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THE MORPHOLOGY OF THE INFLORESCENCE OF RAGWEEDS (AMBROSIA-FRANSERIA: COMPOSITAE)[1,2]

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ABSTRACT

PAYNE, WILLARD W. (U. Michigan, Ann Arbor.) The morphology of the inflorescence of ragweeds (Ambrosia-Franseria: Compositae). Amer. Jour. Bot. 50(9): 872–880. Illus. 1963.—The ragweeds possess an inflorescence which is highly modified in relation to anemophily. Several trends from primitive to specialized character expressions may be seen in the morphology of the unisexual capitula and florets. An evolutionary scheme is presented whereby the catkinlike, acropetally maturing, staminate spike and the sessile, centrifugally developing, fruiting involucre cluster are derived from basic inflorescence types within the Compositae. Morphological evidence suggests that: (1) the taxa *Ambrosia* and *Franseria* should be combined under the older generic name *Ambrosia*; (2) the ragweeds and their relatives as a group appear to occupy a position intermediate between the Heliantheae and Anthemideae, as currently delimited within the Compositae.

THE RAGWEED species, currently divided between the genera *Ambrosia* L. and *Franseria* Cav., possess one of the most highly modified inflorescence types found in the Compositae. This modification has come about primarily through specialization in relation to wind pollination (anemophily). The unusual floral morphology of the ragweeds, similarly expressed in varying degrees by related genera (viz. *Iva, Dicoria, Euphrosyne, Hymenoclea, Xanthium*), has led to taxonomic confusion at all levels from the subspecies to the tribe. The purpose of this paper

is to illustrate the salient features of the ragweed inflorescence, both for its intrinsic interest as an unusual member of one of our most advanced phanerogamic families, and to serve as groundwork for taxonomic treatments to be presented in the future.

MORPHOLOGY OF THE FLORAL STRUCTURES— Ragweeds possess floral heads or capitula of 2 kinds: (1) staminate heads which characteristically bear only pollen-producing florets; and (2) pistillate heads which bear 1 or a few seed-producing florets. Staminate heads are arranged in acropetally maturing, racemelike or spikelike clusters at the tips of the stems and branches. Pistillate heads occur in basipetally (centrifugally) maturing clusters in the axils of leaves immediately below the staminate spikes (Fig. 1A).

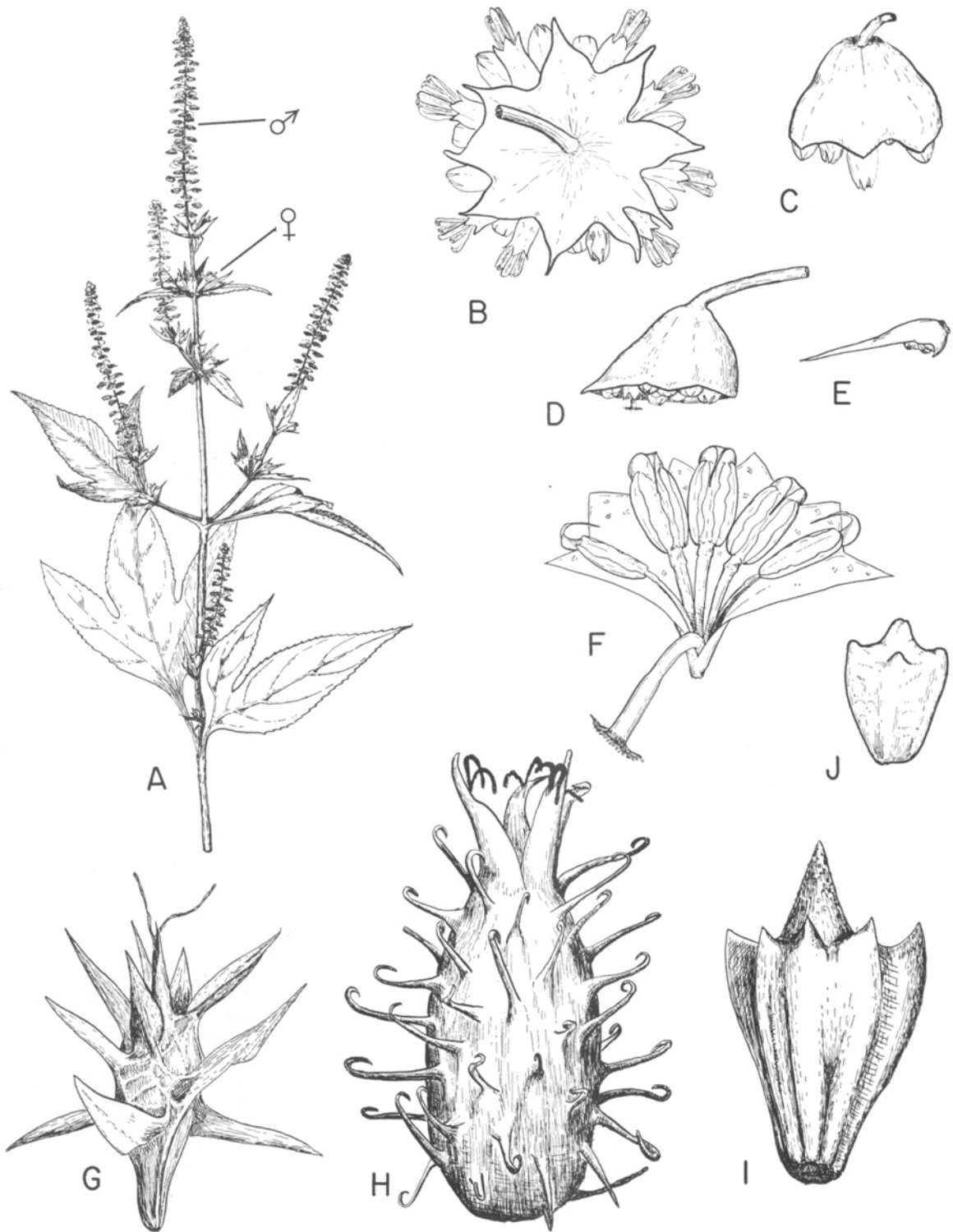*The staminate head*—The staminate heads of most ragweeds are stalked and are not subtended

