

THE ANNALS
AND
MAGAZINE OF NATURAL HISTORY.

No. 135. DECEMBER 1847.

XXXV.—*Observations on the Structure of the Fruit of the Cruciferæ.* By L. C. TREVIRANUS*.

AMONG the Cruciferæ some years since introduced into German gardens, *Æthionema heterocarpum*, Gay. is remarkable from the fact that in certain individuals occur two-celled many-seeded and one-celled single-seeded silicles. The former are flat upon the upper side and somewhat vaulted on the under, and in correspondence with this the upper border of the septum is straight, while the under has a convex form. In the latter the under side is strongly excavated, rendering the whole silicle almost globular; the keel is wanting on this deepened under side, and the solitary seed lies, as in *Isatis* and *Tauscheria*, directly in the middle of the silicle, being attached at the summit of its cavity. This species therefore connects certainly the genus *Æthionema* with *Tauscheria*, only in *Tauscheria* the enlargement of the silicle is above, while that of *Æthionema heterocarpum* occurs on the under side. If however *Tauscheria* is to stand, another genus, namely *Campyloptera*, Boiss.†, cannot I think be retained, since the plants on which it is founded appear to be specimens of *Æthionema heterocarpum*, bearing no other fruit than the one-seeded kind above described.

It is difficult to say what causes this remarkable deviation in some silicles from the normal structure of the others. It cannot be called a monstrosity, since the seed of the one-celled silicle is just as perfect as those which the two-celled yield; the flowers also which produce the former are not less perfectly organized than those from which the two-celled fruits come. I have been induced therefore to institute some researches into the structure of the fruit of the Cruciferæ, and albeit these have not led to the wished-for elucidation, I will nevertheless publish some of the results, which may perhaps possess more general interest.

* From the Botanische Zeitung, June 11th and 18th, 1847. Translated by Arthur Hefrey, F.L.S.

† Ann. d. Sc. Nat. 2 sér. xvii. 194.

It is well known that the two-celled rudimentary fruit of the Cruciferæ is distinctly characterized by the fact that the septum is not directed transversely toward the rachis or the centre of the floral whorl as in other two-celled ovaries of Dicotyledons, *e. g.* of Scrophulariaceæ, Gentianeæ, &c., but lies in the radius of it, and that notwithstanding this, the same position of the two lobes of the stigma occurs as in the families just named, that is, one is curved outward and the other inward, consequently their relative position corresponds with the direction of the septum. If we examine the framework of this fruit in reference to the vascular bundles of which it is composed, we usually perceive four, which spring from the receptacle where it becomes somewhat expanded to receive the fruit, namely two which ascend in the thickened border of the septum on the anterior and posterior sides, and two, one of which enters the middle of each valve. The former give off in their course, in many-seeded silicles, branches passing inward which serve as funiculi to the ovules; they must consequently, according to the division established by Mirbel, be called the trunks of the placental vessels. On the other side also large and numerous lateral branches proceed from them into the valves, there anastomosing with those presently to be mentioned as specially belonging to the valves. Each trunk of the placental vessels is considered by DeCandolle as composed of two cords united together*, and according to the theory which regards the placenta as the border of the valve, agreeing with the double row of ovules on each side, it might be so; but, if I except *Biscutella*, where the vascular trunk appears divided on each side, I have hitherto found it simple in all the ovaries of Cruciferæ I have examined, without trace of division or combination, and the same observation has been made by others†. When the aforesaid cord reaches the apex of the fruit, that is, the place where the valves terminate, it is continued further in the style and ends beneath the stigma in that remarkable manner which I described as occurring in *Primula* and some other genera‡, and have since discovered to be general; namely it spreads out into numerous radiating large and small branches which are of equal height and have thickened clavate terminations. The branches from both sides are collected here, but although they are very closely approximated they by no means unite.

