Bear); 10, dog whipper.

C. Blacks' Bed (laksâfâskàlgi intupa): 11, asimbonaia (Deer); 12, ta'pala (Bird; father Raccoon); 13, hilis tcàlaba (Deer in 1929); 14, tutka oktidīdja (Raccoon in 1929); 15, hilis hoboia (Raccoon in 1929); 16, oīdjawa (Panther in 1929); 17, dog whipper.

18, medicine pots (1st position); 19, medicine pot for boys (2d position); 20, medicine pot for women (2d position); 21, drum; 22, box for tobacco; 23, place where medicine was laid before being used; 24, woodpile; 25, ball post. The dotted line marks the course pursued by the women when they entered to dance.

In this town the Hathagas were the Bird, Alligator, Beaver, Bear, Tàmi, and Wind. The Tcilokis were the Deer, Raccoon, Panther, and perhaps Aktayatci. The two moieties were anciently exogamous.

The particular opponents of this town in regular ball games were the people of Atasi but they also played against Eufaula Hopai, Alabama, Hilibi, and Upper Eufaula. The Koasati Indians are said to have divided up in the ball games, some playing on each side.

The names of the present officers are:

miko	Nokos Miko ("Bear Miko") (Bird)
asimbonaia	Tâstânâk Imała (Deer)
"	Tâstânâk Hadjo (Bird)
hilis haya	Katcutci ("Little Panther") (Panther)
hilis tcàlaba	Nokos Hadjutci ("Little Bear Hadjo") (Deer)
oīdjawàlgi	1. Fus Yàholotci ("Little Bird Yahola") (Bird) 2. Hotàlgutci ("Little Wind") (Bear, father Wind) 3. Halàk Hopai ("Potato Hopai") (Panther, father Raccoon, Raccoon and Potato belonging to the same phratry)
hilis hoboia	1. Itco Ilutci ("Little Deer Foot") (Raccoon, father Deer) 2. Tàlsi Yàhola (Bird)
ta'pala	1. Halàk Yàholá ("Potato Yahola") (Bird, father Raccoon)
"	2. Hotàlgi Hadjutci ("Little Wind Hadjo") (Bear, father Wind)
tutka oktidīdja ...	Itco-ili Imała ("Deer Foot Imała") (Raccoon, father Deer)
yàhaikas	1. Pahos Fiksiko (Raccoon, father Deer with which the Pahosa is affiliated)
"	2. Miko Yàhola (Bear)

If one town wished to play a match game with another, said my Pakan Tallahassee informant, they sent a man to that town with a ball stick, and when the people of town number two had reached an agreement they sent the ball stick back. My informant said that he then had a ball stick hanging up in his house which had been sent by the Alabama.

In the women's dance, the atàsa held by the leading woman is red and has an eagle feather attached to it; that of the second is white and has a feather of the fus hàtki ("white bird"), a bird found down by the creeks, attached to it. They used from 12 to 14 terrapin rattles. During the women's dance the two ta'palas stand about where the two pots nearest the west bed are in the plan. Each carries a wand called sī'dik-kika having a white feather fastened to the end.

The dog whippers used in this dance are taken from any clan.

About 54 men were present at the last preceding busk and 25 women and girls participated in the dance.

At the top of the pokabi in this town was a horse skull. In scoring for this game they draw a line from the ball post to the nearest corner of the south cabin. When the skull is struck, 4 are scored; when the pole under the skull is struck, it counts 2 on the way out and 1 on the way back. They may count it as a game, however, by agreement when they reach the corner post. The women's tallies are marked on one side of the line, the men's on the other.

There is little difference except in detail between the above plan of Pakan Tallahassee and the several I recorded in 1912.

WIOGUFKI

The plan of Wiogufki is given in Figure 6 and a view of the ground from the southwest in Plate 3, Figure 2.

There is a little log house on the grounds in which the pots are stored when not in use to keep them from being broken. There never was a north cabin so far as my informant knew. On the upper end of the ball post is a cow skull.

The women walk four times around the fire; then their leaders stop opposite the singers and they begin to dance.

The hilis tcȧlaba holds office for four years. In this town the place of the miko's henīha is taken by a tȧstȧnȧgi. Indeed all of the tȧstȧnȧgis are considered the same as the henīhas. They are called " the people who are named " and are of the nature of lawmakers and assistants to the miko. The miko's tȧstȧnȧgi is also the same thing as the yatika. There are no istatcagagis (retired leaders who acted as councillors), and no Creek town now has a hoḷibonaia. There are five water boys picked at random. At the front posts of each cabin are four poles with feathers tied to the ends for use in the " feather dance."

The two leading women in the women's dance carry atȧsa. The principal function of the ta'palas is to call the women up for their dance which they do four times. Each has a wand with a little white feather at the end. Their official positions do not end with the women's dance but continue to the end of the busk.

No medicine is now put on the firesticks but it was formerly done. The only medicine they use at the busk is the miko hoyanīdja, to which nothing is added.

The Hathagas and Tcilokis were the same as in Hilibi. They were exogamous, and if the exogamic law was violated the ears of the culprits were cut off.

The towns of Wakokai, Tukpafka, and Talahasutci were all one with this. In regular ball games they always played against Alabama.

Comparison between the plan given above and the two obtained in 1912 shows considerable differences, but since one of the former was obtained from the same man, I think the explanation lies in the smallness of the town and the weakness of many of the clans which has resulted in many changes within a comparatively short time. Nevertheless there is a general correspondence and the allocation of clans to the moieties also agrees except in the case of

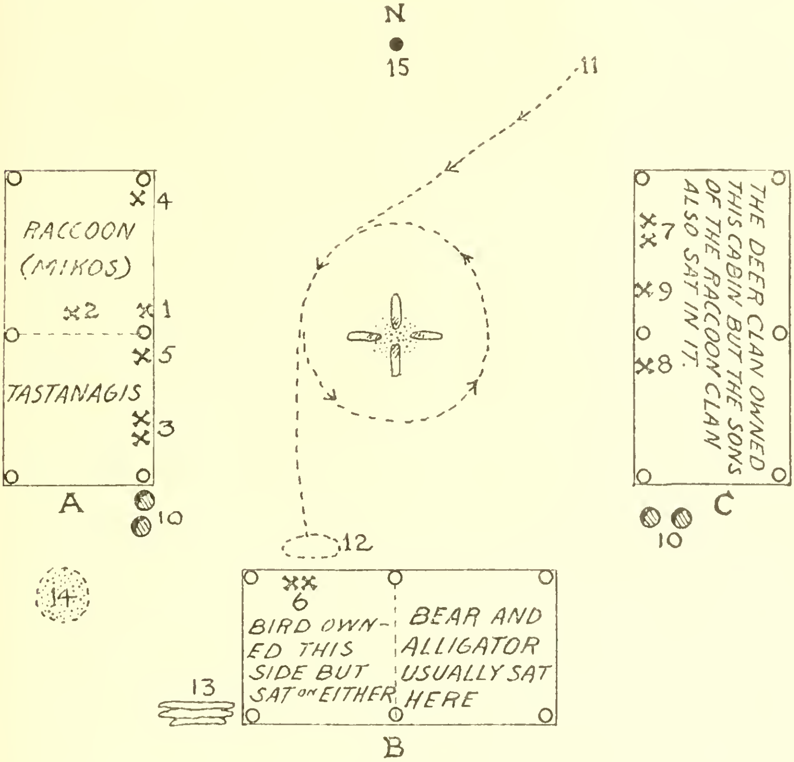


Fig. 6.—Square ground of Wiogufki.

A. Chiefs' Bed: 1, miko (Alligator); 2, hilis haya; 3, hilis tcâlaba (Bear and Deer); 4, hilis hoboia (Panther); 5, a tâstânâgi (instead of henīha) (Raccoon).

B. Whites' Bed: 6, yâhaikas (Deer).

C. Warriors' Bed: 7, ta'pala (Raccoon); 8, hilis hoboia (Deer); 9, tutka oktidīdja (Deer).

10, medicine pots (near bed A for men; near bed C for women and boys); 11, point where women enter to dance; 12, point where women begin dancing; 13, woodpile; 14, ashes of old fires; 15, ball post.

the Panther clan. This is explained by the fact that the Panther was anciently considered a White clan and later came to be regarded as Tciloki.

OKCHAI

Figure 7 shows the arrangement of this square and Plate 4, Figure 1, shows a view of it taken in winter.

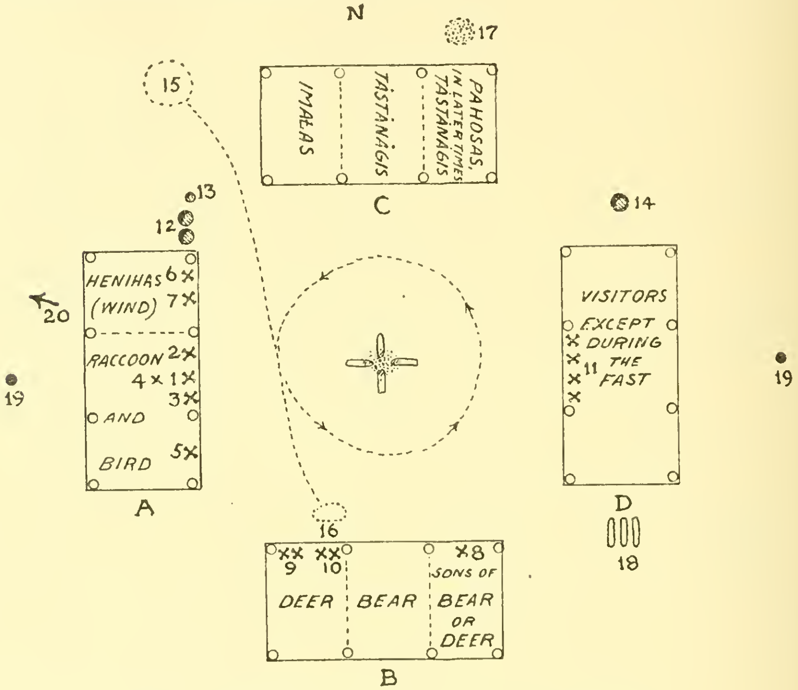


Fig. 7.—Arrangement of square ground of Okchai.

A. Chiefs' Bed: 1, miko (Raccoon formerly; Bear in 1929); 2, henīha (Deer); 3, yatika (Deer formerly; Wind in 1929); 4, hilis haya; 5, ta'pala (any clan); 6, hilis tcàlaba (Bird); 7, tutka oktidīdja (Wind).
B. Henihas' Bed: 8, ta'pala (any clan); 9, hilis hoboia; 10, yàhaikas (any clan).
C. Warriors' Bed.
D. Youths' Bed: 11, oīdjawa (any clan).

12, medicine pots; 13, medicine pot for boys; 14, medicine pot for women; 15, point where women assemble preparatory to their dance; 16, point where women start dancing; 17, ashes of previous fires; 18, woodpile; 19, ball posts; 20, a spring lies in this direction.

The hilis tcàlaba, ta'pala, and tutka oktidīdja changed every four years. The hilis haya was reappointed every four years.

Wiley Buckner, an old informant of mine, was the former yatika. The tutka oktidīdja in 1929 was Hotàlgi Miko.

The medicine was pounded up just in front of the pots at the north end of the chiefs' bed.

The fire was brought from Alabama in the great migration and new fire was lighted from it. They dug up the earth as deep as the arm would reach, put the fire in there, and made the new fire on top. This is the very spot at which they first placed their square in Oklahoma and it has not been moved. The squares of the kindred towns, Łáłogálga and Ȧsilanabi, are not so old.

There were two poles with feathers on the ends at each of the front posts of the cabins all the way round.

Atása were borne by the two women who led in the women's dance.

The tástanágis were law makers. They had charge of the rules governing the taking of medicine and if anyone broke one of these regulations they made him stay in the square ground all night without eating instead of breaking his fast that evening as was usual.

In the various beds of this square ground the "sons of the clan" can sit with their fathers.

The Hathagas and Tcilokis were the same as at Hilibi.

Their principal opponents in the ball games years ago were the Hilibi.

This arrangement agrees substantially with that obtained by me in 1912 (42d Ann. Rep., Bur. Amer. Ethnol., p. 234), the principal difference being in the location of the Bear and Bird clans. My earlier informants placed the Bird and Aktayatci in the middle of the south cabin and the Bear at the east end of the same, while the later ones said nothing of the Aktayatci but placed the Bird clan in the southern section of the west cabin and the Bear clan in the center of the south cabin, the sons of the Bear being located next to them on the east. The arrangement of this square must be taken in connection with the plans of Łáłogálga and Ȧsilanabi.

ŁALOGÀLGA, OR FISH POND

For a plan of this ground, see Figure 8.

The tutka oktidīdja is appointed every four years but always from the Aktayatci clan. The hilis hoboia are chosen every four years and ordinarily from the Aktayatci and Bear clans but this is not necessarily the case. However, if one dies before his four years have expired he is replaced by someone of his clan. The hilis hoboia also act as the hilis tcálaba.

Ta'palas are appointed only when needed. There are no special water carriers, the hilis hoboia calling upon any boys for this purpose whenever water is required.

The two leaders among the women carry atâsa, that held by the first being colored red, that by the second white.

One of the two medicine pots contains pasa; the other the miko hoyanīdja along with wīlana, tutka hiliswa ("fire medicine"), which grows in wet places in swamps and has red flowers, tcâto hâtkutci (four "little white rocks"), and tutka-tcok-hissi (green moss from an old fireplace).

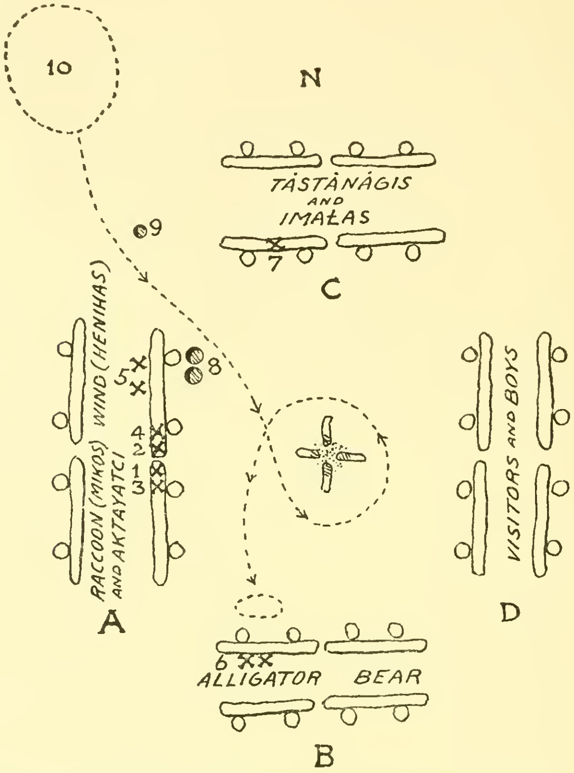


Fig. 8.—The square ground of Łałogâlga, or Fish Pond.

A. Chiefs' Bed: 1, miko (Raccoon); 2, henīha (or 2d chief) (Wind); 3. asimbonaia or yatika (head speaker, drawn from any clan); 4, hilis haya (any clan); 5, hilis hoboia.
B. Citizens' Bed (Tâsikaiâlgi intupa); 6, yâhaikas (no fixed clan).
C. Warriors' Bed: 7, tutka oktidīdja (Aktayatci).

8, medicine pots; 9, boys' medicine; 10, point where women assembled preparatory to the dance.

If one has eaten new roasting ears he is given a little pasa root to chew and then a little pasa in cold water of which he must take four drinks. Then he can take all of the medicines like the others.

Some of the medicine is swallowed, the rest spit out. The doctor sees that the medicines are taken and fines those who neglect to do so.

There is a town policeman called istikonā'ha who carries out the orders of the miko against those who have refused to obey him, and collects fines from them. The incumbent in 1929 was Maxcy Alakotci. When I interviewed them they were using the tástánági as the town miko.

The Hathagas are the Bear, Wind, Bird, and Alligator; the Tcilokis are the Raccoon, Aktayatci, Deer, and Potato.

The Aktayatci are said to have formed one phratry with the Raccoon.

In match games, they played against Tukabahchee, Atasi, Lapłáko, Eufaula, Hilibi, and Kealedji. Alabama was formerly of the same fire but later drew away.

This year (1929) they did not use the pasa. The Àsilanabi square ground is arranged just like this one, but the Okchai differ from these two a little in the use of their medicines. It is thought that Àsilanabi is older than Łáłogálga and that the latter branched off in order to get the extra money that was paid to its six representatives in the national assembly.

Except that there is more detail, the arrangement given here differs only slightly from that which I recorded in 1912 (42d Ann. Rep., Bur. Amer. Ethnol., p. 236). The only noteworthy divergence is in the position assigned to the Deer clan by my earlier informants, but this may be attributed to the fact that the miko apokta was then a Deer and his clan was probably brought over to the west cabin for that reason. As we should expect, the agreement is also close with the arrangement of the Àsilanabi ground though there are minor divergencies in the allocation of clans to the south cabin. All of my authorities agreed well in assigning clans to the two moieties, but the oldest of all of them thought that the Beaver and Alligator were probably Tciloki. This may have been the ancient arrangement.

TUKABAHCHEE

The plan of Tukabahchee square appears in Figure 9 and a view of it as it looked in 1912 is given in Plate 5, Figure 1.

The number of tástánágis is indeterminate. The toba mawīdine were officers not otherwise named who always remained in the cabins. There is one in each of the 12 beds except a part of the southeast cabin as indicated. They were selected from any clan, given names taken from the father's clan, and seated with the latter. Thus, if a man were a Deer and his father a Raccoon, they would give him a name from the Raccoon clan's names and seat him with them. After being so seated these officers were not obliged to do any further work connected with the busk.

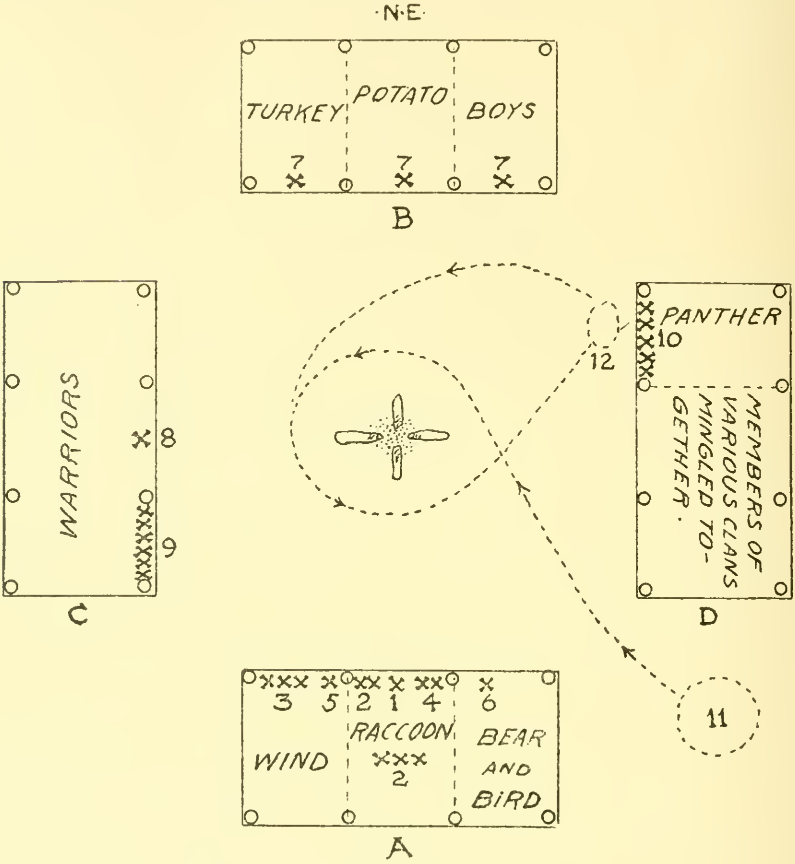


FIG. 9.—Tukabahchee square ground.