Fig. 1. Floral morphology in *Ambrosia*. A. Habit sketch of *A. trifida*; pointers indicate staminate and pistillate portions of the inflorescence, ×0.25. B. Staminate head of *Franseria camphorata* showing central insertion of the stalk and pronounced involucral lobes (phyllary tips), ×5. C. Staminate head of *Ambrosia bryantii* ×5. D. Staminate head of *A. psilostachya* showing eccentric attachment of stalk and reduction of involucral lobes, ×5. E. Staminate head of *A. bidentata* showing loss of stalk and extreme distal prolongation of involucre ×5. F. Dissected staminate floret of *A. artemisiifolia* (stamens have become separated in dissection), × 15. G. Fruiting involucre of *A. acanthicarpa* showing many scattered, flattened spines, ×5. H. Fruiting involucre of *Franseria ambrosioides* with hooked spines, ×5. I. Fruiting involucre of *Ambrosia trifida* with reduced spines in a single whorl below the beak, ×5. J. Fruiting involucre of *A. psilostachya* with vestigial spines, ×5.
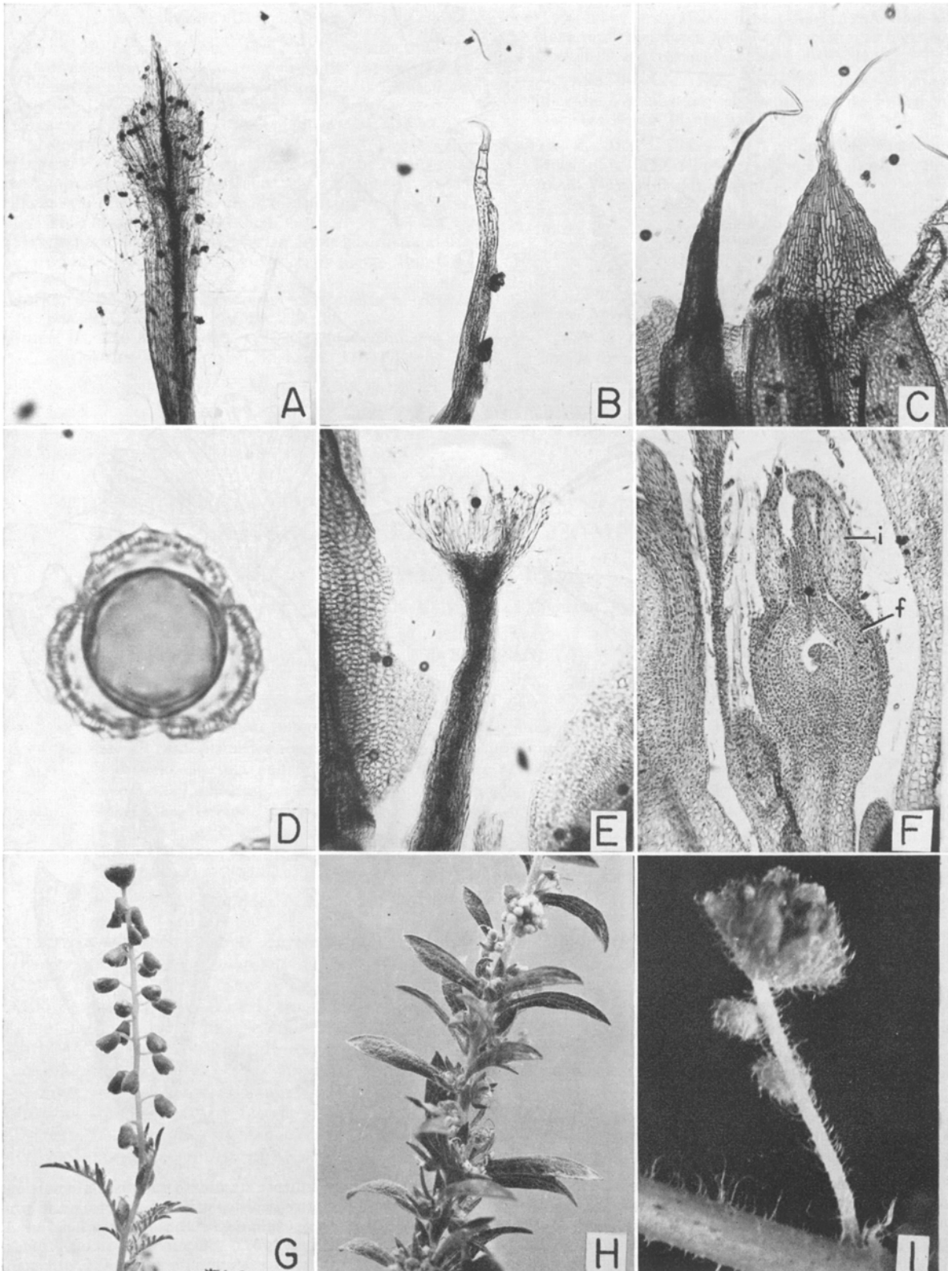
Fig. 2. A. Lanceolate pale of *Franseria chenopodifolia*, × ca. 25. B. Filiform pale of *Ambrosia bidentata* × ca. 50. C. Attenuated anther tips of *A. psilostachya*, × ca. 50. D. Equatorial view of acetolyzed pollen grain of *A. bidentata* showing 3 pores and intercolpoidal air spaces developed between the endexine and ectexine, × ca. 1050. E. Pistillodium from

