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Morphological Notes

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The most interesting plant as regards Scotland, *Hierochloa borealis*, is not mentioned. We know from Robert Dick that the plant occurs along the Boulder Clay of the Thurso river, but it would have been of interest if the occurrence of the species had been noticed from the geological standpoint.

Mr. Crampton gives localities for other Caithness plants which are not localised in any of the published lists, as—

Carex limosa, L.—Small loch in the corrie at Yarehouse, where it grows associated with *C. dioica*, L., and *C. paniculata*, L.

Ranunculus auricomus, L.—Mr. Lillie of Swiney, Lybster, has sent me a specimen of the above species, gathered by one of the children of Boultaich School, and brought to Miss Hamilton, the teacher.

This is an interesting addition to the flora, as it is not on record north of Nairn on the east coast, and of Argyll! on the west coast. In Sweden its distribution is continuous from Skane to Swedish Lapland, in Norway north to 71° 8', and in Russian Lapland to 69° N. lat.

It also occurs in the Faroes, but not in Iceland.

MORPHOLOGICAL NOTES. By K. VON GOEBEL, Sc.D. (Camb.), LL.D. (St. And.), *Director of the Botanic Garden, Munich.* (Plate I.)

I. THE INFLORESCENCES OF THE AMBROSIACEÆ.

The large family of the Compositæ, as is well known, is one of those groups whose individual representatives, in spite of all their variation, still show such a close agreement in the structure of the flowers and the inflorescences that one can offhand recognise them as members of one family. Only a few groups deviate to any great extent, and of these one of the most interesting is the Ambrosiaceæ.

Ecologically they are interesting in the manner in which pollination on the one hand and the distribution of the fruit on the other hand are accomplished among them.

The Compositæ as a rule exhibit insect-pollination, but the Ambrosiaceæ have reverted to wind-pollination.

Hardly any greater contrast can be presented than between the resplendent flower-head of a *Helianthus* or a *Dahlia*, with its remarkable arrangements for dehiscence and for transference of the pollen, and the insignificant male and female floral attire of a *Xanthium* or an *Ambrosia*. There is a clear indication here that, quite apart from the lack of a corolla conspicuous in its coloration, the structure of the floral organs is in strict correlation with their functions. In the flowers no nectar is formed, there is no "concrecence" (in reality it is only agglutination or sticking together) of the anthers, and the pollen is formed in great quantity, as is the case with other anemophilous flowers. The condition of the exine indicates, however, that originally pollination took place by insects as in other Compositæ.

It is well known that the pollen in entomophilous plants is provided with a spiny or sticky exine, whereas in anemophilous plants the exine of the pollen-grains is smooth and not sticky. The Ambrosiaceæ, so far as I have been able to examine them, still show in the exine the remains of spinose thickenings such as are found in numerous other Compositæ, but these are so reduced that the pollen is no longer adapted for adhering.

The male flowers still show on the rudiment of the stigma a hairiness which recalls the "stigmatic brush" of other Compositæ. In the female flowers, in which the stamens have dwindled without leaving a trace, there is no longer any indication of this stigmatic brush. Thus the Ambrosiaceæ, in contrast to other Compositæ, are retrogressive in structure. On the other hand, it is evident that they have developed new characters not attained by other Compositæ. This is seen more especially in the character of the noteworthy envelopes with which the fruit is enclosed. The fruiting heads of *Xanthium* are well enough known to the wool-grower as the detested "burrs" (Kletten), which by means of their bent hooks attach themselves to the woolly coats of animals, and are so dispersed. We shall see that as regards these fruiting heads the other Ambrosiaceæ have also undergone retrogression in contrast with *Xanthium*.

It is not surprising that such noteworthy plants have

repeatedly formed subjects for investigation. So far as the developmental history is concerned, and apart from Payer's¹ contributions, which in the present instance need only be indirectly considered, there are available only the investigations of Rostowzew,² and these I propose in the following to supplement on some points.