A. Chiefs' Bed: 1, miko (Raccoon); 2, mikos (substitutes) (Raccoon); 3, henīhas (Wind); 4, henīhas and yatikas; 5, hilis haya; 6, ta'pala.
B. Potato Bed; sometimes also called Youths' Bed: 7, 7, 7, toba mawidīne.
C. Warriors' Bed: 8, ta'pala; 9, tȧstȧnȧgi łȧkȧlgi.
D. Youths' Bed (Tcibȧnȧgȧlgi intupa): 10, yȧhaikas; 11, point where women assemble preparatory to the dance; 12 point where the women start dancing.

The istatcagagis, most of whom sat in the southeast bed, were like a jury, or like a committee, to settle matters of routine. They comprised both men and women. The admittance of women to this select group is something which I heard from no other informant.

A man was picked out of the bed of the henīhas to speak for others, *i. e.*, the yatikas were selected from the henīhas. None was used in the stomp dance. As payment for his services the yatika was given a deer hide and a ribbon. When he was wanted by the miko he was summoned four times, but he did not start until he had received the fourth call. He set a basket on the ground into which all of the tâsikaias threw bits of tobacco to be taken to the singers for the women as payment for their services.

The hołibonaia was a special speaker used in the ball game and in war. The term asimbonaia was about equivalent to that of yatika. He was a head man chosen from among the tâstânâgis for almost any purpose. He listened to any message which the miko wished to give out and then repeated it aloud.

There were two hilis tcâlaba who sat with their clans and were summoned whenever needed. One was a Raccoon and one a Bear.

There were two oktidīdja who sat with their clans or wherever they belonged until summoned to attend to the fire.

Four hilis hoboia, selected from any clans, were sent to gather the medicine.

All of the tâsikaias shared in getting water.

The famous Tukabahchee plates were taken out and cleaned four years in succession and then left covered for four years.

The feather dance was discontinued at Tukabahchee when my informant was a small boy.

The three leading women in the women's dance carry atâsa. The leading woman has an eagle feather on her atâsa, the second a white crane feather, and the other the feather of a third bird, perhaps a goose. They start one at a time and when the third moves all the rest follow. After they have walked round the fire four times they begin to dance and circle the fire again six times.

The Hathagas were Bird, Wind, Bear, and Beaver; the Tcilokis were Turkey, Alligator, Raccoon, Deer, Panther, and any others.

In olden times the moieties were exogamous. The Raccoon and Potato were then brothers, or rather half brothers, but intermarriage between them is now common. Even today, however, the Beaver and Bird will seldom intermarry. The Bird was the " uncle " of the Beaver and the Beaver the former's " nephew."

A man's children called his father's clan " fathers." One can say anything he wishes to, however disrespectful, about his own clan, but he must not speak against his father's clan or permit anyone else to.

The general arrangement is the same as that obtained from the father of my informant in 1911-12 (42d Ann. Rep., Bur. Amer. Ethnol., p. 244), but the stations here assigned to some of the individual officers are probably more nearly correct, particularly the locations of the mikos.

KEALEDJI

Figure 10 shows the Kealedji square.

The hoktâgi immiko, "women's chief," supervised the women's dance. There are now no regular water carriers. The imałas formerly sat in the north cabin, but now there are no officers so called. The beds are called by the names of the clans which occupy them. If the asimbonaia is wanted to deliver a speech, he is called over to the miko's seat for that purpose. For tâstânâgis the best men are chosen. The ta'palas are changed every four years. In former times they had a regular four days' busk, but now it lasts for but one day and there is no feather dance.

In the match games they played against Okchai, Wiogufki, and Tulsa.

The Hathagas are Wind, Bear, Panther, and Turkey; the Tcilokis are Raccoon, Deer, and Aktayatci. In ancient times these moieties were exogamous.

The names of the present officers are as follows:

miko	Kasihta Yâhola (Raccoon)
henīha	Henīha Imałutci (Wind)
miko apokta	Kayomulgi (Raccoon)
hoktâgi immiko	Wiwohka Yâhola (Raccoon)
henīha	Oīkas Hadjo (Wind)
asimbonaia	Kōsa Fiksiko (Bear)
ta'pala	Tâlmutcâs Hadjo (Bear)
"	Alak Hadjutci (Turkey)
hilis tcâlaba	Kân Tcati (Wind)
" "	Itco Imała Fiksiko (Deer)
tutka oktidīdja	Ahali Imała
hilis hoboia	Tâłkōna Hadjo (Wind)
" "	Hotâlgi Fiksiko (Wind)
tâstânâgi	Tâstânâk Tcâpko
"	Tâstânâkutci
"	Inheniha (= henīha)
"	Tâłkōna Hadjo

The plan of the revived square ground of the Kealedji agrees in all essentials with the one given me in 1912 from memory by a very old man, except that in recent times the Deer clan seems to have lost its importance or died out. It is interesting to find that old and recent informants agree in assigning the Panther clan to the White moiety. They differ, however, regarding the position of the

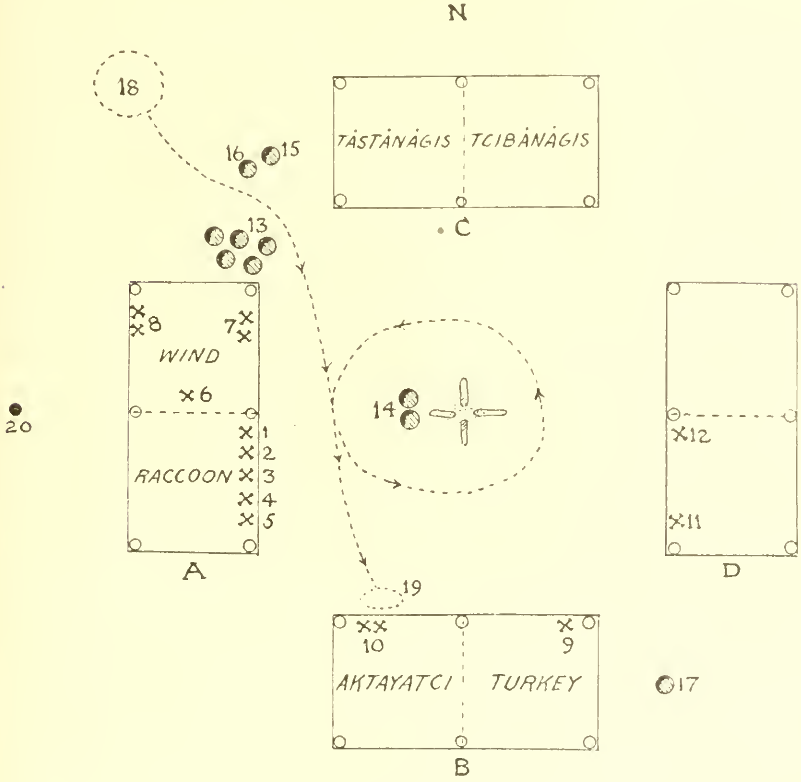


FIG. 10.—The Kealedji square ground.

A. Chiefs' Bed: 1, miko (Raccoon); 2, henīha (Wind); 3, miko apokta (Raccoon); 4, hoktâgi immiko (Raccoon); 5, henīha (Wind); 6, hilis haya (usually Raccoon; Wind in 1929); 7, hilis tcâlaba (Deer and Wind); 8, hilis hoboia (Wind).
B. Youths' Bed: 9, taʻpala (Turkey); 10, yâhaikas.
C. Warriors' Bed.
D. White Bed: 11, asimbonaia (Bear); 12, taʻpala (Bear).

13, medicine pots (1st position); 14, medicine pots for those fasting (2d position); 15, medicine pot for boys (2d position); 16, medicine pot for girls (2d position); 17, medicine pot for women (2d position); 18, point where women assemble preparatory to the dance; 19, point where women start dancing; 20, ball post.

Turkey, which the earlier informant considered Tciloki and the later White. But this clan, together with the Alligator and Tâmi, is known to have been on one side in some towns and on the opposite in others.

ŁAPŁȦKO

Figure 11 shows the plan of this ground.

The two pots of medicine were prepared where they are shown (nos. 4 and 5) and remained there all of the time. The Bird clan sat anywhere. The yatika belonged to no regular clan, and at the present time there is no such officer. There are two hilis tcàlaba who occupy no special seats, and one hilis haya who is taken from any clan of a friendly town. Towns belonging to the other town moiety do not

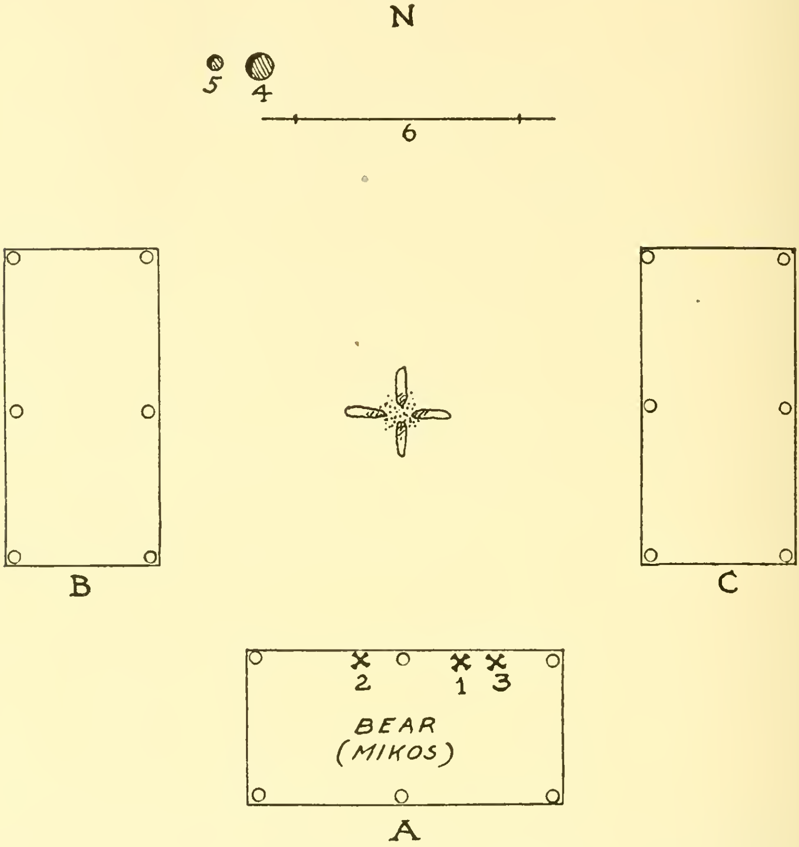


Fig. 11.—Square ground of Łapłäko.

A. Chiefs' Bed: 1, miko (Bear); 2, henīha or miko apokta (Bird); 3, yatika (sometimes seated here).
B. Warriors' Bed. This was usually occupied by middle aged men of various clans.
C. Citizens' Bed (Tàsikaiàlgi intupa). Occupied by various classes, including persons not properly citizens of the town but taking medicine there, men married in the town or adopted into it, and men whose fathers belonged to it.

4, a large pot of medicine for the fasters; 5, a small pot of medicine for the women and children; 6, rack for ball sticks.

take medicine with them and in fact are not invited except in the case of individuals married into the town.

The Hathagas are the Bear (the most important of them), Bird, Beaver, and Wind; the Tcilokis are the Raccoon, Deer, Potato, Aktayatci, Panther, Alligator, etc. Here the Alligator, Turkey, and Beaver can intermarry; in Eufaula they could not. But probably this means that the Beaver could intermarry with the other two, as the Alligator and Turkey were seldom allowed to marry under any circumstances. The Bird and Beaver were classed together in Łapłáko, but this group does not include the Bear or Wind. The Hathaga clans had the reputation of being progressive while the Tcilokis were fullbloods and reactionaries. This characterization probably followed the coming of the white people.

The towns of the opposite group were called Tálipoła, which means " foreign but not unfriendly."

The word Łapłáko indicates a place where there are many marshes filled with canes. This town square, which had been discontinued, was revived in the year 1903 in this way. They had to prepare a ground in order to take medicine before a game with the Nuyaka Indians next year. Later this was improved with regular cabins, but it must have been inconspicuous or have been considered unimportant, as I heard nothing about it in 1912.

Łapłáko and Atasi are now nearly fused on account of the number of marriages between individuals belonging to them. Before the Civil War the Łapłáko had an Atasi Indian named Hotálgi Hadjo married among them as their hilis haya. One of the great men of Łapłáko in former times was Jim Boy (Tástánági Imała) whom my informant remembers to have seen. He thinks he died just before the Civil War broke out. McKenney and Hall (History of the Indian Tribes of North America, vol. 2, pp. 71-74) give a portrait of this chief and a considerable account of his life. He was born in what is now Alabama in 1793 and accompanied the warriors of his town during the Creek War of 1813-14, but was too young for active participation. In the war with the Seminole he was one of the leaders of the Creek contingent which aided the Americans. The exact date of his death seems to be unknown.

The arrangement of the modern ground differs more from those described to me in 1912 (42d Ann. Rep., Bur. Amer. Ethnol., pp. 254 and 255) than any of the others. The first of the latter was obtained from a very old man who should have known the ancient arrangement well, but of course my interpreter and I may have misunderstood him. The cabins are at different points of the compass and more confusion is shown in the later organization, but they agree in stating that the miko belonged to the Bear clan and in placing that clan in the south cabin. My older informant allocated this clan with the Tciloki. This was probably an error on his part but he seemed to insist upon it.

They have had no busk since the Civil War and no women's dance, and the pasa is no longer used, only the miko hoyanīdja. The dances in the square are three stomp dances. Seven days before one of these the "broken days" are sent out and on the day when the sixth stick is thrown away they are all to be at the ground, while on the seventh they are supposed to be taking medicine. Seven days before the dance they also meet and pick out four clean young men, called hilis hoboia, men whose wives are not pregnant, who are not given to intoxicants, and who have not attended to the digging of a grave during the preceding month. These men gather four bundles of medicine (miko hoyanīdja) which they lay down with their tip ends toward the west. First they spread out a bed of leaves called lodja issi, "turtle leaves," which should be taken from hickory trees. The medicine is laid on top of these and more leaves are spread over it. On the morning of the fast day all of those who are to take medicine are supposed to present themselves at the square ground. The fire is built up so that it will not go out all day. Early in the morning the two hilis tcàlaba prepare the medicine, first the medicine for the women and children and then that for the adult men. This is taken four times during the day, the fourth time between one and two o'clock. Before they take the medicine the yatika announces, on behalf of the chief, that each of those intending to take it is to get a stick and throw it into a blanket. These sticks are counted and the yatika announces the number. Four times (or sometimes twice) during the day the men who are to take medicine with the exception of the officials (the mikàlgi, yatika, hilis haya, and the two ta'pala) go out to get firewood so as to be ready for the dance that night. Four men are selected to keep watch of the fasters during the night, to see that no one sleeps or breaks his fast, or drinks or goes with a woman. That is why the numbers are taken. These four men are called istikonā'ha, "men taking away," because they take away the hat of anyone found sleeping (and treat similarly anyone who breaks the taboos in other ways). The hat they carry to the miko and, when the owner comes to get it, he is fined.

After they have taken medicine for the fourth time, they go to the creek for a bath and then return to the square. The yatika talks to them telling them to take care of themselves all of that night, and then they scatter to the camps to eat. Before sundown, however, they are supposed to be back on the ground. The yatika calls to them four times and by the fourth time they are to be in their seats. When all are in their places, the two ta‘pala are selected. The yatika makes a speech on behalf of the miko, calling upon his hearers not to act in an unfriendly way toward the outside friends who are about to be admitted to the dance, not to take liquor, to behave themselves all through the night, not to fight, and so on. This speech is addressed to the town people and outsiders alike. After it the fasters dance four times and then the visitors are admitted. That " kills the fast." All through the day the square is to be kept clean with the idea that the fasters will in consequence be clean. They go up to take the medicine two by two, and those who are ceremonially unclean take the medicine last. They dance until about daybreak. Then all belonging to the town go down to the branch and bathe, after which they return and sit in their respective beds. Then a collection may be taken to defray their expenses and they settle other matters. The night before, the chief of a friendly town may have announced a dance, and, if so, the announcement is now made and advice given as to how they are to help their friends. This advice is uttered by the yatika, speaking for the miko, and he then gives a general talk, advising his people not to use liquor, not to break the laws, and to be good citizens in every sense of the word. Then they disband for the year.

HILIBI

A plan of Hilibi square is shown in Figure 12 and a general view of the ground as it appeared in the winter of 1911-12 in Plate 5, Figure 2.

Two poles with white feathers attached were at each front post. These were used in the " feather dance " and were called " the path," because the path was to be white.

When there are visitors the owners of the east cabin move elsewhere in order to make room for them. When the south cabin is overcrowded, some of its occupants move into the east cabin. In this town the clans were always considerably mixed up in the beds. The ta‘palas can sit anywhere. The tutka oktidīdja does not have a particular seat on account of his official position. He is appointed every four years. The tutka dīdja, who starts the fire, is identical with the hilis haya.

If a man whose father is of the Aktayatci, the miko's clan, is given a busk name, he is brought to the mikos' bed and given a seat there.

The Hathagas are the Bear, Bird, Alligator, Beaver, Turkey, and Wind; the Tcilokis are the Panther, Potato, Deer, Aktayatci, and evidently the Raccoon. The Alligator and Bird are considered as practically one clan.

The two leaders in the women's dance carry atâsa.

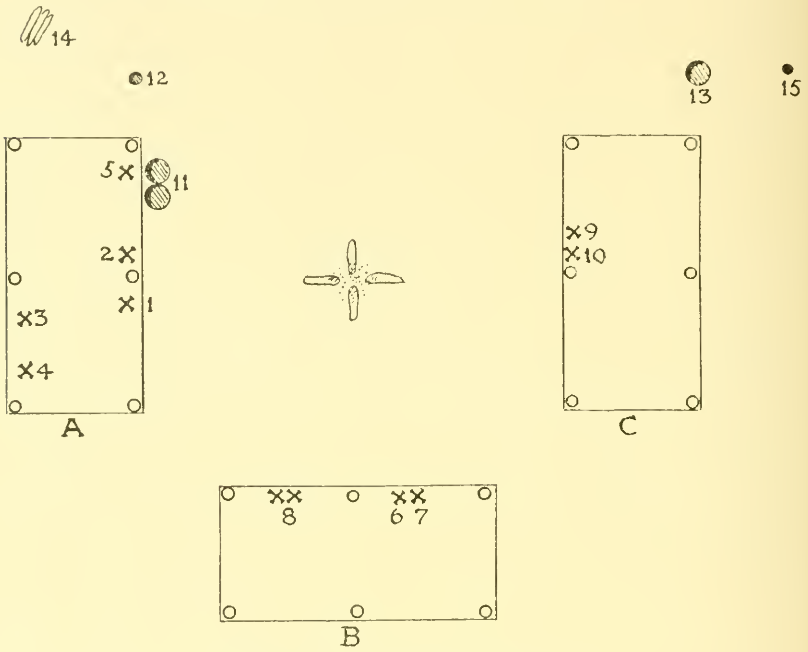


Fig. 12.—Square ground of Hilibi.