by bracts. Orientation of the involucre and florets tends to be outward or downward so that pollen is discharged and falls directly into the air. The phyllaries arise in a single whorl and are laterally connate, so that the involucre is campanulate or saucer-shaped. The tips of the phyllaries may be prominent as marginal teeth or lobes (Fig. 1B), or the margin of the involucral cup may be shallowly lobed or nearly without lobes (Fig. 1C, D). Attachment of the involucral stalk to the involucre varies from central to more or less eccentric. If the latter, the widest portion of the involucre is distal in relation to the main stem. In one species, *Ambrosia bidentata*, the staminate involucre is sessile or subsessile and the distal edge is prolonged into a pronounced tooth as long as or longer than the main body of the involucre (Fig. 1E).

The receptacle of the staminate head is relatively small (usually less than 2 mm in diameter) and bears from 10 to 150 or more florets which mature centripetally in a gradual succession. Each floret is subtended by a bract (pale) which may be lanceolate (Fig. 2A) and longer than the floret or reduced and hairlike (Fig. 2B).

Staminate florets (Fig. 1F) vary from approximately 2 to 4 mm in length. There is no pappus. The corolla is campanulate, 5-lobed (4-lobed forms occur), regular and possesses only commissural veins. It usually bears, in addition to non-glandular trichomes, small biseriate glands (colleters) that are scattered over the outer surface.

The stamens are weakly connate around the style and do not bear basal tails or appendages. Their claws fit together to close the anther ring until the time of anthesis and pollen discharge (Bianchi, Schwemmin, and Wagner, 1959) and may be very attenuated (Fig. 2C). The filaments are inserted alternately with the corolla lobes and are usually free.

Ragweed pollen is tricolpate (tetracolpate grains are not uncommon in certain species) with reduced furrows that commonly extend little beyond the pores. The ectexine is relatively thin and is separated from the endexine between the pores to form bladderlike air chambers (Fig. 2D). These air chambers are the most distinctive feature of the pollen of *Ambrosia* and its relatives, and have not been described elsewhere in the Compositae. The sexine, the outer layer of the ectexine, bears very short or vestigial spines and is homogeneous as seen with the light microscope, but the nexine, the inner layer of the ectexine, is composed of short, compactly arranged baccula (rods, muri).[3]

The pistil (pistillodium) of the staminate floret is highly reduced and modified. Its ovary and stigmatic lobes are essentially lacking, and the columnar style is surmounted by a flat (peltate), brushlike cluster of hairs (Fig. 2E). After initial pollen discharge, the pistillodium pushes through the anther ring sweeping residual pollen from the floret.

The pistillate head—Pistillate heads range from 2 to 25 mm in length. The involucre is typically sessile and, with the exception of the central (terminal) head of a cluster, each is subtended by a more or less leafy bract. The bases of the phyllaries are coalescent to form an obovate or vase-shaped, indehiscent, usually hard conceptacle within which the florets and fruits mature. The tips of the phyllaries of the pistillate involucres of most species are evident as spines or tubercles (Fig. 1G–J).