Thus one topic will be the male inflorescence, while another will be the "fruit" of *Ambrosia*.

A. The Male Inflorescences.

As is known, the Ambrosiaceæ are monoecious to this extent, that the male inflorescences occupy the apex of shoots at the base of which are placed the female ones.

The individual flower-heads ("capitula") of *Ambrosia tripartita* are arranged in large numbers indefinitely (botryose) on an elongated axis, which in turn is terminated by a flower-head.

The lateral capitula have this noteworthy characteristic, that the flowers are not placed as usual on the upper (adaxial) side, but on the under side—that is, the side turned away from the primary axis of the whole inflorescence (abaxial). It is natural, at first sight, to ascribe this occurrence to a *torsion* of the flower-stalk. This is indeed the opinion of Rostowzew, who says that the flower-head undergoes a torsion, in that the peduncle grows more rapidly on its upper side than on its lower.

This interpretation in itself does not agree with the developmental history. If one examines the early stages, it is seen that the position of the capitula is "reversed" at a *very early stage*.

The capitula are differentiated from the embryonal tissue as hemispherical primordia. The cells of the primordia on the adaxial (upper) side pass first into the phase of elongation-growth, with the exception of the terminal part (*a*, fig. 1), which develops as the first leaf. On the other hand, the lower side remains embryonal. This is utilised for the development of the growing-point of the capitulum (*b*,

¹ Payer, "Traité d'Organogénie comparée de la fleur" (Paris, 1857, p. 638).

² T. Rostowzew, "Die Entwicklung der Blüten und des Blütenstandes bei einigen Arten der Gruppe Ambrosiæ" ("Bibliotheca botanica," 20).

fig. 1), except the basal part (nearest the primary axis), which later gives rise to the intercalary meristem in the elongating peduncle of the capitulum.

How shall we interpret this peculiar development? Two different views are obviously possible.

It may be that the first leaf (*a*, fig. 1) arising from the growing-point of the capitulum is the first leaf of the involucre of the capitulum, the individual leaves of which, united together, form an apparently entire envelope. This is the concept of Rostowzew, which, however, has thus far to be supplemented, that the "torsion of the capitulum"—if one assumes such a thing—is not a subsequent event, but it existed from the first; in other words, it is "congenital." Rostowzew does not mention that if this interpretation be assumed, then the lateral capitula of the *Ambrosia* would present one of the rare cases in which the "bracts" (Deckblätter) of lateral shoots have aborted completely. This occurrence is known in the flowers of the cruciferae, etc., in which one can correlate the abortion of the bracts with excessive crowding originally undergone by the flower-primordia before the elongation of the axis of the inflorescence. In the case of *Ambrosia*, this would be all the more striking because the female inflorescences possess well-developed bracts, although they are quite as closely crowded together as the male ones. In no instance have I observed in the male capitula even a trace of a subtending bract.

The second possibility is that the first leaf (indicated by *a* in fig. 1) is the bract (Deckblatt) of the capitulum. The manner in which (*a*) develops from the primordium that gives rise to (*a*) and (*b*) is similar to what occurs frequently in flowers and inflorescences. In this instance the bract, so to speak, is late in being formed. It does not develop in advance of its axillary shoot, but from a primordium common to both. The thing that surprises one is that the axillary shoot should arise on the under side of the bract, and not, as usual, on the upper side. But, after all, this is no more wonderful than the "congenital torsion" already referred to, nor is it quite without precedent amongst other Dicotyledons. The remarkable flowers of *Erythrochiton hypophyllanthus* are situated on the under

side of the leaf; also the axillary branches on the creeping shoots of some of the terrestrial *Utriculariæ* arise on the side of the leaf furthest away from the growing-point.¹

In other respects it may be assumed that the position of the male capitula of *Ambrosia* means the same thing as the torsion (entirely brought about by their weight) of the male inflorescences of *Corylus*, *Alnus*, *Juglans*, or the torsion of the anther of grasses: by this means the shaking out of the pollen is facilitated in all these anemophilous plants.