A. Chiefs' Bed: 1, miko (Aktayatci); 2, henīha (Alligator); 3, hilis haya (Raccoon in 1929); 4, ta‘pala (Bear); 5, hilis tcâlaba (Bear in 1929).
B. Raccoons' Bed: 6, hilis hoboia; 7, tutka oktidīdja (Raccoon in 1929); 8, yâhaikas (any clan).
C. Cabin used by visitors: 9, ta‘pala (Alligator); 10, hilis hoboia (Alligator).

11, medicine pots; 12, medicine pot for boys; 13, medicine pot for women; 14, woodpile; 15, ball post.

The history of this town is as follows. It was founded by a man of the Aktayatci clan who went off to live by himself and then put up a ball post. Many women belonged to his family and he had numerous visitors, some of whom married these women so that it soon grew into a large band of which he was probably the first miko. Anyhow that is the way the Aktayatci came to have the town. After stomp dances had been held there for some time, more visitors came to join them and it grew still larger. Because it was built up very rapidly, its founder called it Hilibi, which means " hurry " (hila'pkis, " I make haste "). Since it was an " illegal " band, a tâlwa fâteasīgo (" town deviating from correctness "), all the clans do not have regular places, having been drawn from so many other bands.

The following notes on some personal names contained in the town roster give an interesting insight into the manner in which totemic names were bestowed:

Fos Hâtki Imała (" White Bird Imała "), so named because he belonged to a White clan, the Wind.

Halak Hopaie. He belonged to the Bear clan, but his father belonged to the Raccoon, hence the name Halak or Ahalak (" Potato "), since both these clans are Tciloki.

Pahos Fiksiko. He belonged to the Wind clan, but his father was a Deer and the Pahosa is of the same phratry as the Deer.

As shown by the native story above given this town was not supposed to be ancient or to have a firmly fixed town organization, and, while it was older than the Hilibi people themselves believed, it seems to have preserved the irregularities which might naturally be associated with a new town. Not improbably the tradition of irregularity preserved the fact. At the same time there is a general agreement between the plan here given and that which I obtained in 1912 (42d Ann. Rep., Bur. Amer. Ethnol., p. 258). The mikos' cabin is to the west, and the mikâlki and henihâlgi were of the same clans, Aktayatci and Alligator respectively. The Alligator and Turkey were classed as Whites from association with the Bird by my later informants, but the earlier ones gave them as Tciloki.

ALABAMA

This was a very simple square of exceptional arrangement as shown in Figure 13.

The Alabama were one of the incorporated tribes with a language distinct from Creek. The clan names in Alabama are: Mahaleha (Wind), Sawaha (Raccoon), Aktayatciha (Aktayatci), Hâtcuntcobaha (Alligator), Konoha (Skunk), Nitaha (Bear), Koīha (Panther), Fociha (Bird), Fitōha (Turkey), Ofâtaha (Beaver).

All of the officers were brought over to the chiefs' bed. Men of the Alligator, Bear, and Aktayatci have been mikos and a man of the Skunk clan was once the henīha. There is no regular rule for either position.

The Hathagas were the Wind, Bear, Panther, Skunk, and Raccoon; the Tcilokis were the Bird, Beaver, Turkey, Alligator, and Aktayatci. The Wildcat was the same as the Panther.

One of the greatest Alabama Indians now remembered was Kȧntcati Yȧhola (Alabama name Tcīsōki), who was the hilis haya. He was born in Alabama and came west with his tribe. He lived until about 1866.

The above plan and the three others I obtained in 1912 and the years immediately following (42d Ann. Rep., Bur. Amer. Ethnol., pp. 263-264) show considerable minor variations but all agree in locating the chiefs' bed in the east and the warriors' bed in the west. Most of them also place the Bear and Panther clans in the latter and the Wind, Aktayatci, and Deer in the former, where they are noted at all. In allocating the clans the above informant agrees with the older ones except regarding the Panther which the men first consulted asserted was Tciloki while it is here given as a White clan, but this is a clan which has been placed on both sides.

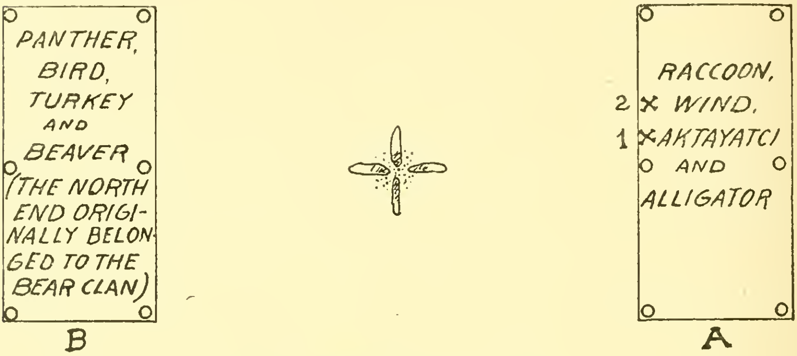


Fig. 13.—Alabama square ground.

A. Chiefs' Bed: 1, miko (Wind); 2, henīha (Raccoon).
B. Warriors' Bed.

KASIHTA

For the plan of Kashita square ground, see Figure 14.

There should be two hilis tcȧlaba, drawn from the Alligator clan, but they are not employed now. Four hilis hoboia for the pasa, four for the miko hoyanīdja, and one tutka oktidīdja are chosen by the miko without reference to clan. There is no definite body of water carriers. Two ta'palas are selected from any clan to serve just for the night. They carry sticks called reels, and their function is to invite the dance leaders to lead dances and see that all take part. There is only one singer for the women's dance. He sits behind the miko.

In 1901 the old square ground was given up and the new one was established in June, 1920. Because the new generation was weak one cabin was cut out. The Coweta square is said to have been the same as that of Kasihta.

Every time anything is brought in or anything repaired they dance all night because thus the two things are joined together, just as two days are united by the night on which they dance. Formerly dances were held every Saturday night, but hard times have put an end to them. The dance which was being held when I paid my visit was because they were then putting up a ball post.

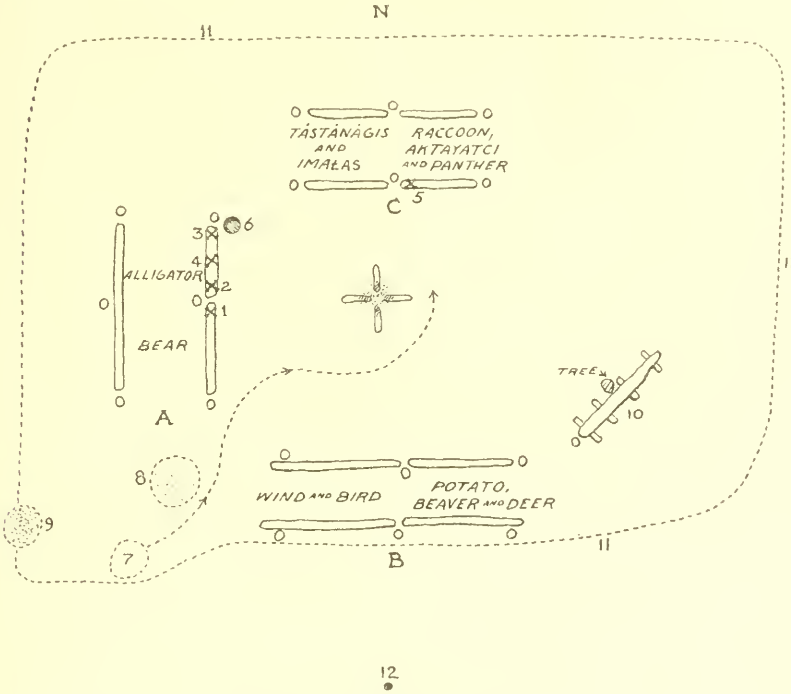


FIG. 14.—Kasihta square ground.

A. Chiefs' Bed: 1, miko (Bear); 2, henīha (Alligator); 3, hilis haya (seat when on duty); 4, asimbonaia.
B. Whites' Bed (Henihálgi intupa), or "Cabin of the Greater Kings."
C. Warriors' Bed: 5, asimbonaia (Aktayatci).

6, medicine pot; 7, point where women assemble before dancing; 8, trash heap; 9, where ashes of old fires were placed; 10, split log where are seated those young men who have broken the rules and are in consequence placed here as a punishment before being allowed to mix with the rest of the people; 11, line of sweepings (tádjo) marking limit of square ground; 12, ball post.

The Hathagas are the Wind, Beaver, Bird, and Deer; the Tcilokis are the remaining clans, yet it is said that the Bear, Alligator, and

Wind were of the same " class." Under the present law they can all marry outside of third cousins.

The Kasihta defeated the Coweta three times in the ball game, the last time in 1878, and after that they took them under their jurisdiction and they have played on the same side.

Comparison of the plan of the new Kasihta with the plans of the earlier grounds secured by Gatschet and myself (42d Ann. Rep., Bur. Amer. Ethnol., pp. 266-268) shows that the old order has been fairly well maintained allowing for the disappearance of some clans, particularly the Fish clan. Incidentally I wish to correct an erroneous statement in my report in which I misquoted Gatschet to the effect that the Kasihta miko belonged to the Alligator clan. While the Alligator clan occupied half of the chiefs' cabin, the miko himself has always been taken from the Bear and was stated to have been so by Gatschet. The allocation of clans to the moieties by my recent informants contains a number of difficulties, for they seem to have placed the Bear among the Tciloki, which is unlikely, especially as it was said to belong to the same " class " as the Alligator and Wind. My own earlier authorities also classed the Beaver and Deer as Tciloki.

The following information will be interesting to those who wish to study acculturation processes in intangibles. It was told me by the Indian considered best able to speak for the town.

> The original four cabins represented the New Jerusalem with its 12 gates. The busk goes back to the time when Jacob set up the altar at Bethel and is traced from him and his 12 sons. All of the Indians in America entered in two migrations, one at the time of Jacob (1500-2000 B. C.) and the second 600 years later, at the time when Jerusalem was destroyed by Nebuchadnezzar. Then they talked face to face with the Great Spirit because they were more obedient to God than any other tribe, but about 700 years after the Messiah they got away from the original law on account of desire for riches. Then they lost the old law and asked for a new government, and by holding a ceremony in midsummer, in the month of July, it was given to them. That new law taught them to tell the truth and be honest with their fellowmen and to raise their children in such obedience, not to touch anything that did not belong to them, not to make a false statement. That is the law which we are trying to follow.

He added:

> We have a hard time because the white men have failed to fulfill their part of the agreement. They have strong laws that we can't begin to understand and our customs are about choked out through grafters who claim to have bought the claims of the allottees on which our squares are located. In order to hold their grounds several towns have to pay rent year after year. If the law makers would cooperate with us and give us full privileges we would raise more substantial, law-abiding young men and young women. That was the custom and the wish of our forefathers.

OCHESEE SEMINOLE

This is the only Seminole ground from which I obtained information during my recent trip. The plan of it is shown in Figure 15.

There are two pots of medicine for the miko hoyanīdja and pasa respectively, but the latter is introduced only at the busk. The women, however, use wormseed (" wīlana "). After they are through with the medicines, whatever is left is poured out at the place where they have been taken.

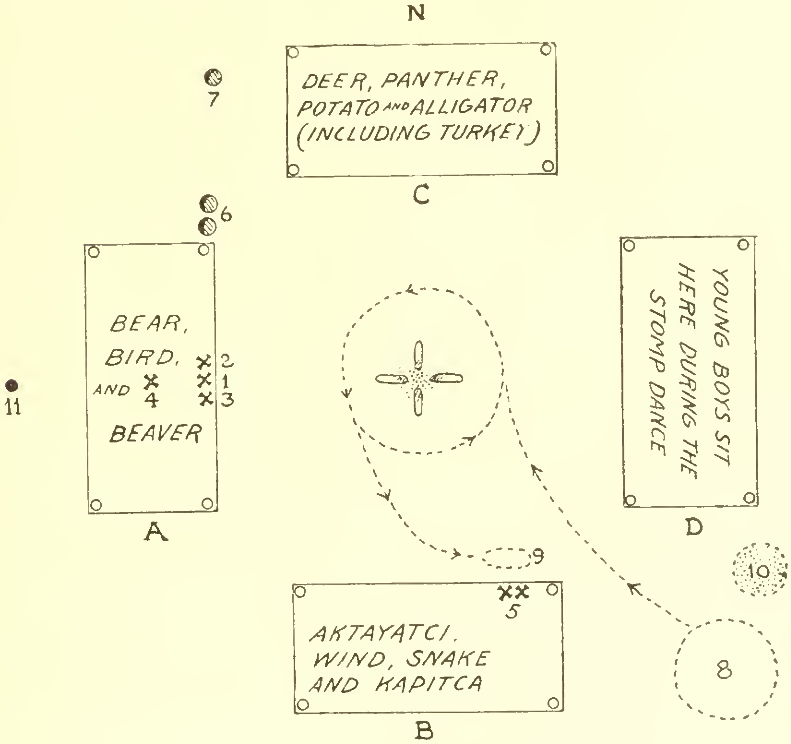


FIG. 15.—Ochesee Seminole square ground.

A. Chiefs' Bed: 1, miko (Bear); 2, henīha (Bird); 3, yatika (Deer in 1929); 4, hilis haya (Wind in 1929).
B. Warriors' Bed: 5, yâhaikas.
C. Warriors' Bed.
D. Youths' Bed.

6, medicine pots; 7, medicine pot for boys (containing red root); 8, point where women gather before dancing; 9, point where women start to dance; 10, ashes of old fires; 11, ball post.

The miko is chosen if possible from the Bear clan, but if they do not find a suitable man of that clan, they select someone from the Beaver clan.

The yatika and hilis haya may be selected from any clan, the former being chosen for his oratorical gifts.

There is now no henīha. The last they had went to live with the Creeks and did not come back.

Two ta'palas are used in the women's dance and hold their position for four years. Other ta'palas are chosen temporarily for the other dances. In the stomp dances they change these ta'palas several times during the night.

There are four hilis hoboia taken from the west, north, and south cabins but from any clan. They keep their positions as long as they choose to serve.

There is one tutka dīdja who can be of any clan.

Five or six boys bring water to the ground.

The two leaders among the women carry atâsa which are painted with white clay annually just before the dance. Women do not take the wīlana internally; they merely wet their faces and other parts of their bodies with it. The boys use only the miko hoyanīdja.

The ashes of the old fire are removed from the square and the new fire lighted on the morning of the fast day.

The Hathagas are the Bear, Bird, Beaver, Wind, Otter and Skunk; the rest are Tcilokis. The Bird and Beaver belonged in one phratry, and so did the Wind, Otter and Skunk; the Alligator and Turkey; and the Aktayatci, Kapitca, and Snake.

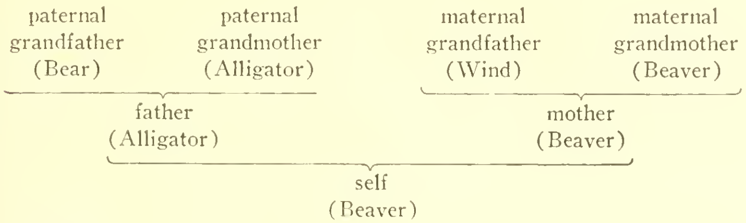
The name of the present miko is Nokos Miko, and his father belonged to the Deer clan. The last henīha was named Henīha Miko, and his father was of the Bear clan. The busk name of the yatika (my informant) is Pahosa Tâstânâgi; his father belonged to the Aktayatci, and his father's father to the Bear.

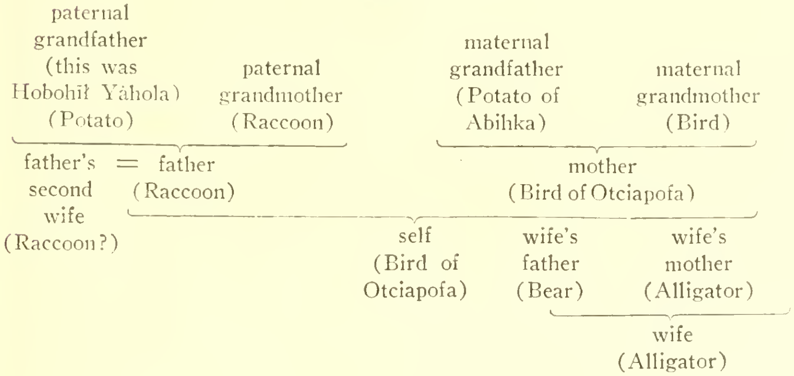
They have a ball post surmounted by a wooden fish. A hit on this fish counts 4, and on the post above a certain mark 2. There have been no regular match games between towns in the lifetime of my informant, but about two years ago the old men and the young men played against each other.

The above plan of the Ochesee ground agrees closely, naturally enough, with that which I obtained from the man whose advice was particularly resorted to in reestablishing it some years ago (42d Ann. Rep., Bur. Amer. Ethnol., p. 283), for in 1912 it had been given up. The main differences are in the seating of the Potato and Alligator clans. In the matter of the moieties the only change is in the case of the Raccoon clan, which I previously set down as White. This is so exceptional, however, that I have always believed that I must have misunderstood my informant.

GENEALOGIES

The two brief genealogies which follow will illustrate in some measure the influence of the clan system on marriage. The first is the genealogy of Jeff Canard of Łapłäko; the second that of Earnest Gouge of Hanna, the latter of especial interest because it includes the famous orator Hobohīł Yâhola.





CONCLUSION

The busk undoubtedly represents a long period of development, and as the stages through which it passed and the elements entering into it have been lost, we can never understand it fully. Its main purpose, however, was evident. It was to restore the connections of the tribe with the universe which a year of civil or profane living had tended to rupture. Hence the new fire, extracted from its abiding place in the wood and not as yet sullied by contact with humanity. Hence the rigorous fast accompanied by administration of medicines divinely revealed to the ancestors, the general pardon of offenders, the sabbath calm prescribed for that period of regeneration, the use of white paint, and the employment of the term white—"the white day," "the white smoke," "the white drink"—in various parts of the ritual. The one discordant note seems to have been provided by the women's dance, since the leaders of that dance carried representations of war clubs, which there is every reason to believe were anciently adorned with scalps, and some of these were painted red. But I suspect that this dance was an attempt to represent war as a protective institution and to thank the being or beings who preside over human destiny for having so well defended them against assaults of the—as usual—perfidious foe. Possibly some element of propitiation also entered into this dance.

The universe with which the Creeks sought reconciliation was not, however, a material one. What they had in mind was rather the mind or minds believed to be operant there. While we know of some supernatural beings connected primarily with the busk and numerous spirits associated with natural objects were anciently believed in, it seems fairly certain that the peculiar patron of the ceremony was a solar, or rather celestial, being generally called Hisagita-immisi, "the breath controller," and also Ibofánga, "the one above," and that the busk fire was in some way an earthly representation of the great solar fire overhead. While it is probable that Hisagita-immisi was not in ancient times the monotheistic deity he has now become, there is every reason to think he was already, before White contact, the supreme being of the Creeks.