Considerable variation in spine development and morphology is found among the different ragweed species. In some the spines are quite phyllary-like, being flattened, lanceolate, and scattered in several whorls over the surface of the involucre (Fig. 1G). In many species the spines are terete and may be hooked (Fig. 1H) or straight. In the most extreme expressions, the spines are blunt or vestigial and are arranged more or less in a single whorl near the apex of the fruiting involucre (Fig. 1I, J).

Pistillate florets are borne in small numbers (2–7) or singly within each pistillate involucre. There are no pales. In those species which bear 2 or more florets per involucre, the florets are set apart by woody walls which divide the interior of the involucre into compartments. The florets are devoid of calyx, corolla, and androecium and

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[3] These observations on pollen and pollen structure are based upon light-microscope studies of acetolyzed pollen of species of ragweeds and ragweed relatives as follows: *Iva* (sensu lato) 9 species (Jackson [1960] lists 15 species); *Dicraia*. 2 species (Rydberg lists 7 species); *Euphrosyne* no species (Rydberg lists 1 species); *Hymenoclea*, 3 species (Rydberg lists 4 species); *Franseria* (sensu stricto) all but *F. nivea* of ca. 24 species (Rydberg lists 39 species); *Ambrosia* (sensu stricto) all of ca. 11 species (Rydberg lists 21 species); *Xanthium*, 5 members of the *X. strumarium* complex (Rydberg lists 21 species, all of which, with the exception of *X. spinosum*, I consider to be in the *X. strumarium* complex). All of these have very similar pollen structure, the most obvious departure being an elongation of the baccula of certain species of *Iva*, including *I. frutescens* and *I. imbricata*. (All the data from Rydberg are from his 1922 publication.)

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staminate floret of *A. psilostachya*, × ca. 50. F. Immature pistillate head of *A. artemisiifolia* showing the single, reduced floret (f) with its developing, anatropous ovule surrounded by the tissue of the pistillate involucre (i), × ca. 25. G. Staminate spike of *A. pumila* with the terminal head enlarged and developing before the lower heads of the spike, × ca. 1.3. H. Teratological spike of *A. psilostachya* showing a mixture of staminate heads and pistillate head clusters on same spike, × ca. 1.0. I. Teratological staminate head of *A. hispida* showing the development of secondary heads along the stalk and a vestigial bract subtending the stalk, × ca. 5.

resemble naked pistils (Fig. 2F). The stigmatic lobes, which are relatively long (up to 1 cm or more) and somewhat papillose on the receptive, inner surfaces, are exserted through beaks at the apex of the involucre to receive pollen. A separate beak serves each floret in most species with multi-flowered involucres, but in a few species, including *Ambrosia bryantii* and *Franseria artemisioides*, a single beak serves all of the florets.

The foregoing comprise the outstanding modifications of the floral structures of the ragweeds. By relating character expressions found among the ragweeds to correlated expressions of less specialized composites, the evolutionary tendencies appear to be as follows: (1) In the staminate heads: (a) from stalked to sessile; (b) from outward to downward oriented; (c) from centric to eccentric attachment of the stalk to the involucre; (d) involucre from deeply to shallowly lobed and from radially symmetric to bilaterally symmetric with distal prolongation; (e) pales from lanceolate to filiform; (f) stamen claws from more or less deltoid to long-tapered. (2) In the pistillate heads: (a) spine arrangement from scattered in several whorls to localized in a single, apical whorl; (b) spine shape from flattened to terete and from straight to hooked; (c) spine prominence from long to vestigial or lacking; (d) number of florets from several to one; (e) several beaks to a single communal beak on multiflowered heads.
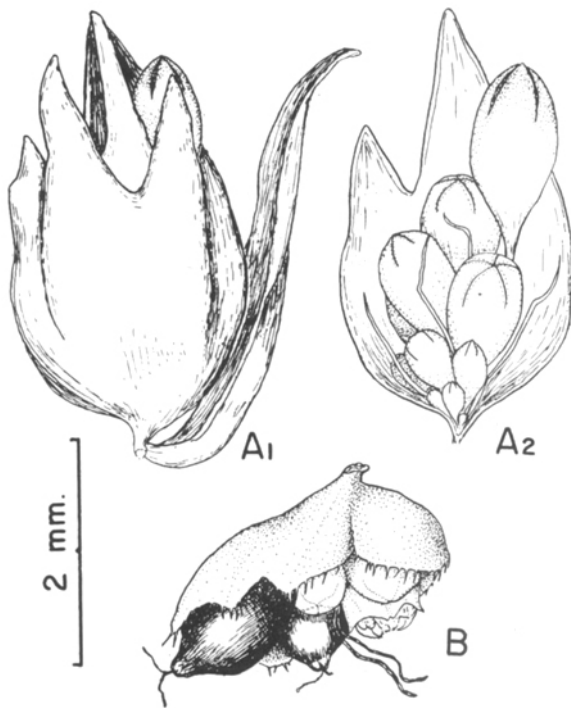

Fig. 3. Teratological heads of *Ambrosia artemisiifolia*. A. Pistillate involucre containing staminate florets; A₁ entire involucre, A₂ cut-away view to expose florets and pales. B. Staminate involucre containing both staminate and pistillate florets.