Returning now to the morphological question, one might, in arriving at a decision, also take the anatomical facts into account. If (*a*) (fig. 1) represents the bract of the capitulum, then one might expect that the normal orientation would be shown in the constitution of the vascular bundle, phloem on the lower side, xylem on the upper. Of course, I do not regard the anatomical conditions as decisive, since, in my opinion, these are determined by the morphological, not the reverse. In the present instance this would mean that, in the event of a relatively limited development and retardation in time on the part of the bract in comparison with the axillary shoot, it appears quite natural that the former (the bract) should be provided with its vascular system from the latter (the shoot). This being so, one expects the xylem to be uppermost, with the phloem underneath.

The conditions actually existing are briefly as follows: The thin, much-flattened peduncle of the capitulum contains two vascular bundles (rarely three); the phloem-groups of these are set towards the narrow margins, and the xylems are turned towards one another and somewhat obliquely downwards (fig. 3). This anatomical structure is interesting because unusual in a shoot-axis.

A certain biassed school of anatomists assumes that shoots are distinguished from leaves by their anatomical structure, particularly in the arrangement of the vascular bundles. The shoot of the capitulum of *Ambrosia* does not differ in structure from many leaf-stalks, except that in the latter the xylem of the vascular bundle is directed upwards.

¹ K. Goebel, *Utricularia* ("Annal. du jardin botan. de Buitenzorg," vii, 1889).

There is little doubt that this anatomical structure is the result of reduction; that is, the peduncle of the primitive type possessed more than two vascular bundles. Linked with these bundles are those which ramify throughout the involucreal leaves and the flower, but I have not followed these in detail. It may be mentioned, however, that the vascular bundles of the involucreal leaves are normally orientated in that their xylem lies towards the growing-point of the capitulum. The orientation is that described above, and for the reasons given it does not seem to me possible to arrive at any definite conclusion as to the morphological interpretation of this leaf (*a*) from the anatomical structure.

It might be advanced in opposition to the view that the leaf (*a*) is a bract, that later on it does not always stand opposite the peduncle; this might, however, result from displacement. In the younger stages I saw it in the median position occupying the whole breadth of the inflorescence-primordium (fig. 4). As regards the further development of the male capitula, two facts may be pointed out. Firstly, that the external side (that on which the letter (*a*) is placed) appeared to be much further advanced than the inner side; this is seen at once in fig. 4. Secondly, that the arrangement of the flowers is not "dichasial" sympodial (as one of the recent authors wrongly states), but corresponds essentially with the other Compositæ. One sees quite clearly the broad growing-point of the capitulum (V., fig. 4), from which the individual flowers arise; some of the outer ones have bracts even now. The characteristic arrangement of the flowers is determined by the fact that the capitulum as a whole is dorsiventral in structure, with a more advanced development on the outer side.

B. The Female Inflorescences.

As indicated by Rostowzew, these are dichasially arranged (fig. 5). Each consists of a single flower enclosed by an "envelope" (fig. 8). To understand their constitution it will be necessary to first compare the inflorescences of other *Ambrosiæ*. Here one finds the following series:—

1. Mixed inflorescences with female marginal florets.
2. Inflorescences with sexes distinct, in so far that in

the female only the marginal florets flower, and only the minority of these, while in the male inflorescence the formation of female flowers is entirely suppressed.

3. There is also a diversity in the arrangement of the female and male inflorescences. Whereas the arrangement was originally indefinite (botryose), this is retained only in the case of the male inflorescences, the female ones showing dichasial arrangement.¹

In *Xanthium* the male inflorescences are orientated normally; the structure of a young male inflorescence in longitudinal section is shown in fig. 6, I. The female capitulum consists of two flowers enclosed in the many-spined envelope. This envelope originates from the fusion of two bracts (*Sa*, *Sb*, fig. 6, II.) in whose axils the female flowers are placed. With reference to the development, the reader is referred to my recent account.² This is noteworthy in this respect, that the two floral bracts entirely monopolise the growing-point of the capitulum (except what is required for the flowers arising in their axils), as is shown in the view from above (fig. 6, IV.), and that the flowers are deeply sunk in the axis of the capitulum.