1. Abihka or Talladega square ground.

2. Tulsa square ground from the southeast.

1. Nuyaka square ground.

2. The three beds of Pakan Tallahassee, from the southwest.

1. Pakan Tallahassee square ground looking between west and south beds, showing chunkey yard and ball post.

2. Wiogufki square ground from the southwest.

1. Okchai square ground in winter from the southwest.

2. Fish Pond square ground.

1. Tukabahchee square ground.

2. Hilibi square ground in winter from the southwest.

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THE DETERMINATION OF OZONE BY SPECTROBOLOMETRIC MEASUREMENTS

(With Three Plates)

BY
OLIVER R. WULF
Smithsonian Institution and U. S. Bureau of Chemistry and Soils

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(With Three Plates)

In the fall of 1930, at the suggestion of Dr. C. G. Abbot, measurements of the transmission of visible light by ozone were made on the solar spectrometer of the Smithsonian Institution at Table Mountain, Calif. This determination of the absorption of ozone in the region of its very weak absorption, practical in the laboratory only by the method of photographic photometry, by which it has been done by Colange,[1] can be accomplished by direct energy measurements on the spectrobolometer because of its great sensitiveness and the extreme intensity of the source. At the same time fluctuations in weather conditions are likewise registered with great sensitiveness and constitute a serious source of error in the measurements. But on the other hand it is favorable that observations may be made of the absorption of controlled amounts of ozone placed in the sun's beam with all other conditions of operation identical with those of the regular solar observations. One of the useful results of this work has been the selecting of a large number of points on the solar bologram which may be satisfactorily used for ozone determination. The present paper has to do for the most part with the results of these measurements as forming a basis for the determination of atmospheric ozone from solar bolograms and not with the results of their application.

The essential apparatus used in this work auxiliary to the spectrometer is shown in Plate 1. A cylindrical glass cell, 20.0 cm. long and approximately 13 cm. in diameter, was mounted in the front room of the spectrometer tunnel in such a way that it could be easily moved in or out of the solar beam as it came from the coelostat mirrors on its way to the first slit of the instrument. The circular windows of this cell were made of high-grade plane plate glass. These windows

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[1] Colange, G., Journ. Phys. et le Rad., ser. 6, vol. 8, p. 254, 1927.

of the cell were covered with diaphragms having vertical rectangular openings sufficient to pass a beam that considerably more than covered the first slit of the spectrometer. The absorption cell was sealed with all glass seals in connection on its inlet side with the ozonizers and on its outlet side with an analytical apparatus for ozone. No alterations of any sort were made in the regular observing conditions except for the interposition of the cell. Tank oxygen was supplied to the ozonizers under a small constant pressure through the capillary of a glass flowmeter having nujol as the manometric liquid, this flowmeter being calibrated in a series of independent measurements. The exit ozone was analyzed by the method described by Wulf and Tolman.[1] The samples, whose volumes were known from the time and rate of gas flow, were collected over potassium iodide solution, set aside, and subsequently analyzed. It is evident that, in the filling of such a cell by sweeping at the low rates of gas flow necessary in such a system for producing ozone of relatively high concentration, a considerable amount of time will elapse before the exit gas attains practically the concentration of the entering gas. To study this circumstance a tube was also brought to the analytical apparatus from before the cell as the gas came from the ozonizers allowing a sample of the inlet gas to be taken, and by means of this it was possible to determine the time sufficient for the exit gas to rise nearly to the concentration of the inlet gas. The concentration of the exit gas was taken, in view of the processes of diffusion and mixing going on in the cell, as representative of the ozone concentration in the cell. The ozonizers were of the familiar silent discharge type. For part of the work one alone was used, while for the rest of the work two were used in series and both water-cooled, these giving the largest concentrations employed. Ordinarily over the period of the taking of four ozone bolograms six analytical samples of the ozone were collected.

Knowledge gained from earlier work on ozone permits a description of the character and position of the absorption.[2] A small fraction

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[1] Wulf, Oliver R., and Tolman, Richard C., Journ. Amer. Chem. Soc., vol. 49, p. 1650, 1927.

[2] *a.* Colange, G., Journ. Phys. et le Rad., ser. 6, vol. 8, p. 254, 1927.

b. Wulf, Oliver R., Proc. Nat. Acad. Sci., vol. 16, p. 507, 1930.

c. Ladenburg, Erich, and Lehmann, Erich, Ann. Phys., ser. 4, vol. 21, p. 305, 1906; Verh. Deutsch. Phys. Ges., vol. 8, p. 125, 1906.

d. Schoene, E., Journ. Russ. Phys.-Chem. Soc., vol. 16, pt. 9, p. 250, 1884; Journ. Chem. Soc., vol 48, pt. 2, abstracts, p. 713, 1885; Chem. News, vol. 69, p. 289, 1894.

e. Chappuis, J., Ann. l'École Norm. Sup., ser. 2, vol. 11, p. 137, 1882; Compt. Rend., vol. 91, p. 985, 1880; Compt. Rend., vol. 94, p. 858, 1882.

of the solar energy will be cut out by the ozone as is illustrated in Figure 1, which represents a normal spectral energy curve roughly similar to that of the sun showing the approximate area removed by the atmospheric ozone in the visible.

However, the actual observing of this reduction of intensity must be made on the complicated solar curve as shown in Plate 2, which is composed of a series of typical bolograms notched by many Fraunhofer absorption lines. The discontinuities in the curves are due to the insertion of rotating sectors in the path of the solar beam to cut down the intensity in the regions of great intensity, to values such that the galvanometer deflections will still fall upon the photographic plate on which these deflections are being continuously recorded in the form of these curves. In addition, at two points a shutter is inserted for the purpose of determining the base line, that is, the line of zero deflection. Owing to the scattering of the rays by the earth's atmosphere the apparent maximum of the sun's intensity is shifted to longer wave lengths. The strong atmospheric absorption in the deep red is conspicuous, while over the region of ozone absorption chiefly the Fraunhofer lines are in evidence.

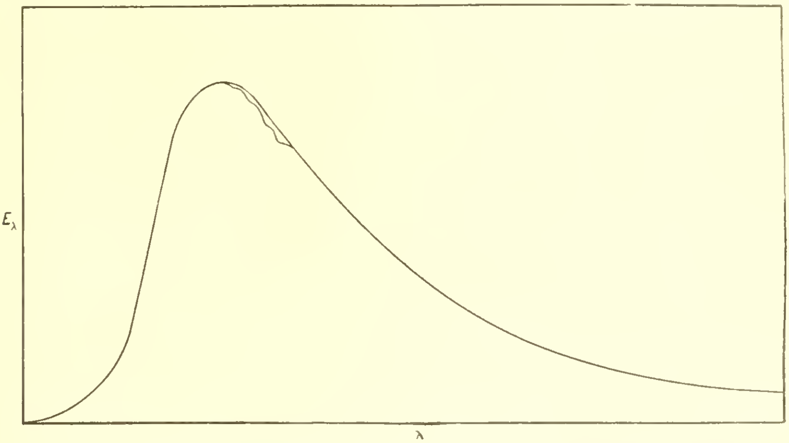

FIG. 1.—Spectral energy curve of black radiator, approximating that of the sun, showing the atmospheric ozone absorption in the visible.

In spite of these complexities, however, comparison of two bolograms, one without ozone in the cell and one with ozone, should show the reduction in intensity caused by the ozone, providing weather conditions remained sufficiently constant between the two. If, for example, we were to take the ratio of ordinates at corresponding points on two such bolograms under ideal conditions this ratio should be unity in regions not influenced by ozone, and somewhat greater than this where the intensity was reduced by the ozone absorption. In view of the exponential decrease in intensity of light passing through an absorbing medium, it is the logarithm of the ratio of ordinates which is proportional to the amount of ozone in the path. This will be zero evidently for those cases where the ratio is unity, and positive or negative as the ratio is greater or less than unity. This proportionality is based on the assumption that Beer's law may be used here. There appear to be no causes concerned with the apparatus and structure of the spectrum which could bring apparent false deviations from this law, since the spectrum is composed of broad diffuse bands,[1] or perhaps more accurately fluctuations in the absorption coefficient without any apparent discontinuities. The question as to whether the ozone absorption actually obeys Beer's law is an important one and, so far as the author is aware, has not as yet been satisfactorily answered, although attention has been called to it by Ladenburg.[2] However, this assumption is contained in all previous determinations of ozone such as we are employing here and must be similarly contained in the present work. Actually, instead of a single bologram in these measurements, four consecutive bolograms were taken with the cell containing no ozone and four more with the cell containing ozone. The average values of the ordinates at corresponding points were compared.

A difficulty enters, however, because of the time which elapses between the taking of the ozone bolograms and the uninfluenced ones which we will call the oxygen bolograms, since a very appreciable change in air mass, or amount of atmosphere traversed, occurs between the two as well as possible weather changes. This was unavoidable with the apparatus at our disposal at the top of Table Mountain because of the nature of the ozone technique, and is not easy to avoid under any circumstances. Under these conditions, the ratio of ordinates outside of ozone absorption would be far from unity and the logarithm far from zero. Standard correction for air mass was, therefore, applied to the average ozone ordinates to bring them to the air mass of the oxygen observations. It is hardly possible, however, to make correction for all differences between the two sets with accuracy sufficient to bring the logarithm of the ratio of ordinates to zero within a quantity small compared to the small ozone effect, and it is not necessary because it is a difference in the logarithm for different wave lengths that is of interest.

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[1] See footnote *2b* on page 2.

[2] Ladenburg, R., Gerlands Beitr. Geophys., vol. 24, p. 40, 1929.

The points shown on the bolograms were chosen as far as possible with respect to the known position of the ozone bands. These bands are shown in Plate 3 as they were obtained in the work described in footnote *2b,* on page 2. The attempt was made to find points on the solar bologram suitable for measurement which lay in every ozone absorption maximum and minimum.

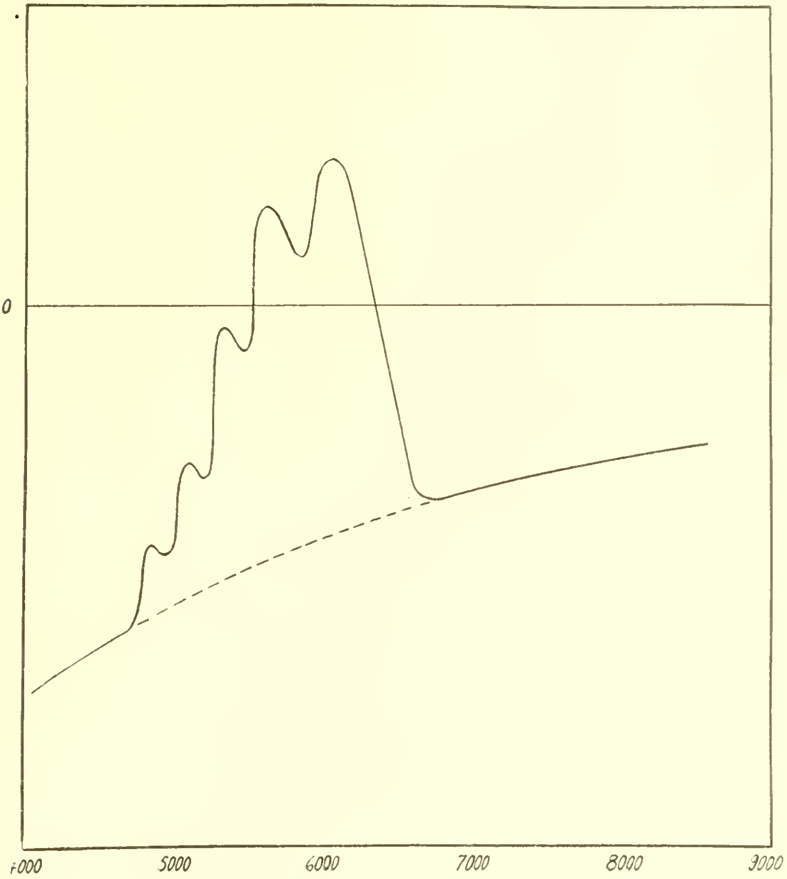

FIG. 2.—Diagrammatic example of ozone area.

From the above considerations, if a plot of the logarithm of the ratio of ordinates is made against wave length, the type of result to be expected is something of the form shown in Figure 2. The failure to make accurate correction for changes in atmospheric transparency or sensitiveness of apparatus will result in the points outside of ozone absorption being something greater or less than zero, here illustrated as less than zero, but this will not obscure the increased value of the ratio in the region of ozone absorption showing as an increase above

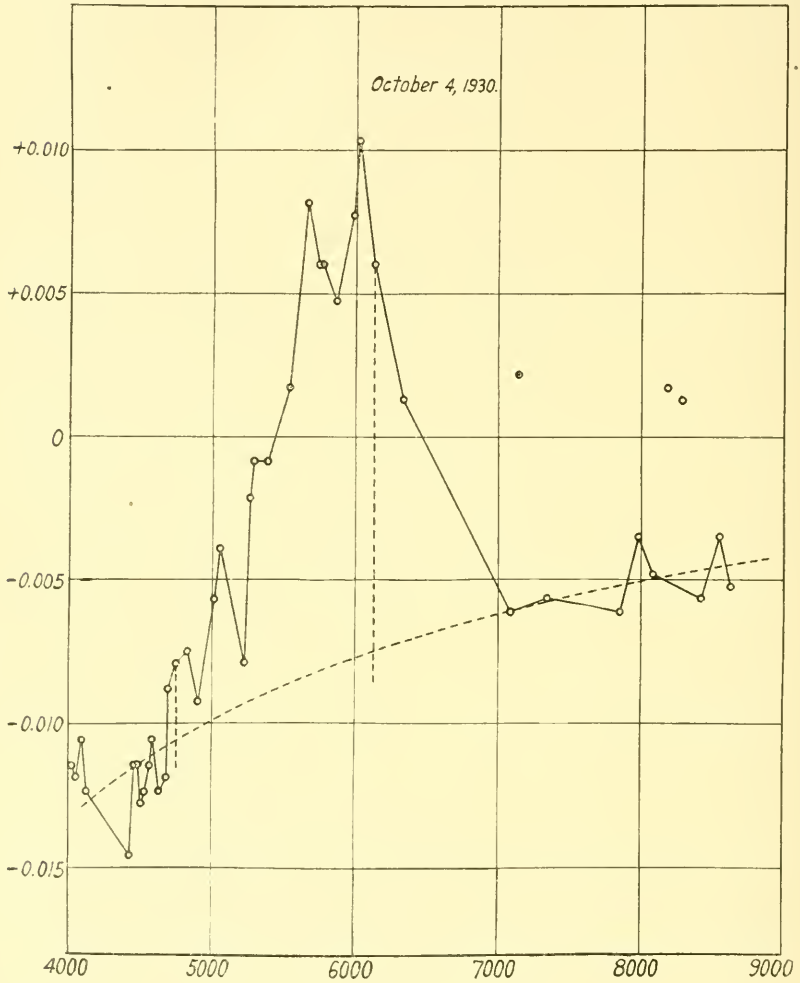

Fig. 3.—Typical ozone area.

the smooth curve passing through the values of the points on both sides of the absorption. It is the area under this curve above the smooth curve which is closely proportional to the amount of ozone in the path.

Figure 3 shows the results of one typical day's observations. For clearness of illustration Figure 2 was made similar to this. In this case an amount of ozone approximately equal to the average atmospheric quantity was present in the cell. Failure to correct exactly for all differences between the two sets of bolograms led to the smooth curve of the points in the absence of ozone absorption being below zero, but the area due to ozone appears clearly and can be measured with sufficient accuracy to be of much use. Several days' determinations were made with larger quantities of ozone in the path, giving areas which can be measured with greater percentage accuracy. On other days smaller amounts were used in order to observe how well such areas could be determined. Included in figure 3 are also three points lying far off the curve which are illustrative of unsuitable points. They lie in weak atmospheric water absorption in the red, which absorption may vary considerably over short intervals of time, rendering the points evidently unsuitable for aiding in ozone determination.

The area under the observed curve should evidently be limited between ordinates whose values are still large compared with the uncertainty in placing the base line. In the blue this has been taken as the value at 4750 Å, while in the red it was necessary to terminate the area at 6135 Å because of the uncertainty in the point at 6335 Å. This limitation was caused by instrumental circumstances which can be altered in the future to include a greater area.

These areas were determined for 10 independent sets of observations, the amount of ozone in the cell being known in each case from the analytical work carried on at the time of the measurements. From these results, shown graphically in Figure 4, a value sufficiently accurate to be useful can be had for the amount of area per unit path length of pure ozone at 0°C and one atmosphere pressure, the common meteorological form of expressing atmospheric ozone. The least-squares solution, assuming the ozone concentration values essentially free from error compared to values for the areas, which method automatically weights the individual values in proportion to the area, leads to the result 21.5 sq. cm. of area per mm. of ozone at standard conditions of temperature and pressure when a plot is made to the scale ordinates 0.001 per cm., abscissa 200 Å per cm. This area can thus be stated as 4.30 Å independent of the scale to which it is plotted. Plotting the data and planimetering the area is a procedure which has the decided advantage of giving a visual record of the amount of ozone which can be judged approximately at a glance. From the results of Colange's data on the absorption coefficient of ozone one can compute this same area, and it may be estimated directly from his published curve of the absorption coefficient. One finds thereby that the value obtained in the present work is about 4 per cent higher than that given by Colange's results, a difference which lies within the limits of error of the present work. With a larger number of sets of observations than the 10 of the present work, and particularly at high ozone values, the accuracy of the determination could, of course, be greatly increased.

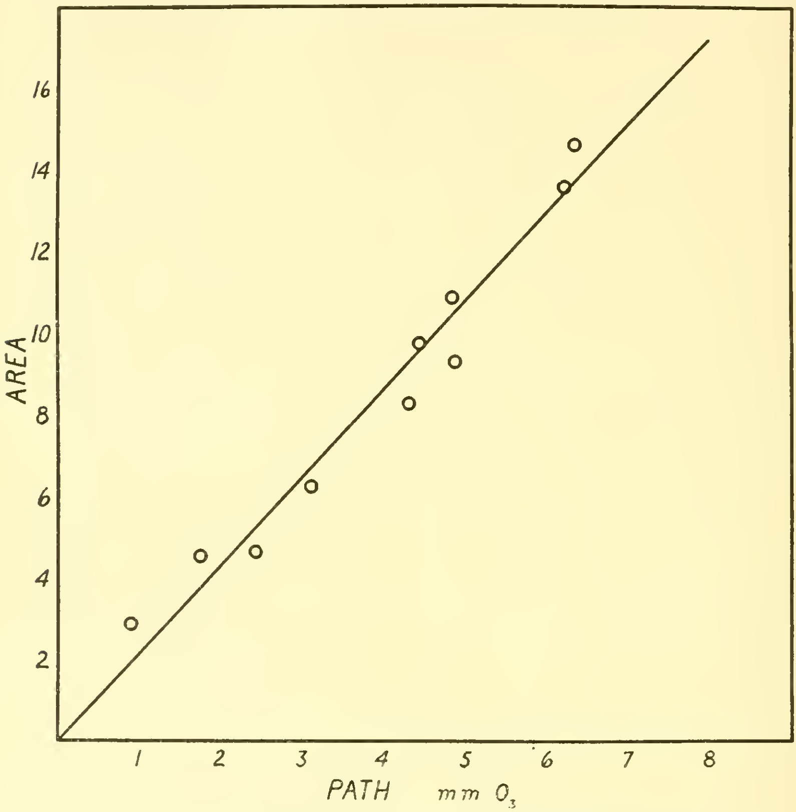

FIG. 4.—Character of the results of the absorption of ozone.