With regard to the two vascular trunks, one of which passes into each valve, and which, following Mirbel, are to be called pericarpial or valvular vessels, these also are apparently never wanting, at all events they are by no means absent in the genus

* Mém. du Mus. d'Hist. Nat. vii. 190.

† Trécul, Ann. d. Sc. Nat. 2 sér. xx. t. 17. f. 3.

‡ Zeitschrift. f. Physiol. iv. 128. t. 9. f. 4.

Cardamine, though they are so small here that they escaped the sharp-sighted eyes of Brown and DeCandolle*. They are most distinct in the boat-shaped valves, for example in those of *Thlaspi arvense* and still more in those of *Megacarpæa*, where each describes a circle in its course and marks the origin of the broad wing, into which numerous branches are given off from it. In flat or slightly elevated valves also they generally give off many branches at right angles which anastomose with those also coming out at right angles from the placental trunks; in its further course however the main trunk becomes more and more attenuated, till finally it terminates in a very minute process inside the apex of the valve of each side without reaching or going beyond the apex itself, which is most striking when this forms a tooth-like projection, often of considerable length, as in the genera *Notoceras* and *Parolinia*†.

The genus *Camelina*, however, as Koch rightly observes ‡, forms an exception to this structure. Here the style is a prolongation of the two valves of the silique, the vessels of which pass into it, so that on the separation of the valves it splits into two halves, each half having in it the end of one trunk of valvular vessels. But in *Cardamine* this trunk is always slender, without distinctly branching, and it is quite lost at two-thirds of the height of the valve.

This course of the two kinds of vessels of the fruit compared with their mode of distribution in other families, as in Primulaceæ, Gentianeæ, Scrophulariaceæ, Saxifrageæ, Caryophylleæ, &c., differs from them in so far, that in the last-mentioned families the pericarpial vessels alone are continued from the ovary into the style, or pass through the style as far as the base of the stigma, while the placental vessels, which in the Cruciferæ exclusively supply the style or the stigma with vessels, do not take the least part in it.

As to the septum, leaving out of the question the funiculi which mostly cohere with it, it has no vessels of its own in the silique; at least it does not possess them in the sense in which this expression is usually taken, as signifying fibrous and spiral tubes, but has a structure wholly cellular, and this of a peculiar kind. It consists of two substances which I will name epidermis

* L. c. 201.

† "Mr. Webb has published an account of a Canary shrub named *Parolinia*, in which the valves are constantly extended into stigmas" (J. Lindley, Veget. Kingdom, 352). Anything but that; Webb's descriptions and illustrations rather show in the most distinct manner that these processes of the valves are not stigmata, but unusually large horn-like appendages, in which the mid-nerve of the valve is continued to the very apex, which is split. (Ann. d. Sc. Nat. 2 sér. xiii. 136. t. 3.)

‡ Deutschl. Flora, iv. 570.

and parenchyma, as these agree in their general peculiarities with those which are so called in leaves. The epidermis forms two lamellæ, whether the septum be thick or thin, between which the parenchyma, which however is often at least partly wanting, is inclosed and distributed in different degrees and abundance. The cells of the first-named substance differ much in their form, position and mode of union. Very often their circumference is more or less drawn out lengthways, as in *Cheiranthus Cheiri*, *Lunaria annua*, *rediviva*, *Farsetia clypeata*, *Vesicaria utriculata*, *sinuata*, &c., and the longer diameter is then never parallel with the axis of the silique, but at a sharp angle to it. The direction however is different in the two lamellæ, and therefore the reticulations, which from the transparency of the septum are visible at the same time, never correspond, but cross one another, a circumstance which Brown* has remarked, and which appears to favour the view taken by DeCandolle†, that the two lamellæ belong to different carpels. In the very thin septa of *Draba*, *Capsella*, *Æthionema* and *Camelina*, the borders of the cells resemble those of the epidermis of delicate leaves, being undulated, which Brown‡ calls amorphous; in those of a firmer structure, on the contrary, for instance in *Cheiranthus* and *Lunaria*, they have a straight course, and are then more or less knotty. This knotty structure, which is not observable in the earliest state of the septum, but is formed subsequently, depends upon a thickening of the cell-walls with a simultaneous perforation of them by canals, which run from within outward in a manner resembling that which Meyen delineates as the structure of the punctated cells of some plants§; but usually the pore-like marks, lying in long rows, are only observable when the wall of a cell is seen from the side, where it is united with another. Several observers have also remarked pores upon the septum usually similar to the pores of epidermis, for example Hartig and Schleiden in *Capsella Bursa-pastoris*, Trécul in *Cheiranthus Cheiri*; I also have perceived the same in the last-named plant, and most clearly in *Octadenia lybica*, Br.; in most of the Cruciferæ however I have sought them in vain, and hitherto have only observed them in the vicinity of the border of the septum, never in the middle of it. Here in the middle the two lamellæ lie pretty close together, while at the borders they inclose, in common with the placental nerves of each side, a space filled with a parenchyma which from thence spreads out further into the septum. This has some affinity to the parenchyma of the under side of a leaf, consisting of anastomosing rows of elongated cells, which sometimes even contain granular