Comparing this inflorescence with that of *Ambrosia*, it will be found to have undergone still further reduction. Firstly, we see that the spines or barbed hooks outside the envelope are here reduced to a few small processes (figs. 7 and 8, *st*); secondly, each envelope contains only one flower. The processes referred to can no longer be of use in the dispersal of the fruits by animals.³ How dispersal is effected can only be ascertained in the native land of the plant. The fruits are relatively light, and float in water for a short time at least, and they may even be rolled to a distance by wind.

It is evident that the envelope of the fruit of *Ambrosia* corresponds to that of *Xanthium*. But is it, like the

¹ With regard to diversity of male and female, compare Goebel, "Ueber sexuellen Dimorphismus bei Pflanzen" ("Biolog. Centralblatt," p. 657, 1910).

² Goebel, *l.c.* ("Biolog. Centralblatt," xxx., 1910, p. 722).

³ They might, of course, become lodged between the claws or in the hoof.

former, a double one, or is it single? That there is some suggestion of a double envelope is evident by the fact that the apex of the envelope (originally laid down as a closed ring; see fig. 7, right-hand figure) is distinctly two-lobed in the later stages of growth. This indicates that two leaf-primordia take part in the formation of the envelope. Only one of these, however, has an axillary flower-primordium. Obviously a characteristic retrogression has taken place here: the flower monopolises the whole area within the envelope; hence it arises not as a lateral outgrowth on the growing-point of a capitulum, but is terminal. There are, of course, many examples of an organ genetically lateral in origin becoming ultimately terminal. We may cite the spikelets of many grasses, also the carpels which in many flowers monopolise all the residual part of the growing-point of the flower, and the terminal stamen of *Naias*, *Callitriche*, etc. *Ambrosia* is, however, a specially well-marked example of this procedure. The development of the female flower need not be described further, except to point out that there is only a mere trace of the corolla, while the stamens and calyx have disappeared without leaving a trace.

Thus we see that *Ambrosia* has carried still further in its female inflorescence that reduction already indicated in *Xanthium*. Even in *Xanthium* the male organs of the capitulum are completely suppressed and the number of female flowers is reduced to two. As new structures there are present the hook-like spines on the outside of the concrescent floral-bracts, which, taking the place of the pappus originally present, facilitate dispersal of the fruit. In *Ambrosia* these spines dwindle to a few rudiments and the number of flowers diminishes to a single one.

In the male inflorescences, however, the number of capitula is probably increased considerably in comparison with the type-form with hermaphrodite flowers. With this may also be correlated, that these male capitula have departed from the prevailing scheme of development, and as seen in their "reversal" have progressed along new lines. Thus with no great effort, and with a basis of facts admissible in any new speculation, we are able to trace, in what seems to me a satisfactory manner, the historical evolution of the structure

of the inflorescences of *Ambrosia*. At the same time, the case dealt with here illustrates once again the phenomenon to which the author has frequently made reference; namely, that our phylogenetic series, so far as we can depict them with any degree of probability, all represent a reduction-series.

The following may be advanced in support of this:—

1. In a descending series we have a definite starting-point (that is, some one of the more completely equipped forms as distinct from the more reduced ones) with which we can compare the less completely equipped members of the series.
2. In many instances the organs in question may still be recognised as rudiments.
3. The descending series arise latest; hence they are more completely preserved and easier to recognise than the ascending with a history extending much further back, and whose members are as a rule very incompletely preserved.