THE ORGANIZATION OF THE INFLORESCENCE—Considering the Compositae in general, it is apparent that the composite head has been derived from a less complex inflorescence of individual flowers by processes involving compaction, coalescence and modification of the floral structures. Cronquist (1955) has stated (p. 482): "Since the head in the Compositae represents in reality an inflorescence, it seems reasonable to expect the hypothetical prototype to have few or solitary, numerously flowered heads," and this assumption has met with general acceptance in the United States. By its nature as a modified inflorescence, the head terminates the stem or branch upon which it is borne, i.e., the head arrangement may be said to be determinate (Fig. 4A). Further, in those composites with branched inflorescences, all orders of floriferous (capitulous) branches are determinate and maturation of the branches and capitula is basipetal (Fig. 4B). This and derived arrangements of heads predominate in the Compositae and may be considered representative for it, although numerous specialized arrangements have come about in the family.

As stated above, the staminate and pistillate head clusters of *Ambrosia* and its relatives mature in opposite directions, acropetally and basipetally, respectively. This phenomenon has undoubtedly puzzled workers for some time, especially as the more obvious, acropetal maturation of the staminate spike is the opposite direction from that which is typical for the Compositae. Confusing homologies, apparent between structures of the staminate and pistillate portions of the inflorescence, lend additional ambiguity. Homology between the staminate and pistillate heads is demonstrated by 2 phenomena: (1) the frequent occurrence of heads of one sex in positions normally occupied by heads of the other; and (2) by teratological heads in which involucres of one sex bear florets of the other (Fig. 3) (Jones, 1936; Payne, 1962a). The relative frequency and varying degrees of mixture of sexual types in such irregular heads leaves no doubt as to the real homology of the staminate and pistillate heads. However, inflorescences are frequently found in which staminate heads and clusters of pistillate heads are borne intermixed on a single spike (Fig. 2H). This indicates that the stalked staminate head is also homologous with the sessile cluster of pistillate heads. Although these observations seem to be contradictory, they are reasonable if one conceives the organization of the ragweed inflorescence to have evolved as it is diagrammed in Fig. 4.