* Observ. on the Pl. of Central Africa, 13.

† L. c. 190.

‡ L. c.

§ Physiol. i. t. 1. f. 2, 5, 10, 11.

matter ; and the delicacy of this cellular tissue is the cause why (which sometimes even occurs spontaneously, for instance in *Iberis*) the layers are so easily separable, which is impossible in those cases where it has a firmer consistence, as in *Thlaspi cochleariforme*, M. B. Brown first observed what he has called nerves in the septum. "In some cases," he says, "the axis of the septum displays itself either as a single nerve or as two separate parallel nerves, and from this axis tubes often pass off which have the aspect and ramification of the veins of leaves and commonly terminate within the border. This is most distinctly the case in *Farsetia*. The central vessels are here very closely approximated, so that they form a single cord ; they extend from the apex of the septum to its base, and the veins are as numerous as unusually distinct. Approximations to this structure of *Farsetia*, more or less evident, occur in some other genera, as *Parrya*, *Savignya* and *Koniga*. But in the last-mentioned genus, the nerve which, as in all cases, arises at the apex, runs scarcely, even in the many-seeded species, beyond the middle of the septum, and the far less distinct veins are decurrent*." Of the plants here named I have been able to examine *Farsetia ægyptiaca* only dried, but *Koniga* (*Octadenia*) *maritima* as well as *K. (Octad.) lybica* (if *Draba nummularia*, Eb., be the same plant) in a fresh condition. In the *Farsetia* the septum certainly has something which looks very like a central nerve, about as it is represented by Desfontaines†, and I observe the same condition of the part in *Octadenia maritima*, except that the veins running out to the side have a somewhat different, that is, a curved course. In *Oct. lybica* each mid-nerve descends to about opposite the insertion of the ovule on the border ; but ramifications go from it to all sides and are distributed over the whole of the septum ; they form an intricate network by their regular anastomoses, and are often distinguishable by a reddish colour. In *Cochlearia anglica* also, likewise in *Vesicaria grandiflora* and *V. gracilis*, B.M., a nerve may be observed in the septum descending from the style. In *Cochlearia* it loses itself in the lowest parts of the septum where the funiculi arise, but in the two *Vesicarias* it only goes to the middle, and by no means gives off branches, but after becoming gradually attenuated suddenly terminates. In all these cases it was evident that the said nerve took its origin where the style ended, appearing to be an immediate prolongation of the central substance of that organ ; it reached also either only to the middle or beyond the middle, but never to the base of the septum. Dr. C. A. Meyer, in his important work on the Cruciferæ of Altai‡, has devoted particular attention to the septum and found

* *L. c.* 13, 14.† *Fl. Atlant.* ii. t. 160, f. 6.‡ *Ledebour, Fl. Alt.* iii. 1-219.