An area such as that illustrated in Figure 3, and pertaining to atmospheric ozone only, can be obtained from atmospheric transmission coefficients, if combined with the knowledge that there is no important atmospheric absorption except ozone across this spectral region. That atmospheric transmission coefficients show unmistakably the ozone absorption has been pointed out and used by Fowle and others.[1]

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[1] Fowle, F. E., Smithsonian Misc. Coll., vol. 81, no. 11, pp. 1-27, 1929. Cabannes, J., and Dufay, J., Journ. Phys. et le Rad., ser. 6, vol. 7, p. 257, 1926.

Figure 5 shows an area analogous to the one shown earlier, determined from the transmission coefficients for March 24, 1929, as a typical day used simply as an illustration. The logarithms of the transmission coefficients for this day, read for all the wave lengths selected in this work, were plotted against wave length and a smooth curve passed through the values lying to both sides of the ozone absorption, and the differences of the points lying in the ozone region from the smooth curve were read. These differences were then plotted against wave length to the scale used above, yielding the area

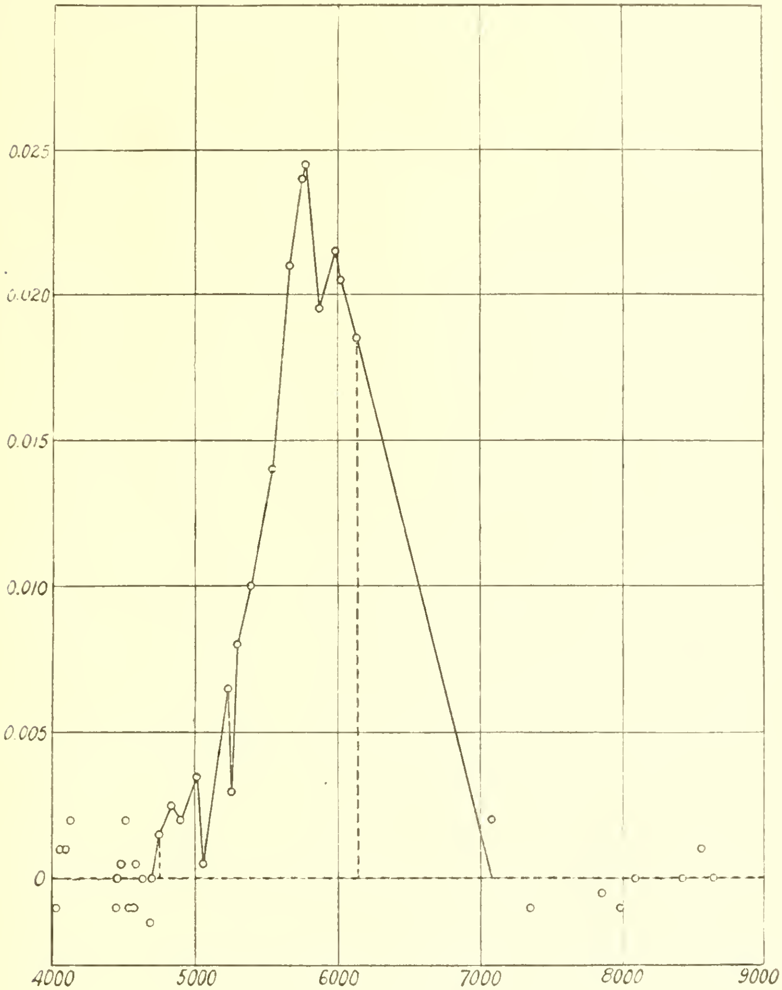


FIG. 5.—Ozone area for March 24, 1929.

shown in Figure 5. Thus the ordinates are the logarithms of the ratio of the intensities before and after passing through the atmospheric ozone. Referring this area so obtained to the results of these present measurements pictured in Figure 4 affords a method of determining the atmospheric ozone based on direct intensity measurements, and yields for this day over Table Mountain, Calif., an ozone value of 3.8 mm., while the value given by Dobson for Table Mountain on this same day was 3.42 mm. A somewhat more satisfactory extension of this method of determining the ozone transmission may be employed, whereby the curved base is reduced to a straight line. Instead of plotting the logarithm of the atmospheric transmission coefficients against wave length and determining the difference of the observed points from the smooth curve in the ozone region, the logarithm of the logarithm of the transmission coefficients may be plotted against the logarithm of the wave length, yielding very closely a straight line, except for points in the ozone region. This fortunate circumstance is due to the approximate inverse λ^n dependence of the logarithm of the transmission coefficients on the wave length. The ozone transmission can be determined from this plot in a similar way from the difference of observed points from the straight line. The transmission coefficients for March 24 were treated independently in this second way. The area resulting was very closely the same as that shown in Figure 5, yielding 3.9 mm. ozone path. It is believed that the application of this method to data of days which give good transmission coefficients affords a satisfactory method for determining atmospheric ozone from direct intensity measurements.

In order to make a somewhat more extensive comparison of ozone values determined by this method with those previously known from observations made with the Dobson apparatus, a series of eight days in 1928 and 1929, for which values by the Dobson method have been obtained at Table Mountain, was treated according to a somewhat abbreviated form of the above method. For these days there were available the atmospheric transmission coefficients as regularly read and already computed from the " long method " observations at Table Mountain. These values are not given at all points used in the determination of the area defined in this present work, but at the regular spectrum points ordinarily determined in the solar-constant work. These relatively few points are scattered over the spectrum in such a way as to outline, somewhat less accurately to be sure, essentially the same area as that defined in the present work. In particular there were but four ordinates lying in the ozone region, but if these values were sufficiently accurate the area of ozone absorption outlined by them, and lying between the wave lengths specified above, would be sufficiently close to the area defined in the above work to yield a satisfactory determination of the ozone.

For these eight days, then, the logarithms of the logarithms of the transmission coefficients were plotted against the logarithm of the wave length and a straight line passed through the values lying to both sides of the ozone absorption. The differences of the antilogarithms of those points lying in the ozone region from the antilogarithms of the corresponding points on the straight line were read. These differences were then plotted against wave length to the same scale as that described above and the areas planimetered and divided by the area corresponding to 1 mm. of ozone path, determined as the result of the work described in this paper. Thus an approximate determination of the ozone on these days was afforded, utilizing an area practically the same as that described above, defined by the positions in which these points lay. The results are shown in Table 1. For these eight days the values of the ozone over Table Mountain as determined by the Dobson method were also available and they are given in this table for comparison. From these results it appears that the average amount of ozone given by the two methods is essentially the same. The independent values, however, are not in good accord, which may be entirely due to the uncertainties in the present determinations. It must be emphasized that this is due to the insufficiency of the data used to make such a determination, which had been collected from solar-constant work, and not to the method employed. It is to be noted especially that differences in the *relative* values for the eight days obtained by the two methods of Dobson and of Wulf cannot be due to the *method* of the ozone absorption measurements described in this paper, but must be contained in the roughness of the data. For quite independent of the evaluation of the areas in terms of ozone, these areas should be closely proportional to the ozone values on these days. That they are not is actually due largely to the uncertainties in

TABLE I.—*Atmospheric Ozone for Eight Days*

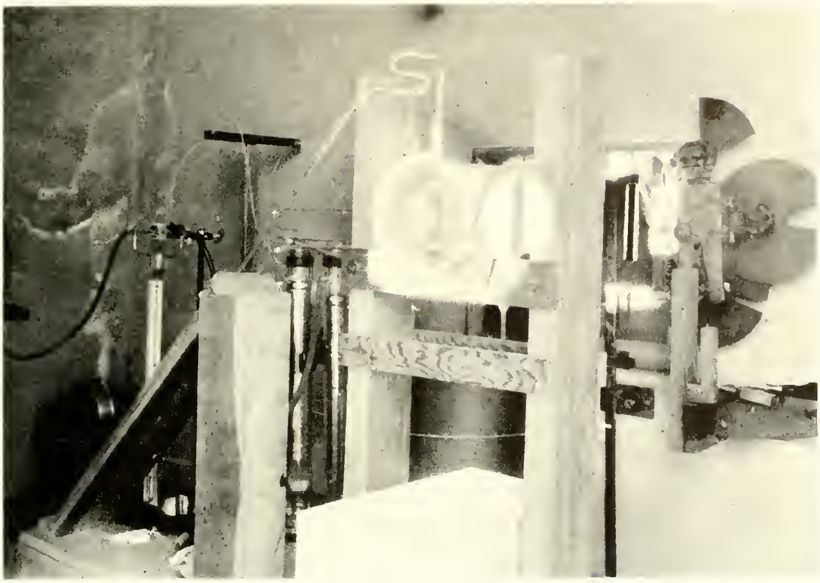
	Path mm. O_3	
Date	Present work	Dobson
Aug. 1, 1928	2.1	2.24
Oct. 3, 1928	2.9	2.28
Nov. 4, 1928	2.5	1.97
Dec. 8, 1928	1.9	1.98
Dec. 18, 1928	1.8	2.53
Dec. 19, 1928	2.4	2.43
Mar. 24, 1929	2.8	3.42
Apr. 23, 1929	2.4	3.08
Mean	2.35	2.49

the transmission coefficients, which in this case define the ozone area. This is shown by a comparison of the March 24 value in this set of eight with the value for this same day as given above, which was determined from the transmission coefficients at all the points chosen in the above work. The former value is 2.8 mm., while the latter 3.9 mm., and the latter is, as stated above, believed to be a satisfactory determination. The cause of this discrepancy appears to lie chiefly in the fluctuations in the few observed transmission coefficients. To summarize: The use of the few single values of the transmission coefficients as regularly determined in the solar-constant work only suffices to define an area which gives the approximate amount of ozone and is not ordinarily competent to show the fluctuations from day to day within an error small compared to the fluctuations.

SUMMARY

The transmission of ozone for visible light has been determined from spectrobolometric data using the solar spectrometer of the Smithsonian Institution at Table Mountain, Calif., with the sun as the source and introducing chemically determined quantities of ozone in the path of its rays. The results are in close accord with the laboratory results of Colange. Using the results of this study the amount of ozone over Table Mountain for one typical day as an illustration has been determined. By an abbreviated method, using only the transmission coefficients normally measured in the regular solar work, the value for the ozone over Table Mountain has been determined for a series of eight days. The mean of these eight days presumably gives a good value for the mean amount of ozone, but this abbreviated method is not ordinarily sufficient to show the fluctuations in the ozone, since the possible error in a single determination is of the order of the fluctuations. The mean value for the eight days differs but about 6 per cent from the mean value for the same days determined by the method of Dobson. It is very interesting that the bolographic method depends on ozone absorption in the yellow, while Dobson's photographic method employs the ultraviolet ozone absorption.

The author wishes to express his sincere thanks to Dr. C. G. Abbot for suggesting the problem and for his continued interest and help throughout the work, and to Mr. J. A. Roebling for a financial grant which made the work possible. The efforts of a number of people have contributed directly to the completion of this work, especially Mr. Alfred F. Moore, Mrs. Beatrice J. Wulf, Mr. Fred Greeley, and Mr. George Cox. The author is grateful to the members of the Smithsonian Astrophysical Observatory for their frequent kind assistance.



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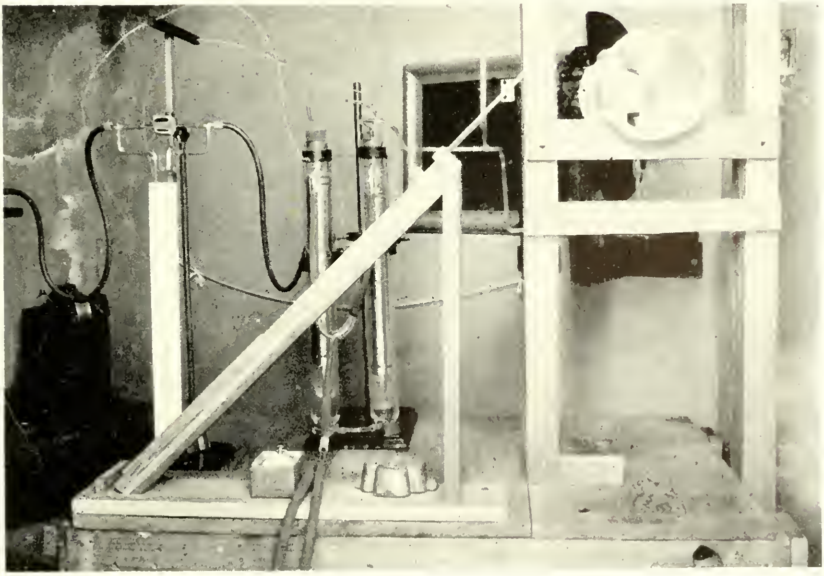

2

Two views of absorption cell and auxiliary apparatus.


-7 -6
-3 -5
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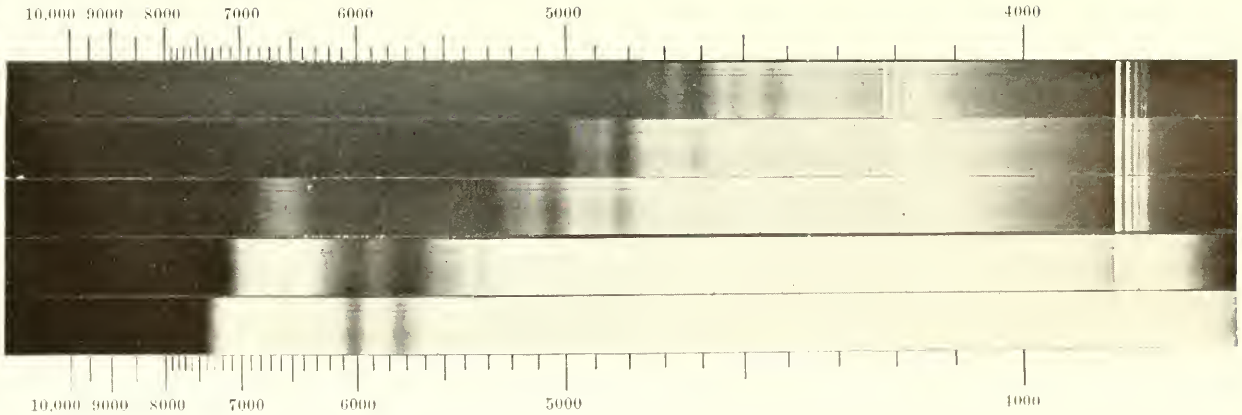

Absorption spectrum of ozone in the visible.

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HUMAN HAIR AND PRIMATE PATTERNING

(With Five Plates)

BY
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Curator, Division of Mammals, U. S. National Museum

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HUMAN HAIR AND PRIMATE PATTERNING

By GERRIT S. MILLER, JR.,
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(With Five Plates)

Few problems have caused more perplexity to anthropologists, physicians, and zoologists than those presented by human hair. Why is it that only some relatively small areas of the human skin are normally capable of bearing a hair growth dense enough to be in any way comparable with the fur of other mammals? Why do men have beards and women not? Why are beards better developed in some races than in others? What is the cause of baldness, and why is there no certain cure for it? Why does baldness commonly occur on the crown and rarely on the sides of the head? Why do we turn gray? Why does grayness usually show itself first on the temples or in the beard? Why does the moustache often remain dark after the beard has turned gray? Why do we have hairy eyebrows, and why, when there is a difference in color between the hair of the eyebrows and that of the head, are the eyebrows usually the darker of the two? Why is the hair of the scalp often different in quality from that of other parts of the body? Why are there several types of hair—kinky, curly and straight?

To all of these questions so many and such unsatisfying answers have been suggested that it would be a huge and useless task to try to list them. Variable and inconclusive though they are, most of the answers possess one quality in common, namely, they have in their background the tacit assumption that all these peculiarities of human hair are things that arise from man's special constitution and its reaction to the natural environment or to the artificial conditions that man has imposed upon himself. It has, for instance, been urged that the general bareness of the human skin comes from the widely prevalent habit of wearing clothes; that baldness comes from barbers and tight-fitting hats; that women have less baldness than men because women have for centuries taken better care of their scalps than men have; that graying hair is the result of a lessening bodily energy supposed to go with increasing civilization or "domestication;" that the axillary and pubic tufts of hair were once useful for babies to cling to; that eyebrows exist for the purpose of keeping sweat from running down into the eyes; that men are bearded to protect their throats from cold weather; that women are beardless because they look better that way. All of which gives evidence of ingenuity if of nothing else.

But not one of the explanations that I have been able to find in print has taken into consideration the zoological possibility that many features of the human hair system may be generalized primate traits instead of specifically human developments. By this I mean the possibility that they may be characteristics that are forced on man because they are common property of the Primates, the animal group to which man pertains. Their explanation, in that event, would have to be made less in terms of human activities and requirements than in terms of the great heritage of characteristics that man shares with all his primate relatives. Each one of these creatures has modified his portion of this heritage in such a way as to make it his own; or, in more technical language, each one of the 800-odd kinds of living apes, monkeys, and lemurs has developed " specific " characters by which it can be distinguished from all the others while remaining none the less a primate among primates. That man should have done the same thing would be far from strange.

This paper is a brief summary of a study on which I have been engaged for several years with the result that I have become convinced that the chief peculiarities of human hair are best and most simply explained as special examples of primate " patterning."

WHAT IS MEANT BY " PATTERNING "

Patterning is familiar to every systematic zoologist because it is seen in every group of animals. It consists in the arrangement of (a) contrasted colored areas on the surface of the body, or (b) contrasted long and short outgrowths from the surface of the body, or (c) combinations of colors and outgrowths, in such a manner that the resulting patterns of color or form are sufficient to distinguish one related species from another.

Familiar examples of patterning are furnished by the color markings of butterflies, or of the American wood warblers, by the minute surface sculpture on the shells of some mollusks, and by the spiny outgrowths on the back and head of the different species of iguana and horned-toad. Among mammals, striking instances are provided by cats and squirrels with their diverse stripes, spots, mottlings, and plain colors, and by African antelopes with their stripes and spots as well as their maned necks, fringed throats and briskets, and tufted tails.

The making of patterns appears to be a process quite distinct from that by which a general harmonizing of animals with their natural surroundings has been effected. Nearly allied, pallid, desert species, for instance, may be distinguished from each other by details of individual pattern as obvious as those that serve to mark richly colored species living in humid forests. General types of color and surface may have their relations to the surroundings in which animals pass their existence; but the special patterns of the species that conform to any one type cannot be shown to have such relations. It may be plausibly argued that the blotched and spotted color schemes of arboreal warblers and the streaked color schemes of grass-living finches have something to do with the unlike surroundings in which warblers and finches pass their lives. But this argument would not apply to the differences between the patterns of Blackburnian and black-throated green warblers nesting together among the same evergreens, nor to those between savannah and grasshopper sparrows living in one meadow. Still less would it be possible to explain, on grounds of special needs, why species of horned-toad differ from each other in the number and form of the spiny outgrowths on the head, or why one species of gnu has a fringe on the brisket and another has not. Patterning, therefore, seems to be something physiologically inherent in animals rather than something that the environment has imposed upon them.