To achieve the inflorescence type of *Ambrosia*, it is necessary to have a change in the order of maturation of the primary capitulous branches of the generalized composite so that the lowermost mature first. Such inflorescences are encountered in a number of composite genera (although they are not necessarily representative for them) in-
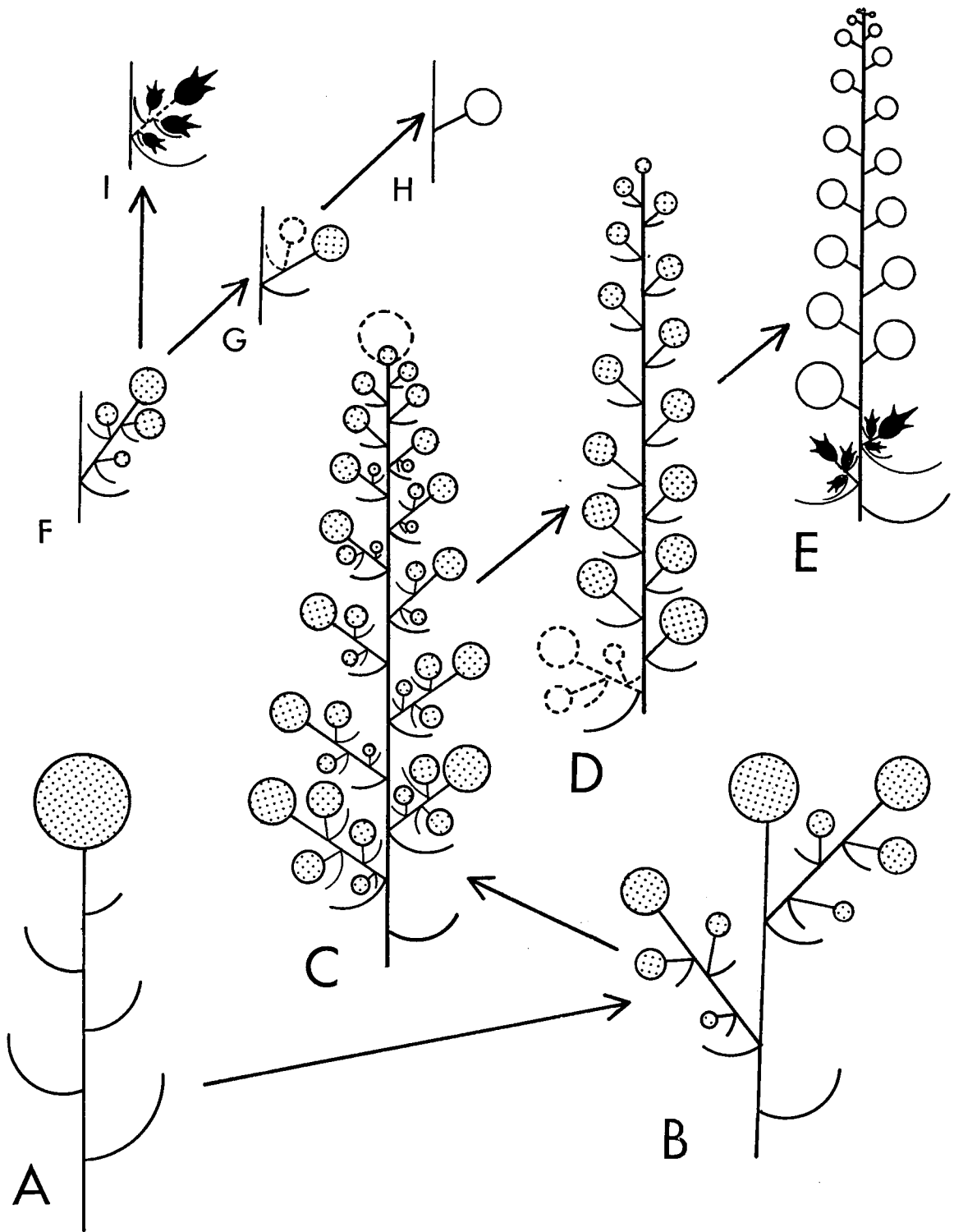
Fig. 4. Diagram illustrating development of the *Ambrosia* type inflorescence from more primitive types within the Compositae. Circles and tridentate ellipses represent heads. Stippled heads = bisexual; open heads = staminate; black heads = pistillate. A. Primitive composite type with large head terminating stalk or branch. B. Derivative type in which capitulous branches are produced at nodes immediately below the terminal head. Note that development of the branches as well as maturation of heads on a single branch system is basipetal. C. Derived form in which development of primary branch systems is acropetal. D. Reduced form with at least the upper primary branches bearing only a terminal head. E. *Ambrosia* type in which upper heads are entirely staminate, the bracts have been lost and, in at least some expressions, the inflorescence organization is truly indeterminate; the lower branches are shortened to clusters of modified pistillate heads. F through I. Modification of primitive, primary branch system to give the types found in *Ambrosia*.

cluding *Artemisia, Aster, Cichorium, Eupatorium, Prenanthes, Solidago* and others. Such an arrangement is shown diagrammatically in Fig. 4C. It may be noted in the figure that although the primary branches of the inflorescence mature acropetally, the heads of an individual primary branch mature basipetally, the terminal head developing first.

A spikelike arrangement of heads, similar to that which is characteristic of *Iva*, the least specialized genus known to be related to *Ambrosia*, may be achieved through loss of the lower heads of at least the upper primary branches (Fig. 4D). The inflorescence of *Ambrosia* is attained by loss of the bracts which subtend the upper branches, by segregation of the staminate and pistillate florets in heads of the upper and lower branches respectively and by further modification of the heads (Fig. 4E). The changes in the generalized composite inflorescence branch which lead to the 2 types found in *Ambrosia* are diagrammed in Fig. 4F–I.

In the derived expressions (as diagrammed in Fig. 4C–E) the development of the branches may be truly indeterminate with, theoretically, unlimited potential for continued development. Also, it would be possible to homologize each of the lateral branches of the acropetally developing inflorescences with an entire, determinate inflorescence of less specialized groups. Within the scheme, a shift has occurred from regular, determinate inflorescence growth to the indeterminate pattern of the vegetative shoot.

Thus, the staminate spike of *Ambrosia*, which appears to be simply an elongate cluster of acropetally maturing, staminate heads, is actually an indeterminate, spikelike arrangement of reduced, 1-headed, determinate branches which develop acropetally. Each cluster of pistillate heads is a single, shortened branch which has retained the tendency for production of more than one head. Although the staminate and pistillate heads are themselves homologous, the staminate head and its stalk (a reduced branch system) is homologous with the cluster of pistillate heads (a shortened branch system), and the difference in directions of maturation may be explained thereby.