it mostly nerveless; in *Draba grandiflora*, however, and *confusa*, *Syrenia siliculosa*, *Smeloskia integrifolia*, &c., with one nerve; in *Parrya exscapa*, *Macropodium nivale* and *Sisymbrium Sophia*, furnished with two of them. In his 'Catalogue of Plants found in the Caucasus, &c. in 1829 and 1830, Petersb. 1831,' he gives also to *Sisymbrium binerve* "dissepimentum hyalinum, fasciis binis longitudinalibus insignitum" (p. 189). Of the plants here-named I had at my disposal good specimens only of *Macropodium nivale*, *Sisymbrium Sophia* and *S. binerve*, and in these I remarked the following points:—In *Macropodium* there extended through the middle of the whole septum a brighter streak free from the tissue of rows of anastomosing cells which occupied the sides, and which, above, where it originated from the base of the style, had on each side a border of rows of more thickened cells, and these borders appear to have been described by Meyer as two nerves. In *Sisymbrium Sophia* also a tolerably broad band runs through the whole length of the septum; it is not however brighter but less transparent than the remaining substance, at the same time it is more transparent in the middle than on the two lateral borders, and these borders have undoubtedly been taken for the two nerves by Meyer. *Sisymbrium binerve*, C. A. M., has much the same condition, only the band is not so broad here as in *S. Sophia*. If we understand by nerves, cords of fibrous tubes and vessels, there is no trace of such in that which appears as a nerve of the septum; they are rather only bundles of long-jointed cellular filaments, like those of which the central cellular tissue of the style, the so-called conducting tissue, is composed, as a prolongation of which, therefore, I do not hesitate to consider those nerves, though unable at present to say in what kind of relation to fertilization they stand in their distribution through the septum. It is true that we observe no distinct nerves in the septum of the majority of the Cruciferæ, which however must exist if these had the important destination alluded to; but in all siliques and silicles, if I am not mistaken, cellular filaments may be discovered, which are distributed in a reticulated manner between the two lamellæ of the septum, and mostly toward their borders where they retreat from one another, while in the middle portion they are usually in close contact. The idea which, on account of their distribution in a descending direction, is the first that must present itself, that they are pollen-tubes, is opposed by their being evidently composed of single elongated utricles, and I have never succeeded in making out a continuation of them to the ovules like that which Hartig figures from *Capsella**.

If we seek to trace back the formation of the silique according

* N. Theorie, 39. f. 26, 27.

to the general mode of origin of fruit, and if we regard, with Brown and DeCandolle, the many-celled fruits as originally composed of as many carpels as they have chambers, we must assume that the silique also consists regularly of two, very rarely, as in *Tetrapoma*, of four carpels, united in an apparently simple manner. But the question then arises, whether the placenta is an appendage of these carpels or an independent part, that is, a member of an inner whorl, the members of which alternate with the carpels as belonging to a more external whorl;—whether therefore it is, as some like to express themselves, an appendicular organ or a product of the axis. Assuming the former, the greatest difficulty is found in attempting to explain the production of the septum in the silique. De-Candolle regarded it as an expansion of the two placentas, and he sought to support this view by pointing out that the septum is always found to be thinner in the middle; that here it is readily torn in the direction of its length as in *Thlaspi arvense*, or is actually slit as in *Cheiranthus Cheiri*, or has a hole in the middle as in *Farsetia ægyptiaca*, *Octadenia lybica*, *Vesicaria gracilis*, &c., or is wanting in the middle and only present along the placentas as in *Tetrapoma*. But leaving out of the question that this by no means justifies such a conclusion, such an expansion would not agree with the original assumption, which settles the placenta to be a marginal production of the mere carpels. A. Brongniart* has described a monstrous form of the silique of *Cheiranthus Cheiri*, where instead of ovules small leaflets and indeed free leaves were produced. But how the formation of the silique is to be conceived so as to agree with this observation has not been stated by the author, who also holds that the theory of the production of the ovules from marginal teeth of the carpels is not applicable to all fruits, for instance not to the Primulaceæ, Myrsinaceæ, &c. Kunth has set forth the opinion that the silique is a structure composed of four leaves grown together at their margins, two of which have been perfectly developed outwards, but two are only developed inwards, because their growth outward is prevented by the pressure arising from the crowded position upon the axis, so that they produce seeds and may easily become united and form a septum †. Bernhardt also, citing a remarkable malformation of the fruit of *Ricotia* observed by himself, considered the silique as the product of four leaves grown together, two of which are arrested in their development ‡. But more recently he has given up this theory, since perfectly formed siliques are found with four