PATTERNING IN PRIMATES

Though patterning occurs in all groups of mammals—even in rhinoceros, hippopotamus, elephant, and cetacean—it is among the primates that the tendency attains its greatest development. In no other group does it make such full use of its chief materials, namely, the color of the skin, the color of the hair, and the contrasts that can be obtained from differences in quality and length of hair. No better example of this process could be given than the one furnished by the head markings of monkeys grouped on Plate 1. The animals there represented are nearly related species that live under essentially uniform surroundings in the great African forest belt. No two of them have the same arrangement of dark and light areas on the head; three have conspicuous white stripes over the eye; one has a black stripe in the same place; in five the cheeks are white, while in three they are not white; one (fig. 2) is bearded, while seven are not; one (fig. 4) has a moustachelike mark of white in the skin of the upper lip; another has a boldly contrasted spot of fine white hairs on the nose. Other patterns in primates come from lengthening, shortening, and varying the direction of growth of the hair on different parts of the crown, also from varying the length and quality of the hair on the chest, shoulders, tail, and legs, and from making contrasts, often more striking than the one seen in the white-lipped guenon shown on Plate 1, in the color of different portions of the skin itself. All of these elements of color and hair growth are combined and recombined in a variety that seems to be without end.

On no part of the primate form is patterning so conspicuously developed as on the head, where strikingly marked color designs of both hair and skin are profusely exhibited, and where tufts, beards, moustaches, whiskers, and crests are brought into varied contrast with areas of short hair and bare skin.

PATTERNING ON THE HUMAN HEAD

In conformity with this universal primate trait human patterning shows itself more conspicuously on the head than on the body or limbs.

The human head pattern is not exactly duplicated by any other primate, but all the elements that enter into it can be easily found in nonhuman members of the order. The usual head pattern of the young adult Caucasian is shown in Plate 2, Figures 1 and 2. Characteristics that both sexes have in common are the completely haired cranium, the bald forehead, nose, and upper median part of the cheeks, and the presence of a narrow transverse hairy strip on the forehead over each eye. The female's pattern differs from the male's in an extension of the bare area downward over the entire lower part of the face and sideways to the ears.

In most primates the forehead and face, except the region immediately bordering the eyes, nose and mouth, are thickly haired. The first step in the process of baring the forehead is shown by one of the Celebean macaques, *Magus hecki* (pl. 2, fig. 3). Other steps have been taken by some of the South American monkeys; while an essentially human forehead can be found in the orang (pl. 2, figs. 4, 6). The bare or nearly bare lower part of the face seen in the females of all human races, and in the males of those races in which the beard is slightly developed, is presaged by the very common occurrence among other primates of a short-haired, nearly bare area around the mouth (shown by all of the monkeys represented on pl. 1). Extensions of this bare area on the cheeks may be seen in the great apes. It is carried farther in some of the South American monkeys, culminating, apparently, in the " cotton head," *Oedipomidas oedipus* (pl. 2, fig. 5), which has reached a stage slightly more advanced than that of the human female.

Though a bare or nearly bare condition of the mouth area is the usual condition among nonhuman primates, it is not universal. Beards like those of the male Caucasian or Australian occur in the orang (pl. 2, fig. 6), in the bearded African guenon shown at the top of Plate 1, and in a South American monkey (*Pithecia chiropotes*) of which I have not been able to obtain a photograph. Moustaches are not common among primates. Even that of the full-bearded orang is poorly developed. But the South American *Mystax imperator* (pl. 2, fig. 7) goes far to make up for this deficiency. While neither moustache nor beard is peculiar to man the strong development of both together appears to be a human specialty.

Nothing exactly like the human eyebrows is known in other primates, but the brow region is one where patterns are made in great profusion. Sometimes these brow patterns take the form of light or dark stripes (as shown in pl. 1 and in pl. 4, figs. 10 and 13); sometimes they are made by lines of hair differing in quality and direction from that of the head (pl. 2, fig. 8), thus showing a near approach to the condition found in man. Human eyebrow hair, as is well known, often differs in color from the hair of the crown. In such cases (pl. 4, figs. 11, 12) it is usually darker than the crown hair, after the manner of the gray-cheeked mangabey (pl. 2, fig. 8) or the Himalayan langur (pl. 4, fig. 10); rarely if ever is it conspicuously lighter, after that of the white-browed gibbon (pl. 4, fig. 13).

This normal human pattern does not always remain constant throughout life. Changes of two kinds usually take place; and the courses of both kinds tend to follow lines that can be traced through the group of primates at large.

TURNING BALD

With arrival at full maturity a considerable percentage of human males undergo a modification of their hair pattern that serves to differentiate them still further from the females. The forehead line begins to rise, either uniformly along its entire extent (pl. 3, fig. 1), or, more commonly, by pushing back a blunt reentrant wedge on each side (pl. 3, fig. 4). Frequently a bare spot begins to form at the same time on the top of the crown (pl. 3, fig. 6), and the hair of the entire median part of the crown becomes sparse. These changes may continue until the bald forehead area has been carried back over the dome of the head, leaving a well-haired border extending around the sides and across the nape (pl. 3, fig. 8).

This series of maturity changes in the hair covering of the human male head has been the subject of endless speculation. By a few writers it has been recognized to be, like the beard, a secondary sexual character,[1] but, so far as I am aware, no one has hitherto shown that it follows the lines laid down by the patternings of other primates. The uniform raising of the forehead line can be found as a specific character in the bald chimpanzee; it is exactly paralleled by the pattern of short and long hairs on the head of one South American monkey, *Pithecia monachus* (pl. 3, fig. 2), and by the color pattern of another, *Cebus hypoleucus* (pl. 3, fig. 3). The development of the two blunt wedges results in a pattern much like the one present in the Celebean black ape, *Cynopithecus niger* (pl. 3, fig. 5). The bald spot on top of the crown is an occasional character of the toque macaque, *Macaca pileata* (pl. 3, fig. 7). The completely developed human bald area (pl. 3, fig. 8) is perfectly outlined in the South American monkey known as *Cacajao rubicundus* (pl. 3, figs. 9 and 10). The long dark hair at the side and back of the head of this animal occupies the area that remains haired in normal human baldness, while the light hair on the median area corresponding with the human bald spot is so short and sparse that it does not conceal the skin of the scalp in the living animal (two have recently been on exhibition in the National Zoological Park). Finally it is to be noticed that the human bald area follows the outline of the dark cap of the West African gorilla (pl. 5, fig. 5) as well as that of a color pattern not infrequently seen in blond men. This pattern, (which appears to occur in women also, but is obscured by long hair) is produced by an obviously paler tint of the hair that grows on the bald-spot area. It is visible as a faint but accurate picture of the color pattern made by a bare scalp contrasted with dark side hair. At the Harvard commencement exercises of 1930 I saw it on the heads of seven of the young men awaiting the conferring of their degrees.

TURNING GRAY

Another change in the human hair that begins at or slightly after the attainment of full maturity is seen in the familiar process of turning gray; this may lead in the end to a stage when all the pigmented hairs of the entire body have been replaced by colorless ones.

This loss of color, like baldness, has given rise to conjecture without end. And, as in the case of baldness, its near relation to primate patterning seems to have passed unnoticed. Nevertheless, it can be

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[1] The examination of many hundreds of photographs makes it appear probable that the males of races with strong beards tend to show the highest percentage of baldness, thus differentiating themselves most fully from the females.

shown to have the same tendency to follow the main lines of primate pattern making.

When gray hairs begin to replace the pigmented ones they do not appear uniformly all over the body. " A vigorous man just beginning to show a touch of gray on the temples " is an often-heard phrase that unconsciously recognizes this fact. When beards were common among us everyone knew how usual it was for them to turn gray before the scalp.

As they increase in numbers the gray hairs tend to form patterns. These are sometimes nothing more than faint sketches or suggestions. Often, however, they develop into striking color contrasts. The faint and fugitive human patterns are not always easy to correlate with the patterns of other primates, but the definite ones rarely present any such difficulty.

Eight of these well defined human color patterns with their primate homologues are shown on Plates 4 and 5.

The first and second (pl. 4, figs. 1 and 3), consisting of a white beard contrasted with a dark crown, are frequently seen. In the first the mouth area is white. In the second it is dark. Both occur in many species of monkey, two of which, the African *Erythrocebus pyrrhonotus* and *Cercopithecus l'hoesti*, are shown in Figures 2 and 4. The identity is so obvious that it requires no comment.

The third pattern (pl. 4, fig. 5), consisting of a white chin beard sharply contrasted with dark whiskers and head, is less common. Sometimes the white involves the moustache. It is then exactly the same as the white area in the African monkey *Cercopithecus brazzae* (pl. 4, fig. 6). I have seen several examples of this human pattern with white moustache, but have not yet secured a photograph.

The fourth pattern (pl. 4, figs. 7, 8, 9) is merely a dark mark on the cheek margin of a gray beard accompanying a gray or bald head. Insignificant though this marking may seem, it is surprisingly common. On April 21, 1930, I visited the Jewish pushcart market district in New York City, one of the few convenient places where many full beards can now be seen, to look for this mark. I found it in no less than 47 out of 55 men with gray or white beards. The same dark line at the edge of the longer hair on the cheeks is found in many of the monkeys that have a partly bare median facial area. An example is shown in Plate 4, Figure 10, the Himalayan langur (*Pygathrix schistacea*). It may be easily observed in immature Japanese macaques, animals that are often exhibited in zoological gardens.

The gray human temple spot (pl. 5, fig. 1) is a common feature of primate color patterning. It is particularly well developed in the gelada baboon (pl. 5, fig. 2).

As they increase in size the temple spots often extend backward along the sides of the head until they cover the entire area that remains haired in normal baldness. The pattern thus formed—dark cap contrasted with grizzled sides and back of head (pl. 5, figs. 3, 4)—is a common one among non-human primates. It is particularly well developed in the West African gorilla (pl. 5, fig. 5. The specimen represented by this photograph is an unmounted skin with the head not filled out to natural form). Occasionally this pattern may be seen reversed. The grizzling is then confined to the area of the normal bald spot, while the hairs at the sides and back of the head remain dark. When this happens the color scheme of the cacajao monkey (pl. 3, fig. 10) is reproduced.

White locks situated on or near the forehead line (pl. 5, figs. 6, 7) are not uncommon, but on other parts of the head they are rare. They may be present without other signs of the graying process (as in fig. 6) or they may appear as a step in that process (as in fig. 7). In either event they are usually confined to some part of an area where patterning occurs in nonhuman primates (pl. 4, fig. 6, pl. 5, fig. 8[1]).

PATTERNING ON OTHER PARTS OF THE HUMAN BODY

The process of turning gray usually begins on the head and extends gradually downward over the body. As it advances it often passes through a stage, particularly well represented in Figure 9 of Plate 5, in which the gray area ends abruptly at the middle of the chest, leaving the hair of the arms and lower part of the body dark. The general lines of a pattern found in an African colobus monkey, *Colobus polycomos,* and in an Asiatic macaque, *Macaca albibarbata* (pl. 5, fig. 10), are then closely followed.

Turning to other parts of the human body we find that the same correspondence with widely distributed primate tendencies holds good.

The pubic region is an area of pattern formation in widely separated nonhuman primates. Young chimpanzees have a white pubic patch contrasted with the black surrounding hair. It disappears by becoming black before the animals reach full maturity. Some species of gibbon have no pubic mark whatever. Others display a black spot

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[1] The spider monkey represented in fig. 8 of pl. 5 has a band of white extending along the entire frontal border of the true head-hair. The forehead-hair is also white, but it differs from the head-hair in quality and in direction of growth. Before photographing this skin I darkened the forehead-hair with ink.

that stands out against its pale surroundings. Still another gibbon has the hair of this region so greatly lengthened that, in adult males, it may form a tassel reaching almost to the knees. A South American monkey (*Oreonax hendeei*) has a long yellow hair tuft in the male and two shorter tufts in the female. In both sexes the tufts are rendered very conspicuous by contrast with the dark belly and thighs. By specializing the hair of this region man has, therefore, merely followed one tendency of his tribe.

The last conspicuous hair-pattern feature of man is the tuft in the arm pit. This, perhaps, comes the nearest of all the patterns to being an exclusively human trait; I have not yet seen an exactly similar development in any other primate. But, on gently blowing the hair of the axillary region of a freshly dead African monkey, *Cercopithecus aethiops,* I once found that the hairs growing in the deepest part of the pit tended to separate themselves from the surrounding fur by a slight difference in quality and in the direction of growth. More recently I have been able to see, in several adult chimpanzees,[1] that these animals have a definitely specialized axillary tuft confined to the region of greatest glandular activity. To produce the human condition it would merely be necessary to suppress the long surrounding hair.

SOME OTHER FEATURES OF HUMAN PATTERNING

A few other points about human patterning require brief mention.

(a) The general bareness of the human body.

Why the human body lacks a protecting general coat of fur is a question that has been often asked and variously answered. A final explanation seems to be as remote now as ever; but it is possible to recognize the fact that human bareness is only an exaggeration of a tendency that is found in other primates,[2] and that it is no more essentially mysterious than the bare face of one tropical American monkey (pl. 2, fig. 5) when compared with the fully haired face of another (pl. 2, fig. 7). In neither instance can it be shown that a special need of the species is served by the bare skin; but in both it is evident that the tendency found throughout the primate group to form patterns by contrasting long-haired areas with short-haired areas has been carried to an extreme.

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[1] At the Yale University Anthropoid Experiment Station, Orange Park, Fla., an opportunity for which I have to thank Professor Yerkes and Dr. Tinklepaugh.

[2] On this subject see Schultz, Human Biology, vol. 3, pp. 303-321, September, 1931, and Sci. Monthly, vol. 33, pp. 392-393, November, 1931.

The general distribution of longer and shorter hair on the body of gorillas rather closely coincides with the human scheme. By continuing the process along the lines marked out in this great ape a stage would eventually be reached in which the body would become bare while the arms and legs retained traces of their original coat.

(b) The different face pattern of men and women.

The sexual hair pattern on the human face is another subject of age-long speculation. No one has ever been able to show that its presence has aided man's career as a species. Equally impossible would it be to show that the analogous sexual patterns in other primates have given these species any advantage over their relatives that lack them. But it seems clear that in this respect man has developed in the same general way as the white-cheeked gibbon of Siam, the orangs of Borneo and Sumatra, the black howler monkey of South America, and the macaco lemur of Madagascar, all of which have sexes that differ from each other in appearance. That is to say, man and these other primates have followed a tendency that may crop out anywhere in the group of animals to which they all belong.

(c) Racial differences in hair pattern and in general color of the hair.

It is well known that not all races of man are exactly alike in hair pattern. Some have better developed eyebrows, beards, pubic patches, or axillary tufts than others; some appear to be not as subject as others to grayness and baldness. Racial tendencies toward darker or lighter colored hair are also well known. These racial characteristics have never been satisfactorily explained on the basis of the special needs of different peoples. On the other hand, as examples of the slight differences that are everywhere found among races of primates nearly related to each other they are readily understood.

The differences between the two races of orang, for instance, are of this nature. The United States National Museum contains 6 males and 6 females of the Sumatran orang, 6 males and 10 females of the Bornean race, all adult or nearly adult. These two series show the same kind of differences that are shown by races of men. In the first place, the beards of the males are much better developed than those of the females. Then, when the beards of the Sumatrans are compared with those of the Borneans they are at once seen to be larger, so much so that an adult male from either island can usually be recognized at once by this feature alone. Finally there is a general difference in the color of the hair on body and head, this being more tawny in the Sumatran race, more mahogany brown in the Bornean.

These two races of orangs inhabit separate parts of one climatic zone, exactly as Caucasians and Mongolians inhabit opposite ends of another. Therefore the differences in hair growth can be no more attributed to the influence of unlike natural surroundings in the second instance than in the first. But it seems clear that the two races of orang and the two races of men are both in early stages of species differentiation, and that the manner of their differentiating is one that is common to the whole primate group.

(d) Total graying.

Often, though not invariably, the process of turning gray culminates in a stage of complete whiteness. But even when a human being has turned gray over the entire body or even has lost all hair color he has done nothing that is essentially new or peculiar for a primate. Light gray or nearly white species of primates have arisen in both Asia and South America. These animals are not albinistic nor in any way individually abnormal. Their near relatives, living in the same regions, are richly colored; and there is nothing to indicate that either light or dark has any advantage over the other. General graying and whitening in man seems likely to be nothing more than another example of human submission to a rule that some other primates have followed. Therefore the strong tendency present in the " white race " of man for the hair to lose its color at an early age may be part of a racial process of depigmentation that has already almost whitened the skin and that may be destined, in the future, to bring about permanent whitening of the hair as well.

CONCLUSION

For the present I wish to avoid detailed discussion of the published attempts to explain those peculiarities of human hair that have just been passed in review. Most of the authors who have considered the subject have done so from the view-point that these peculiarities must have originated from conditions (pathological or cultural) or needs (physiological or esthetic) that pertain exclusively to man. That this view-point is wrong seems to be sufficiently indicated by the evidence here selected from the large mass that I have assembled. This evidence points to the probability that man has these characteristics because, as a primate, he cannot avoid them. They are common property of the great group of mammals to which he pertains, and neither he nor any other member of this group can wholly escape from the tendencies imposed on all of them by their primate heritage. With regard to no nonhuman primate can it be shown that the possession of any special assortment of these characteristics makes a species better, more efficient, or more at ease in the world than one that has another assortment. So also with man.

The similarities that I have shown to exist between some hair characteristics of man and those of particular monkeys and apes must not be supposed to indicate any special relationship between man and these other primates. When superficial features of this kind are common to a whole group they will often appear in almost identical form in two animals whose relationship is shown by their anatomical structure to be remote.

EXPLANATION OF PLATES

All figures greatly reduced, not to scale

Plate 1

Color patterns on the heads of eight species of African guenon (*Cercopithecus*). From Elliot, after Pocock.

Plate 2

The human head-hair pattern and its characteristics as they occur in other primates.

Figs. 1, 2. Young adult Caucasian.
Fig. 3. Partly bare forehead of a Celebean macaque (*Magus hecki*).
Fig. 4. Bare forehead of an orang.
Fig. 5. Bare face of a "cotton head" (*Oedipomidas oedipus*).
Fig. 6. Beard of an orang.
Fig. 7. Moustache of a marmoset (*Mystax imperator*).
Figs. 8, 8*a*. Eyebrows of a mangaby (*Cercocebus albigena*).

Plate 3

Types of human baldness and the corresponding conditions in other primates.

Fig. 1. Raised human forehead line.
Fig. 2. A South American monkey (*Pithecia monachus*) with hair pattern corresponding with the raised human forehead line.
Fig. 3. A South American monkey with color pattern corresponding with the raised human forehead line.
Fig. 4. The two reentrant forehead wedges in man.
Fig. 5. The two reentrant forehead wedges in the Celebean crested macaque (*Cynopithecus niger*).
Fig. 6. Bald spot at middle of crown—human.
Fig. 7. Bald spot at middle of crown—toque macaque (*Macaca pileata*).
Fig. 8. Complete, normal, human bald crown area.
Figs. 9, 10. Nearly bald crown area in a South American monkey (*Cacajao rubicundus*).

PLATE 4

(a) Human color patterns formed during the process of turning gray and the corresponding patterns in other primates.

FIG. 1. White face contrasted with dark head in man.

FIG. 2. White face contrasted with dark head in an African monkey (*Erythrocebus pyrrhonotus*).

FIG. 3. White face contrasted with dark mouth area and dark crown in man.

FIG. 4. White face contrasted with dark mouth area and dark crown in an African monkey (*Cercopithecus l'hoesti*).

FIG. 5. White chin and lower lip contrasted with dark face and head in man.