The hypothesis is further supported by 3 observations. (1) Clones of *Ambrosia pumila* grown at the University of Michigan Botanical Gardens commonly produce spikes on which the apical head is the first to mature (Fig. 2G). This may be interpreted as a carry-over from the inflorescence type in which the terminal head of the axis always develops first. An identical phenomenon is found in *Cichorium intybus*. (2) Specimens of *Ambrosia artemisiifolia, A. hispida* and *A. trifida* have frequently been observed to produce abnormal staminate spikes on which the stalks of the lower heads bear secondary heads below the terminal one (Fig. 2I), an indication that the stalk actually is a reduced branch system. Also,

in many of what may be considered less specialized species of ragweeds, on the basis of primitive and derived character expressions presented earlier (including *Franseria divaricata, F. artemisioides, F. dumosa* and others), the lower stalks of the staminate portion of the inflorescence often bear 2 or more heads and may be subtended by bracts. In *F. divaricata*, the pistillate heads are arranged on elongate branches which are clearly homologous with the staminate branches above, and in *F. dumosa* each stalk of the inflorescence bears a terminal staminate head with 1 or more pistillate heads located below. Such expressions may be considered primitive for the ragweeds. (3) In several species of ragweeds (including *Ambrosia acanthicarpa, A. artemisiifolia, A. bidentata, A. confertiflora* and *A. psilostachya*) spikes are occasionally found in natural populations, and I have frequently observed them in cultivated plants, in which the tip of the staminate spike has reverted to the vegetative condition and produced entire shoot systems. This phenomenon confirms the theoretical ability of the shoot to continue growth beyond that normally encountered in the spike and indicates the essentially vegetative nature of the organization and development of the spike.

Modification similar to that of *Ambrosia* may be seen in the inflorescences of *Cichorium intybus* and *Eupatorium capillifolium* and will probably be encountered elsewhere in the Compositae.

DISCUSSION—Many of the modifications of the inflorescence and floral structures of the ragweeds are obviously associated with adaptation for anemophily, as mentioned earlier. The arrangement which has been achieved, i.e., an elongate, catkinlike cluster of staminate heads located above the pistillate heads, is eminently suited for wind-pollination and affords at the same time a high probability of outbreeding. This reproductive apparatus is remarkably similar to certain wholly unrelated, wind-pollinated plants, such as the oaks, and is a graphic example of convergent evolution. Downward orientation of the staminate heads and florets and the structure and action of the pistillodium insure discharge of pollen into the air. The reduced pore areas of the pollen grain may slow water loss to the air beyond a certain point (although water loss immediately after discharge of the grain is considerable), and the bladderlike spaces within the walls of the pollen grain increase its buoyancy. The elongate stigmatic lobes of the pistillate florets are adapted to receive air-borne pollen.

Other modifications involve the loss of unnecessary structures, viz., the ovary and pappus of the staminate florets, the bracts subtending the staminate involucres, and all structures of the perianth and androecium of the pistillate florets.

The bur which is formed by the pistillate involucres of most species undoubtedly functions in animal dispersal. This is especially true of those

with hooked spines. A very bizarre spine modification is found in the Mexican species, *Ambrosia bryantii*, where a proportion of the fruiting involucres, which are armed with very long, sharp spines, are permanently retained on the stems where they serve as protective thorns (Payne, 1962b).

While the details of ragweed classification and relationships must await treatment, it is relevant to point out at this time certain hypotheses which are suggested by morphological evidence. (1) The similar taxa *Ambrosia* L. and *Franseria* Cav. are distinguished only on the basis of the number and arrangement of spines on the fruiting involucres, the former tending to have few spines arranged in a single whorl at the apex and the latter tending to have many spines scattered over the surface. Shinners (1949), Gebben, Payne, and Wagner (1962), and Payne (1962a,b) have indicated that this distinction cannot be justified, and, indeed, leads to considerable systematic confusion and error. Many of the species possess an intermediate morphology so that it is very difficult to reconcile their placement in either taxon. Several lines of evolution can be traced from franserioid to ambrosioid species-groups, so that maintaining the distinction leaves *Ambrosia* (sensu stricto) a highly polyphyletic group. These, as well as breeding experiments carried out between the 2 taxa (which demonstrate very close chromosomal homology [Gebben et al., 1962]) indicate that they should be combined under the older name, *Ambrosia*. This combination will be made in a later paper, at which time the arguments will be elaborated, transfers made and a resumé of species and transfers presented. (2) Although the ragweeds and their relatives are commonly included in the tribe Heliantheae (Fernald, 1950; Cronquist, 1952; Munz, 1959; etc.), the position and relative status of this group of plants have long been the subject of debate and conjecture. Bentham (1873) established the treatment of the group as a subtribe of the Heliantheae but stated (p. 435) that they "form so distinct and natural a subtribe that it has been repeatedly proposed to raise them to the rank of an independent tribe, suborder or even a distinct order; and . . . the separation would seem justified; . . . but after a detailed examination of all the surrounding genera, I have felt compelled to admit that the majority of synantherologists are correct in placing them under the [tribe] Helianthoideae. They are without doubt, connected with *Artemisia* [of the Anthemideae] as well as with Melampodineae [via *Parthenice* and *Parthenium*] but geographically as well as structurally the relationship to Melampodineae appears to me to be the closest." Some workers, including Cassini (1834) and Delpino (1871), who may have been among those alluded to by Bentham, recognized them as a distinct tribe, while still others, such as Small (1913, etc.) and Rydberg (1922, etc.), considered