* Ann. d. Sc. Nat. 3 sér. i. 29.

† Abhandl. d. K. Acad. d. W. zu Berlin f., 132; Lehrb. d. Botanik, i. 397, 458.

‡ Ueb. den Begriff d. Pflanzen, art. 47.

valves and four septa*, and in fact the genus *Tetrapoma* is of this kind, in which the number of parts which the silicule usually possesses is exactly doubled. Bernhardt therefore in his latest memoir on the subject † regards the perfect ovary of Cruciferæ as composed of four pieces with the same number of septa, cells and placentas, but two of which are usually suppressed; not explaining himself definitely as to the origin of the septum, that is, whether it is a prolongation of the valves of the fruit or of the axis. The latter view however seems to be most favoured by Bernhardt, and in fact it is also in my opinion that alone which is sufficient to explain the structure of the fruit of the Cruciferæ. In them, says Aug. St. Hilaire, the axis divides into two branches which traverse the ovary and again unite at the point to form the style. These are the two pistillary cords which bear the ovules, and the carpellary leaves, which when ripe separate from them, are independent of them. The ovary has therefore the simplest possible structure here; it consists of two carpels and two parietal placentas ‡. According to this view the septum must be regarded as the substance of the axis compressed to a mere plate, in and on which the cellular tissue, conducting the fertilizing matter, is prolonged from the style, and which in fact is itself only a modification thereof for this particular purpose. The double lamellæ of the septum can as little be made an objection to this view, as the often remarkable attenuation, slits or opening in the middle of it, or even the total absence of a septum; since, as to the first, each of the two cavities should be formed independently; and with regard to the second, it is well known that it does not occur more frequently than cavities in the middle of the pith, which may reach to a total disappearance of the same.

From this point of view also I hold the anomalous forms which occur in the silique to be most satisfactorily explicable. Assuming as the normal structure, that a silique is two-celled with a perpendicular septum, it will become one-celled and single-seeded either by the total absence of a septum, the place of which is occupied by the cavity with the single seed, or by only one remaining in the ripe fruit of two one- or more-seeded cavities, since generally only one seed becomes developed. The first case occurs in *Isatis*, *Clypeola*, *Tauscheria*; here there is in reality no trace of a septum, and the single seed hangs down therefore from the apex of the cavity, which usually occupies the centre of the silicule. It is the same condition that we meet with in the anomalous fruits of *Æthionema heterocarpum*, with the difference that

* Flora 1838, no. 9.

† Ueb. d. Metamorphose d. Pflanzen; Flora 1843, Nos. 3, 4.

‡ Leçons de Botan. 493, 494.

the cord of the umbilical vessels is wanting on the depressed lower side of the much-inflated silicle, the other alone being present, running over the elevated side. The second occurs, for instance, in *Neslia paniculata*, *Rapistrum rugosum*, *Crambe orientalis*; and indeed in the two last-named the silicles are only two-celled in the upper joints, from the presence there of a perpendicular septum which is wanting in the lower. In *Myagrum perfoliatum* and *Erucaria aleppica* no seed is developed in either of the two chambers which occupy the uppermost part of the silicle. This absence of the septum in the lower part of the fruit has its analogue in the slit or opening which exists in the septum in that situation in *Farsetia* and other genera, in the whole central part in *Tetrapoma*, and it indicates the necessity of an uninterrupted union between it and the style or the stigma; while on the other hand an interruption at the other end, namely the lower, appears to be attended with no detriment to the formation of the fruit.