FIG. 6. White chin and mouth area contrasted with dark face and head in an African monkey (*Cercopithecus brazzae*).

FIGS. 7, 8, 9. Dark area at edge of light cheek hair in man.

FIG. 10. Dark area at edge of light cheek hair in an Asiatic monkey (*Pygathrix schistacea*).

(b) Eyebrow patterns, human and simian.

FIGS. 10, 12. Dark eyebrows contrasted with light head hair.

FIG. 11. Dark eyebrows contrasted with hair that has turned white.

FIG. 13. White eyebrows contrasted with black head (white-browed gibbon, *Hylobates hoolok*).

PLATE 5

Human color patterns formed during the process of turning gray and the corresponding patterns in other primates (continued).

FIG. 1. The human gray temple area.

FIG. 2. The gray temple area in the gelada baboon (*Theropithecus gelada*).

FIGS. 3, 4. The human gray temple area extended around the head.

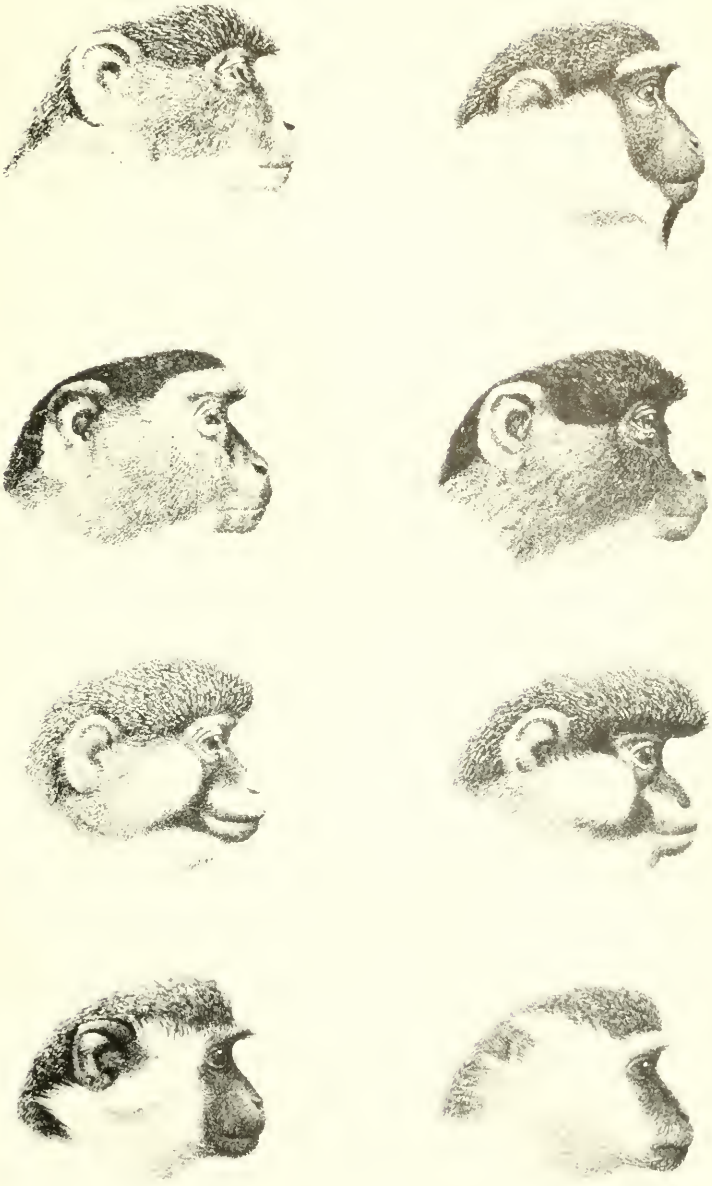
FIG. 5. Color pattern on the head of the East African gorilla.

FIGS. 6, 7. White locks on the human forehead line.

FIG. 8. White stripe along the forehead line in a South American spider monkey. (*Ateles hybridus*).

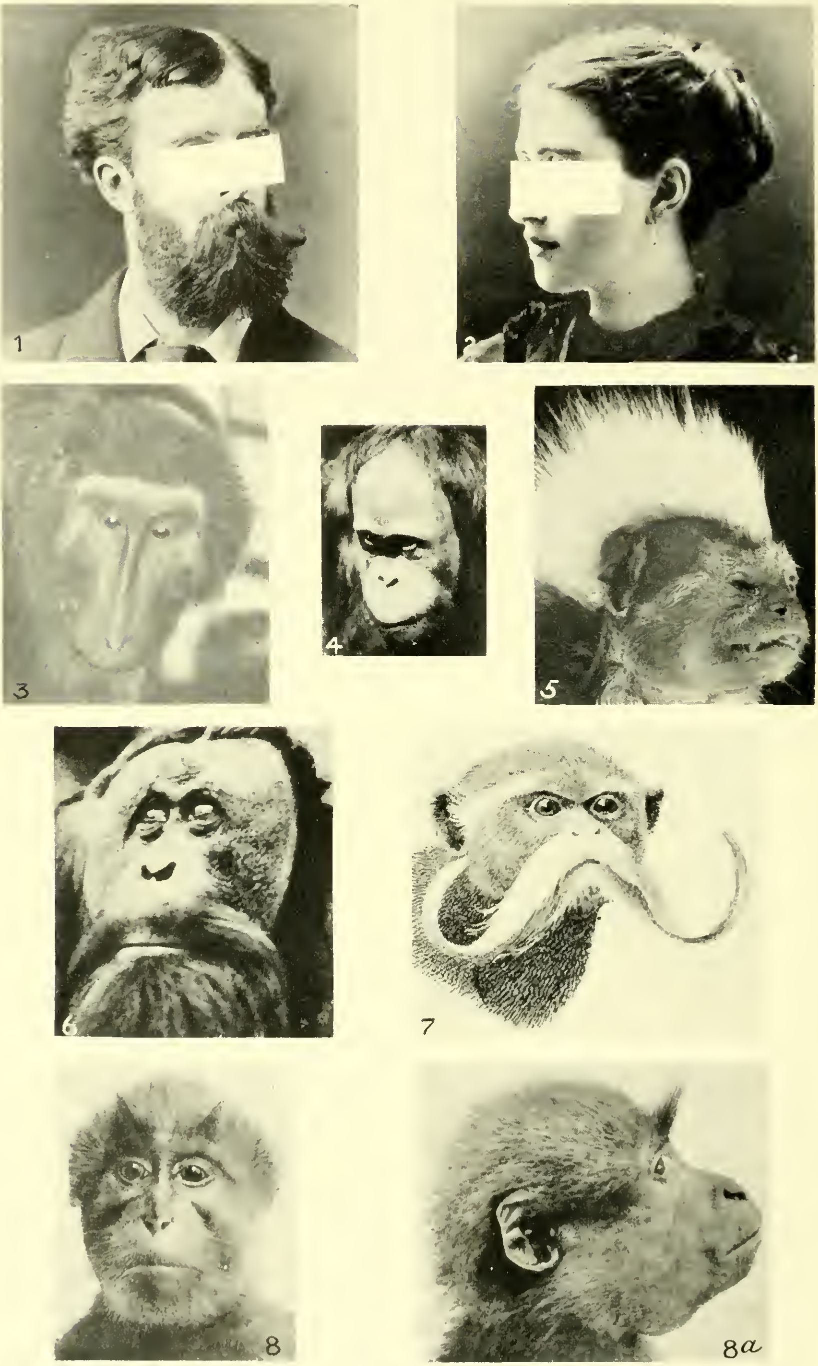
FIG. 9. Gray area extending downward from head to middle of chest in man.

FIG. 10. Gray area extending downward from head to middle of chest in an Asiatic monkey (*Macaca albibarbata*).



Patterning on the heads of eight species of African monkey.

(For explanation see p. 12.)

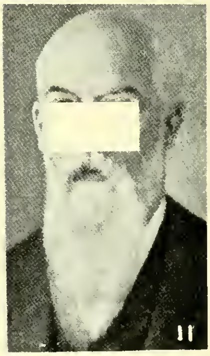


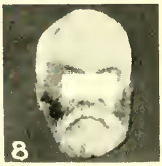
Human face patterns compared with the analogous patterns of five kinds of nonhuman primates.

(For explanation see p. 12.)

Human baldness patterns compared with the analogous patterns of five kinds of nonhuman primates.

(For explanation see p. 12.)

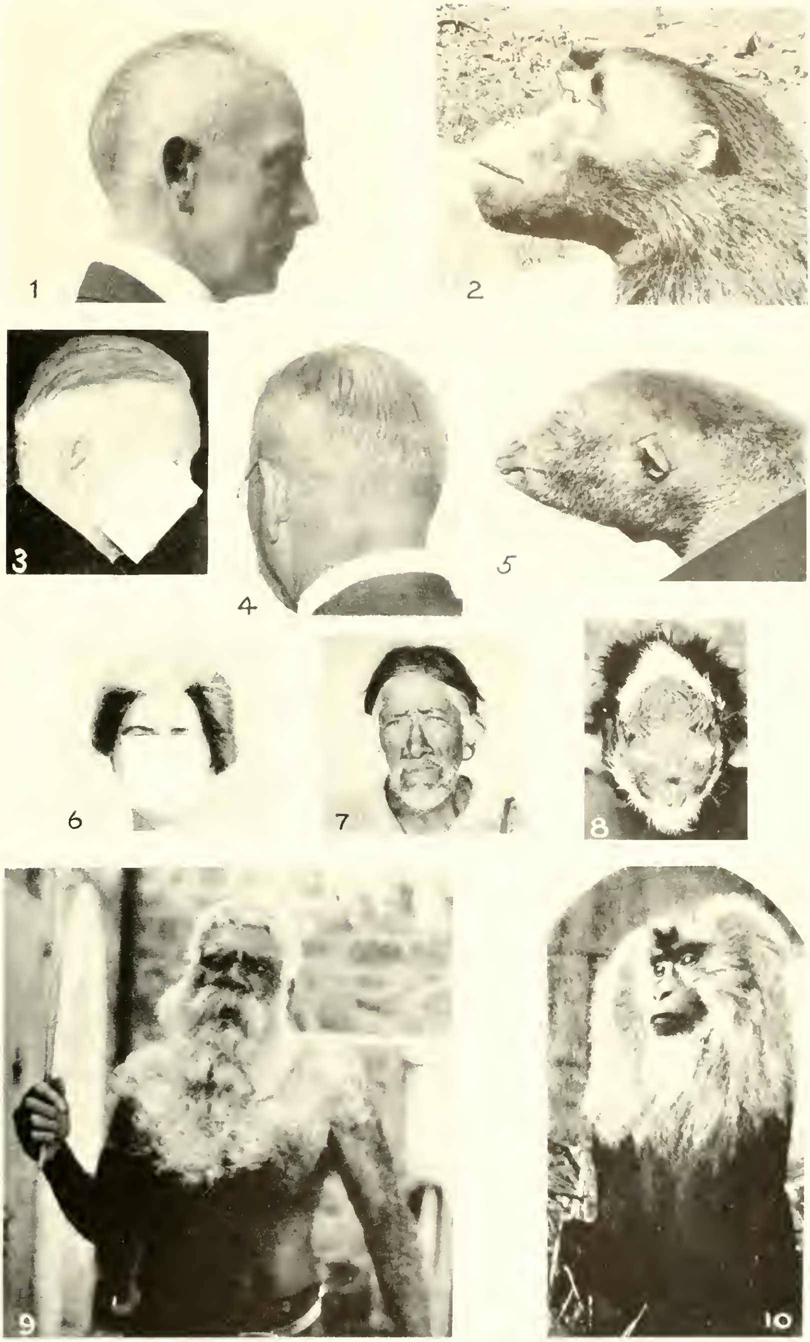




Figs. 1-10.—Human grayness patterns compared with the analogous patterns of four kinds of nonhuman primates.

Figs. 10-13.—Eyebrow patterns, human and simian.

(For explanation see p. 13.)



Human grayness patterns compared with analogous patterns of four kinds of nonhuman primates.

(For explanation see p. 13.)

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SUPPLEMENTARY NOTES ON BODY RADIATION

BY
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SUPPLEMENTARY NOTES ON BODY RADIATION[1]

By L. B. ALDRICH

WALL TEMPERATURES AND BODY RADIATION

In present-day ventilation, three basic factors are considered: (1) air temperature, (2) relative humidity, and (3) air movement. The results of my previous report indicate that, in addition, consideration should be given to a fourth factor, the temperature of the walls and surrounding objects.

For normal indoor conditions, with the surrounding objects all at the temperature of the air in the room and with the subject clothed and at rest, the radiation loss of a human subject is nearly one half of his total heat loss. This radiation emitted from skin and clothing has been shown to be nearly that of a "black body." We may assume that, by virtue of repeated reflections from the other walls and surrounding objects in a closed room, the radiation from the walls to the subject is also nearly "black." Then the radiation loss of the subject is proportional to the difference of the fourth powers of the absolute temperatures of the subject and the surroundings, in accordance with the Stefan-Boltzmann law. Suppose the mean surface temperature of a clothed subject to be 32° C. and the mean temperature of surrounding walls and objects to be the same as the air temperature, 23° C. The difference of the fourth powers of the absolute temperatures is 977×10^6. Now imagine the air temperature, humidity, and air movement to stay constant and the wall temperature to be lowered 10°. The difference of the fourth powers becomes 1963×10^6, an increase of 100 per cent in the radiation loss. On a winter day the temperature of exposed walls might easily be 10° below air temperature, and the inner surface of window panes probably would be considerably more than 10° below air temperature. Thus a subject, particularly if on the exposed side of the room, would radiate at least twice as much on one side as on the other, and his total loss of heat would be increased some 25 per cent or more.

Of even greater importance is the consideration of surrounding objects which are at higher than air temperature. As before, suppose

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[1] See A study of body radiation, Smithsonian Misc. Coll., vol. 81, no. 6, 1928.

the air temperature, relative humidity, and air movement to remain normal but let the surrounding walls be raised to a temperature of 32° C. Radiation loss from a human subject would now be negligible, the normal balance between heat produced and heat lost would be destroyed, and until readjustment is made, a condition of discomfort results. In actual schoolroom conditions, a student near an unshielded steam radiator or other artificial heat source is exposed to a temperature much higher than his surface temperature. In classes, the student is surrounded by other students and the summation of the solid angles subtended at a point on one student by the other students may be very appreciable.

As a rough example, assume a class of students placed in rows, with spaces of 2 feet between students in a row, and the same distance between rows. To simplify matters, imagine each student to be cylindrical, 1 foot in diameter and 4 feet high. The four students nearest to a given student would occupy roughly 10 per cent of the total space to which the central student is radiating. The four next nearest students exposed to the given student would occupy an additional 5 per cent, and the eight next nearest another 4 per cent. Summing up, the amount of space occupied by surrounding students would be about 20 per cent of the total space to which the central students radiate. If we reduce the space between students to only 1 foot instead of 2 and proceed to sum up in a similar manner, the area occupied by the other students increases to about 35 per cent of the whole. For a spacing of 3 feet between students it reduces to only 10 per cent. In other words, when students are spaced 1 foot apart, the total radiation loss of each student is some 35 per cent less than if he were alone in the room. When the spacing is 2 feet between students the radiation loss is 20 per cent less than if he were alone, and when the spacing is 3 feet the radiation loss is 10 per cent less. These rough figures serve in a general way to show the relationship between the spacing of students and the radiation loss of individual students.

For a given wall temperature, what air conditions produce maximum comfort? Evidently if the walls are cold an increased air temperature is indicated, and vice versa. A further study of the effect on a subject of various wall temperatures under controlled air conditions is needed. Such a study should tell us to what extent one's radiation loss may be altered without producing discomfort and should furnish evidence as to the minimum spacing advisable in classrooms without injurious reaction resulting from decreased heat loss.

ACCURACY OF SKIN TEMPERATURE MEASUREMENTS

In the study of body radiation above referred to, skin and clothing temperatures were measured by a special thermoelement device suggested by Dr. C. G. Abbot. For convenience I quote the following illustrated description of the instrument from my previous publication:

> For the direct measurement of skin and clothing temperatures, a special device was prepared with the help of Mr. Kramer, the Observatory mechanician, and embodying Dr. Abbot's suggestions. The device is shown in Figure 1.[1] It consists of a specially mounted copper-nickel thermoelement of fine drawn wire. A frame of German silver is bent as shown in the figure and fastened in a wooden handle, *W*. Two silk threads are stretched to form a cross between the four spring-wire posts, *p*. The thermoelement wires are fastened symmetrically to these silk threads with the junction straddling the lengthwise thread. The wires lead out through fibre rings, *F*, and through the wooden handle. The copper wire (see fig. 2) leads through a switch to a sensitive type Leeds and Northrup D'Arsonval galvanometer and thence to the constant temperature junction in a stirred kerosene bath as shown in Figure 3. The *Cu-Ni* wires are sufficiently long so that all desired positions can be reached without moving the constant temperature bath. Holding the device by the wooden handle, one presses lightly the four prongs of spring wire *p* upon the surface whose temperature is desired. This places the junction in excellent contact with the surface. There is no backing to the junction save a single silk thread, and thus no possibility of heat piling up and causing too high temperatures. For about $\frac{1}{2}$ cm. on each side of the junction, the wire also touches the surface and assumes the surface temperature, thus eliminating error due to cooling of the junction by conduction along the wires.

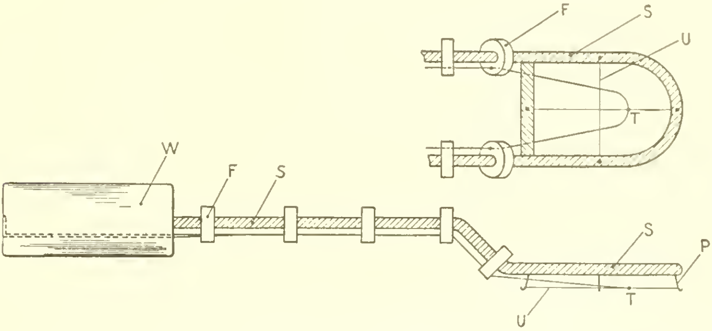

FIG. 1.—Thermoelement device for measuring surface temperatures.

F—Fibre rings.
S—German silver frame.
W—Wooden handle.
P—Spring steel projection.
U—Silk thread.
T—Thermoelement.

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[1] The figure numbers of the original publication have here been changed to accord with the arrangement in this paper.

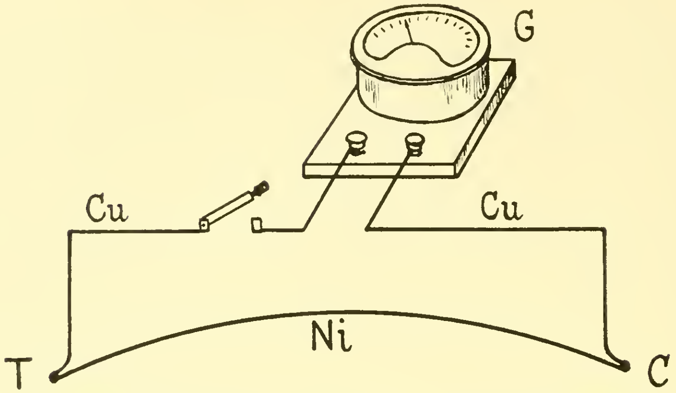

FIG. 2.—Diagram of electrical connections of copper-nickel thermoelement.