them to comprise a distinct family. Presently available knowledge allows us to go very little farther than did Bentham. The outstanding modifications of the ragweed group, particularly as seen in the more advanced genera *Hymenoclea* and *Ambrosia*, may warrant elevation of the group to the position of a tribe within the currently accepted tribal structure of the Compositae. These include the loss of corolla and androecium of the pistillate florets, separation of the sexes in different heads located on different parts of the plant, the development of a woody bur from the involucre of the pistillate head, the occurrence in all genera of bladderlike air spaces in the pollen grain wall, the weakly connate nature of the anthers of the staminate florets, prolongation of the anther tips of many species, acropetal maturation of the inflorescences of all genera, and their essentially American origin and distribution. However, the basic question of relationship remains. The pistillodium is duplicated in both the Heliantheae (*Parthenium*, *Parthenice* of the Melampodinae) and the Anthemideae (*Artemisia*). Baccula have been found in the pollen wall of the Heliantheae (Larson, via B. L. Turner, personal communication), but I have observed them to be more truly representative of the Anthemideae, as have Stix (1960) and others. Colleters (the biseriate, glandular trichomes) occur in both *Parthenium* and *Parthenice* of the Melampodineae, although they are not typical of the Heliantheae and are typical of the Anthemideae. The possession of subtending pales on the receptacle of the staminate head relates the ragweed group to the Heliantheae, as do, perhaps, the occurrence of opposite leaves at the lower nodes of some of the advanced species. The strongly resinous odor of the ragweeds and their relatives and similar allergic response in humans relates them to the Anthemideae. Turner (personal communication) has suggested that perhaps *Parthenium* and *Parthenice* really belong to the Anthemideae and that the Ambrosieae are related to these genera and depart from the Anthemideae at or near their junction. At any rate, it may be stated that the ragweed group, whatever its rank, appears to occupy a position intermediate between the Heliantheae and Anthemideae (although it does not form a connecting link between them) and is somewhat removed from both through specialization. It is hoped that further comparative work on these taxa will provide evidence for a more concrete taxonomic and evolutionary treatment in the future.

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HETEROTHALLISM AND SEXUALITY IN ASCOBOLUS STERCORARIUS[1]

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ABSTRACT

BISTIS, G. N., and J. R. RAPER. (Harvard U., Cambridge, Mass.) Heterothallism and sexuality in Ascobolus stercorarius. Amer. Jour. Bot. 50(9): 880–891. Illus. 1963.—The steps in the sexual development of the heterothallic ascomycete, Ascobolus stercorarius, are: (1) induction of antheridial hyphae and antheridia; (2) induction of ascogonial hyphae and ascogonia; (3) directed growth of the trichogyne; and (4) plasmogamy. Although this sequence occurs in each of the 2 reciprocal combinations (A–antheridial/a–ascogonial and a–antheridial/A–ascogonial), several differences between the 2 combinations have been found. The differences are especially apparent with regard to antheridial induction and the pattern of proliferation of ascogonial hyphae. A study of the specificity of the agents regulating the sexual reactions between the 2 mating-types has confirmed previously described class-specificity at antheridial induction (sexual activation). Experiments utilizing substituted oidia have demonstrated an absence of mating-class specificity in trichogyne attraction and even at plasmogamy. The incipient fruiting bodies which result from illegitimate fusions (a × a and A × A), however, stop growing after 24 hr. This cessation of development suggests the presence of a second block to self-fertility in the sexual process of this species.

THE PHYSIOLOGY of sexuality in the higher Ascomycetes is a field that has received little attention despite considerable information on the comparative morphology of the sexual structures of the group. The lack of physiological information, furthermore, has kept the biochemical genetics of sexuality in relative obscurity. This latter field, unlike the well-mapped biochemical pathways for the vegetative phase, has progressed only to the identification of a few of the underlying genetic factors.

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Although Edgerton (1914) was the first to study the inheritance and role of genetic factors in the sexual phase of an ascomycete (Glomerella cingulata), it was Dodge's discovery of heterothallism in Ascobolus magnificus (1920) which gave impetus to this field. Of particular significance were the 2 conclusions which Dodge made in this paper. First, he equated the 2 mating types with specific genetic factors, namely, 2 alleles (A,a) at a single locus. This simple genetic control of mating pattern has, subsequently, been found in all heterothallic ascomycetes examined and corresponds to Whitehouse's (1949) category of bipolar, 2-allele heterothallism. Second, Dodge suggested that, since sexual organs appear only in A × a contrasts, these genetic factors must play their determining role in some preplasmogamic stage of the