If this be the correct view of the septum, it will then always, at least originally, have a perpendicular position in the silicle. In *Bunias orientale* indeed, where the ripe fruit is two-celled and two-seeded, one cell with its seed lies over the other with an almost horizontal septum*, but this is a consequence of development. For in the earliest state of the fruit, when the stamens have scarcely fallen off, the septum here is vertical as usual, and the cells therefore originally lie side by side and not one above the other. In *Bunias Erucago*, DeCandolle finds the silicles two-celled in the young state, in a certain measure four-celled in the fully developed, as each cell is frequently again divided into two by a transverse septum†. But if a perpendicular section is made through the somewhat oblique silicle, at the period when the calyx, corolla and stamens fall off, in such a manner that the section crosses that oblique position, the four cavities are already visible. A membranous septum descends obliquely from above downwards, which by projecting in and out forms two curves, from each of which a fleshy transverse process runs to the outer wall. The septa of both kinds are present therefore when the fertilization is yet scarcely complete, so that we certainly cannot consider the production of any of them an after-growth.

In the genera *Cakile*, *Crambe* and *Rapistrum*, the silicle is divided into two joints by an apparent articulation in the middle, the upper being commonly externally of a different structure from the lower. By this means its cavity is indeed divided into an upper and lower cell, but the two cells are never perfectly separated, for there always remains an actual, though very narrow, communication between them, as the apparent articulation con-

* Gärtn. d. Fruct. ii. t. 142.

† Syst. Natural. ii. 670.

sists merely of a projection inward of the substance without an actual growing together or formation of a cross septum. That a longitudinal septum however occurs in the upper joint, at least in *Crambe* and *Rapistrum*, with the two cavities, one alone of which is perfected, has already been noted. An ovule is present both in the upper and the under cell, but in the upper it is erect, in the lower suspended: the two funiculi arise at about the same height, but on opposite sides of the cavity. Frequently the upper ovule alone is developed into a seed here, while the lower is often, and in the genus *Crambe* pretty constantly, abortive.

However great therefore the multiformity of nature appears in the silique, it may still be expected that we shall be able to trace back the aberrant structures to simple typical forms when we shall have discovered the transitional modifications. It would be in the highest degree interesting to examine more closely many cases of unusual forms of the fruit. Thus for example in *Stenopetalum robustum*, Endl., the seeds grow upon the base of the septum, in which a tripartite nerve is visible*. In *Pugionum cornutum*, G.,—a plant found, apparently, by no one but J. G. Gmelin,—Gärtner found an “arillus chartaceus” which completely inclosed the solitary seed†; but Ledebour has ascertained, from the examination of fruit in good condition in the collection of A. W. Martini, who was Gmelin’s companion, that the part which Gärtner took for an arillus was nothing else but the inner layer of the pericarp, which had become so detached from the outer that it was only connected by some fibres ‡.

XXXVI.—*Horæ Zoologicæ*. By Sir WILLIAM JARDINE, Bart.,
F.R.S.E. & F.L.S.

[Continued from p. 334.]

Birds of Tobago.

CROTOPHAGA RUGIROSTRIS, Swain. s. §

FOR our observations on this species we would refer our readers to the ‘Annals’ of 1839, p. 160; and in a letter received from Mr. Kirk since these observations were made, we have the following remarks on the incubation of this curious species:—“On a reperusal of your ‘Horæ Zoologicæ’ of 1839, in regard to the incubation of *Crotophaga*, I have now my doubts, and although

* Enum. Pl. Huegel. 4.

† De Fruct. ii. 292. t. 142. f. 3.

‡ Math. physical. Abhandl. der Münchener Acad. d. W. iv. Bd. 3 Abtheil.

§ Species marked n. are also found in North America; s. in South America; and n. s. in both.