G—Galvanometer.
T—Thermoelement junction.
C—Constant temperature junction.

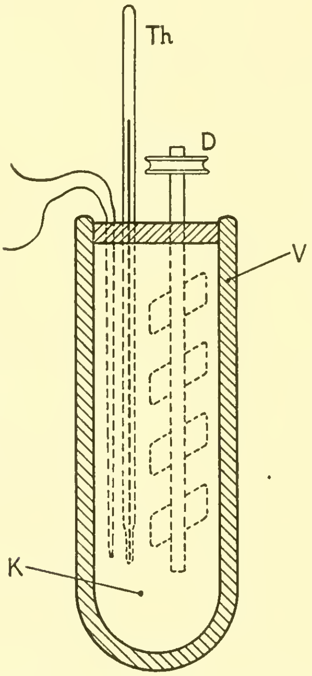

FIG. 3.—Bath for constant temperature junction.

Th—Thermometer.
D—Stirring device.
K—Kerosene bath.
V—Vacuum flask.

The instrument has recently been recalibrated. In mounting for calibration and comparison, the constant temperature junction was fastened against the bulb of a mercury thermometer. The thermometer was then inserted in a metal tube and lowered into a stirred kerosene bath, surrounded by a vacuum flask. In calibrating, the thermoelement device was placed in a well-stirred kerosene bath whose temperature was measured with a second mercury thermometer. A sensitive-type Leeds and Northrup D'Arsonval galvanometer was used with the instrument. The calibration curve, plotting galvanometer deflections against temperature differences, is nearly a straight line.

As certain systematic discrepancies had been noted between skin temperatures observed with this thermoelement and corresponding ones computed from observations of body radiation with the melikeron, it was desired to ascertain whether the thermoelement was in any considerable degree influenced by air temperatures in making such measurements. The instrument was accordingly tested in the following manner by measurements on a skinlike membrane of known temperature.

In the vertical copper calorimeter previously used (see Smithsonian Misc. Coll. vol. 81, no. 6, p. 15) three holes were made in the side at equal altitude, each 6 cm. in diameter. These holes were closed with rubber diaphragms, cemented in with waterproof cement. The thickness of the diaphragms was as follows (determined with micrometer gauge):

0.18 mm.	(thinnest dental dam)
0.36 mm.	(sheet rubber)
1.20 mm.	(composite sheet rubber used for gaskets)

Rubber was chosen because it is pliable, simulating the surface presented by the skin or clothing. The calorimeter as before was filled with water kept thoroughly stirred and a record of its temperature determined by a mercury thermometer.

It is evident that the surface of the thickest diaphragm will be appreciably lower in temperature than the water in the calorimeter, and that the thinner the diaphragm the more closely the surface temperature approaches the temperature of the water. By obtaining a series of surface temperatures of the various diaphragms, a curve may be plotted and extrapolated to zero thickness. The more nearly correct the thermoelement temperatures, the more closely the zero diaphragm value will approach the calorimeter water temperature.

A series of comparisons is summarized in Table 1. Each value in the table is the mean of three separate determinations. Air motion was produced by a fan in the same manner as in the body-radiation experiments above referred to, and velocities (given in feet per minute) determined as before with the Hill katathermometer. Before drawing conclusions from the data in Table 1 it appeared advisable to obtain more comparisons with other thicknesses of diaphragm. Pieces of rubber of the 0.18 and 0.36 mm. thickness were stretched for several days and then cemented into the calorimeter holes previously filled by 0.18 and 0.36 diaphragms. The new thicknesses measured 0.12 and 0.27 mm. A series of comparisons with these new diaphragms is summarized in Table 2.

TABLE I.

Date 1929 Aug.	Room temp. C.	Calorimeter Water Temp. C.	Water temp. minus thermoelement temp. at diaphragm thickness of			Air motion (in ft. per min.)
			.18 mm.	.36 mm.	1.20 mm.	
3	20°.50	31°.82	°.92	1°.32	2°.46	0
	21.40	32.47	1.03	1.50	1.80	
4	25.10	31.50	.73	1.10	1.43	
	26.83	28.32	.40	.40	.57	
5	20.70	35.63	1.27	2.43	3.87	
6	26.20	35.73	.97	1.70	2.20	
	24.77	33.30	.80	1.33	1.77	
10	23.27	34.00	1.27	2.73	3.97	80
	24.00	30.80	.73	1.67	2.57	
	27.80	29.83	.57	.93	1.40	
7	22.57	32.73	1.27	3.27	5.17	180
	22.43	31.97	1.20	2.90	4.63	
8	23.73	30.60	1.00	2.07	3.00	
	23.63	29.27	1.00	1.77	2.67	
	24.17	26.97	.70	1.03	1.53	
9	24.97	35.07	2.00	3.80	5.63	280
	22.30	28.30	1.20	2.20	3.07	
	23.77	26.50	.47	1.13	1.43	
	23.93	29.37	1.40	2.73	3.27	

From Tables 1 and 2, preliminary plots were made of the differences calorimeter temperature minus room temperature and calorimeter temperature minus thermoelement temperature, for each thickness of diaphragm, and for the four conditions of air velocity, viz, 0, 80, 180, and 280 feet per minute. As would be expected, the difference between the calorimeter temperature and the surface temperature determined by the thermoelement appeared to be a linear function of the difference between the calorimeter temperature and the surrounding room temperature. For each of the plots the best straight line was drawn through the points and the origin. From each of the plots values of the calorimeter temperature minus thermoelement temperature were read off at two places, 5° and 10° calorimeter temperature minus room temperature. These values were then replotted as shown in Figures 4 and 5, using thickness of diaphragm as abscissae and calorimeter temperature minus thermoelement as ordinates.

Partly from experimental error and partly because of differences in conductivity of the various diaphragms, the individual points in Figures 4 and 5 do not all lie on the curves. Smooth curves are drawn however with fair certainty. In each case the extrapolation to zero thickness yields a zero value of the difference calorimeter temperature minus thermoelement temperature. This result is gratifying since it indicates that the thermoelement device measures correctly the surface temperature. It confirms satisfactorily the substantial accuracy of the skin temperature measurements reported in my previous paper cited above.

Table 2.

Date 1929 Sept.	Room temp. C.	Calorimeter water temp. C.	Water temp. minus thermoelement temp. at diaphragm thickness of		Air motion (in ft. per min.)
			.12 mm.	.27 mm.	
22	17°.00	24°.00	°.47	°.93	0
26	29.60	37.97	.43	.73	
28	22.87	28.47	.33	.57	
	24.63	27.70	.20	.40	
	25.97	36.67	.57	.97	
30	20.50	32.70	.93	2.00	80
Oct. 2	23.30	27.43	.40	1.30	
5	22.77	33.50	.87	2.17	
	22.30	29.63	.60	1.77	
Sept. 30	21.37	28.10	.73	1.83	180
Oct. 2	23.43	27.07	.37	1.23	
5	22.90	33.13	1.10	2.90	
	22.30	29.37	1.17	2.33	
2	23.50	26.87	.43	1.33	380[1]
5	23.07	32.53	1.10	3.97	
	22.30	29.03	1.33	2.80	

[1] This velocity was intended to be 280 ft. but through an error was found to be 100 ft. per minute too great. In Figures 4 and 5, the calorimeter minus thermoelement temperature was adjusted to an air velocity of 280 ft. per minute.

The following conclusions also are drawn from the surface temperature measurements summarized in Tables 1 and 2:

(1) With the Smithsonian thermoelectric device, the flexibility of the surface measured is an important factor as the air motion increases. On a soft, flexible surface the instrument appears to give nearly correct temperatures for all air motions. On a stiff surface it probably reads nearly correctly for zero air motion but increasingly too low as air motion increases.

(2) In appreciable air motions, the device shows large, irregular drift, making readings difficult.

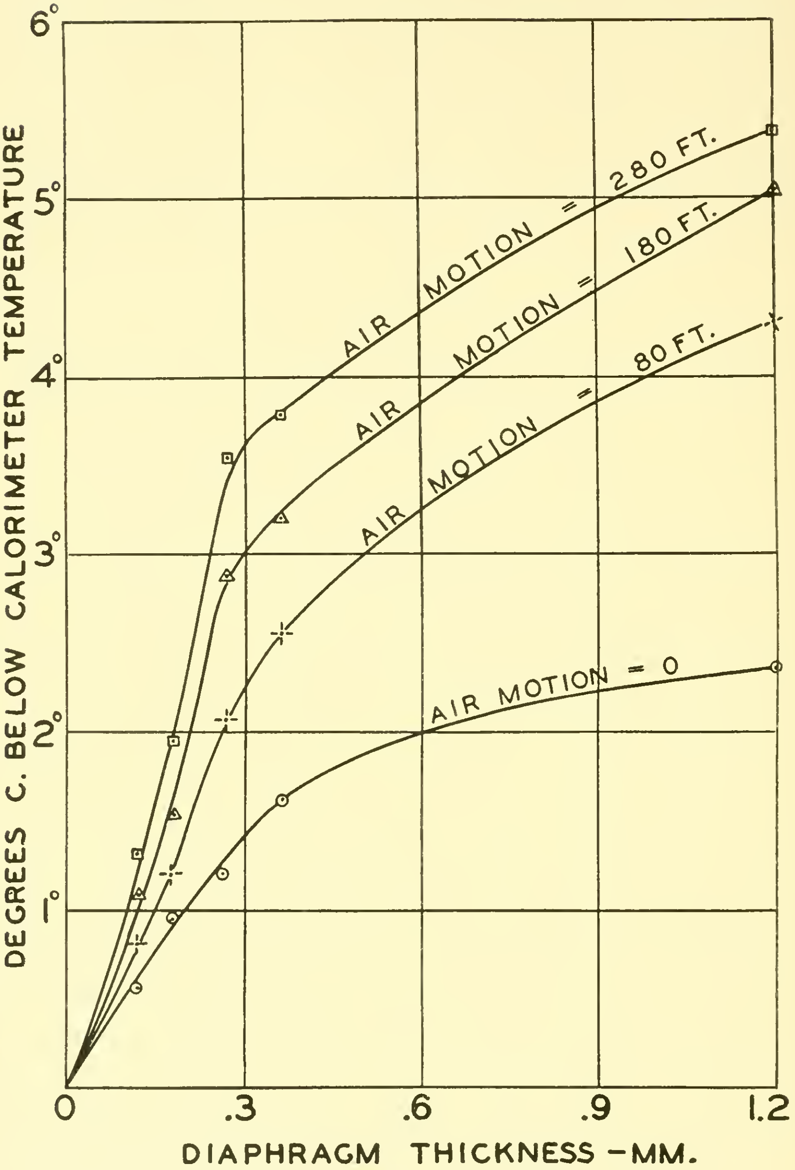

FIG. 4.—Calorimeter minus Room Temperature = 10° C.

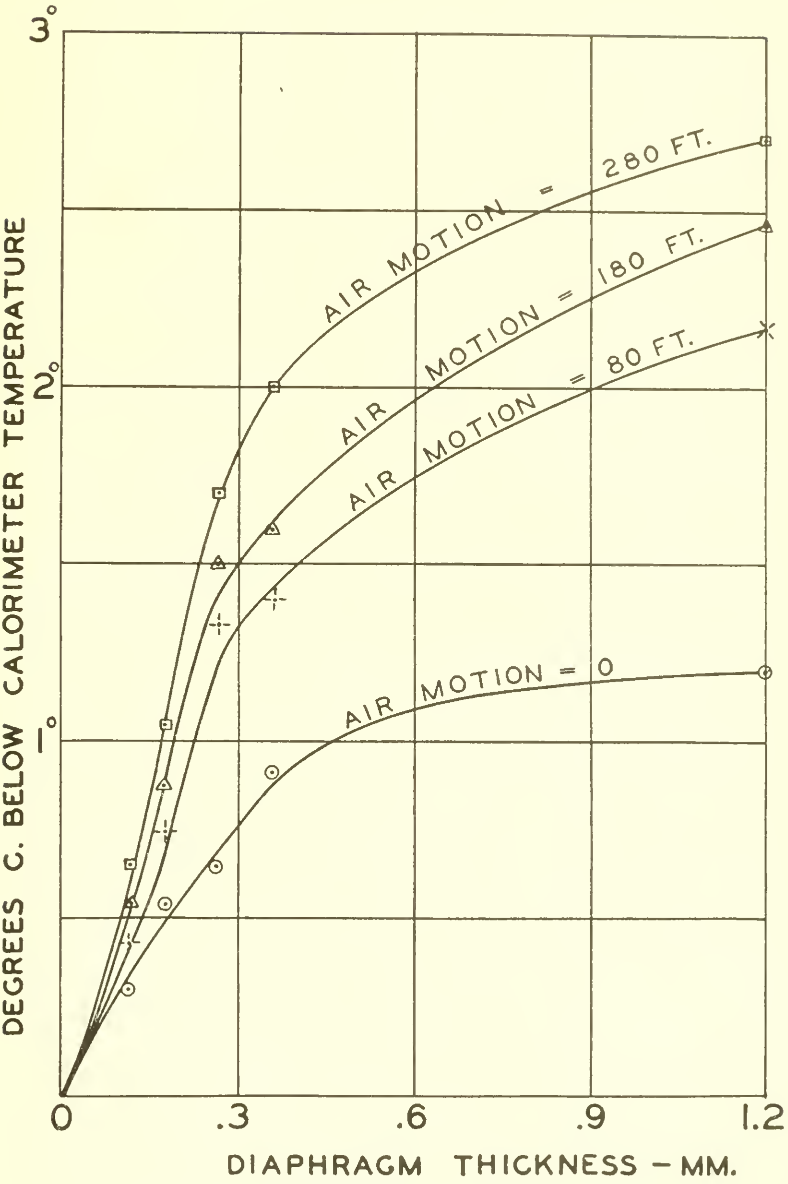

FIG. 5.—Calorimeter minus Room Temperature = 5° C.

TRANSMISSION OF RADIATION THROUGH THE SKIN

In measurements previously made comparing temperatures by the thermoelement device with temperatures computed from melikeron radiation measurements, it was noted (see Smithsonian Misc. Coll., vol. 81, no. 6, p. 19) that in measurements on the uncovered skin the computed temperatures were about 1° C. higher than those measured by the thermoelement. In measurements on clothing and calorimeter this difference appeared to be much smaller. It was thought that possibly the skin was sufficiently transparent to long-wave radiation so that the melikeron in reality received radiation from a warmer layer below the outer surface. To test the transparency of the skin the following arrangement was prepared:

Pyranometer S. I. 8 (for description and use of pyranometer see Smithsonian Misc. Coll., vol. 66, nos. 7 and 11) was mounted without glass hemisphere and with the absorbing strip vertical. A grid, cut from platinum foil and blackened, served as a source of low temperature radiation. The resistance of the grid at room temperature (22.5° C.) was 2.68 ohms. A voltmeter measured the potential fall across the grid, and an ammeter measured the current flowing. The temperature of the grid was roughly determined from its increase in resistance as computed from the voltmeter and ammeter readings. A doublewalled screen close to the grid exposed 8 sq. cm. of grid surface. The distance from grid to pyranometer was 10 cm., which permitted the interposition of two filters and a double-walled shutter.

The accepted procedure with the pyranometer is to use the first swing of the galvanometer as proportional to the incident radiation. When the shutter is opened, exposing radiation to the pyranometer strip, the galvanometer spot immediately starts to move and, if the radiation remains constant, swings to its maximum deflection in a definite time. In the galvanometer used (Leeds and Northrup Type R) this first swing required 3.53 seconds (mean of many trials). It was noticed that when certain more or less opaque filters were interposed the galvanometer spot did not start to move immediately and took appreciably longer than 3.5 seconds to reach maximum deflection. This delayed deflection was due to a combination of the direct radiation transmitted by the filter and of the radiation from the filter itself due to its increased temperature when exposed to the grid. To minimize this indirect heating effect, a stop watch was used and only those readings retained in which the maximum deflection was reached within $\frac{1}{2}$ second of 3.5 seconds. Temperatures of the grid source were varied in the range 75° to 170° C.

The ratio: $\frac{\text{deflection with a filter interposed}}{\text{deflection without the filter}}$ is a measure of the direct transmission of the filter, plus a small quantity diffusely transmitted. Tests of the transparency of various screens were made. These are summarized in Table 3.

TABLE 3.

Transmission of various substances. Temperature of source between 75° and 170° C.

Material	Thickness	% Transmitted
Rock-salt	6.0 mm.	85.
Fluorite	5.5 “	44.
Mica	.03 “	50.
Tissue paper	.03 “	About 45.
Blotting paper	.4 “	Negligible.
Hard rubber	.13 “	Very small.
Rubber dam	.17 “	Less than 10.
Lampblack	One coat, painted on rock-salt.	6 (partly due to pin holes) of rays transmitted by R. S.
Lampblack	Two coats, painted at right angles, on R. S.	Less than $\frac{1}{2}$% of R. S. rays.
Camphor smoke	Smoked on R. S. plate, so thick a lamp filament is invisible through it.	20% of rays transmitted by R. S. plate.
Camphor smoke	Very thick coat, flaking off.	6% of R. S. rays.
Skin, freshly removed	About 2 mm.	Negligible.

Through the interest of a surgeon in a local hospital, a piece of human skin was obtained immediately after removal from the body. Its transmissibility was measured before it had materially lost its moisture. The piece obtained was about 2 mm. in thickness, with some fatty tissue adhering to it. When inserted as a screen in the arrangement described above, its transmissibility was found to be wholly negligible. Bazett and McGlone in a paper entitled "Temperature gradients in the tissues in man" (Amer. Journ. Physiol., vol. 82, no. 2, p. 415, 1927) have shown that in general an increase of 1° above surface temperature is found at a depth of something over 3 mm. below the skin. Forsythe and Christison (General Electric Rev., vol. 34, no. 7, p. 440, 1931) and others have pointed out that flesh, since it consists largely of water, would be practically opaque to the longer wave lengths, just as water is. It seems evident then that the higher melikeron skin-temperature values are not due to the instrument receiving radiation from deeper and warmer layers beneath the surface.

The melikeron is an instrument which responds sluggishly and is rather difficult to manipulate. Furthermore, temperatures computed from its readings depend upon the Stefan radiation constant and upon the assumption that the radiation measured is similar to that of a black body. For these reasons the melikeron-computed temperatures should not be given equal weight with those measured by the thermoelement, and the 1° difference noted may not be entirely real. There are, however, three factors each of which tends to make the melikeron skin temperature higher than the thermoelement values on the skin, namely:

(1) Due to the ridges and roughness of the skin surface, the thermoelement touches the outer and cooler parts of the ridges, whereas the melikeron views both ridges and hollows.

(2) As shown by Bazett and McGlone (loc. cit., p. 433) the temperature 1 mm. below the surface of the skin may be as much as .6° C. higher than the surface temperature. Since the outer layer of skin is scaly and comparatively dry, it may well transmit a small but appreciable amount of radiation coming from the moist and warmer layer below.

(3) Each measurement with the melikeron requires several minutes. The involuntary, psychological reaction resulting from so long an exposure of skin near the instrument aperture may tend to raise the temperature of the exposed skin.

Our conclusion then is that the 1° higher temperatures on the skin resulting in the mean from the melikeron observations would probably be reduced to about ½° if all experimental error were removed. Due to the combination of the three tendencies just mentioned, temperatures at least several tenths of a degree higher than those measured by the thermoelement appear to result from the melikeron readings on the skin.