Descending series of this kind are known to every botanist, since they appear again and again in almost every family. Other facts also indicate that organisms become modified mainly through retrogression and simplification: thus “mutations,” for example, are essentially of this nature, since in them there is a loss of some definite characteristic.¹

Has then the “*nisus formatoris*” of the ancient philosophers itself become antiquated? Not at all; botany at least has remained youthful. To be convinced of this, one need only glance at what is only possible where youthful aspirations exist, namely, the construction of genealogical trees from below upwards. “Alas, alike in their tenure of life, they are mostly ruins, not of the trees, however, but of the ephemeral day-flies!”

¹ E. Baur, “Einführung in die experimentelle Vererbungslehre” (Berlin, 1911), says: “The large majority of mutations which have been closely investigated depend simply on the loss of some single Mendelian unit character. I have not found up till now, any absolutely certain case in which one or more unit characters have arisen *de novo*.”

EXPLANATION OF THE FIGURES.

Fig. 1. Longitudinal section through an inflorescence of *Ambrosia tripartita*. V, growing-point of the male inflorescence; the individual capitula (with the exception of the terminal one) are placed laterally on the primary axis. *a*, the first leaf of a male capitulum of which *b* is the growing-point. *Bl*, female flower with its envelope, H.

Fig. 2. *Ambrosia tripartita*. Longitudinal section through an older male capitulum. V, the growing-point.

Fig. 3. Transverse section through the peduncle of a male capitulum of *Ambrosia tripartita*. The xylem in each of the two large conductive bundles is shaded.

Fig. 4. Capitulum of *Ambrosia tripartita* seen from above. Around the growing-point, V, there are seen fifteen embryonal flowers in various stages of development; the involucre surrounds the whole.

Fig. 5. *Ambrosia tripartita*. Transverse section through a young female inflorescence-group. In the axil of a bract (Deckblatt), D, is a one-flowered female inflorescence, I, with its envelope, H; this has two prophylls (Vorblätter), V, in the axils of which other inflorescences are present.

Fig. 6, I.-III. *Xanthium spinosum*.

- I. Longitudinal section through a young male inflorescence. B, male flower with its bract, S.
- II. Longitudinal section through a female inflorescence. *Sa*, *Sb*, the bracts (Deckblätter) of two flowers, *Sa*₁, *Sb*₁, which on the side towards the incurved margins of the bracts are proceeding to develop the floral organs.
- III. Older inflorescence in which each female flower has now the stigma developed, *st*.
- IV. *Xanthium strumarium*. A young female inflorescence seen from above.

Fig. 7. *Ambrosia tripartita*. On the left a female inflorescence, seen from the outside. *st*, primordia of the spines which remain rudimentary. H, the envelope (clearly two-partite). *Bl*, flower-primordium seen through the envelope (which is regarded as transparent). On the right a young inflorescence seen from the outside.

Fig. 8. *Ambrosia tripartita*.

- I. Fruit with its envelope, bisected longitudinally. H, envelope; *st*, spines; P, pericarp; S, seed-coat (very thin); E, embryo.
- II. Fruit with envelope seen from outside.

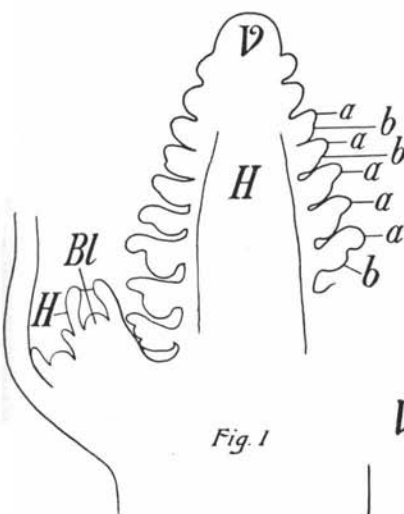


Fig. 1

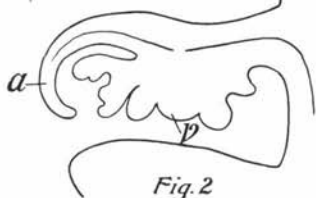


Fig. 2

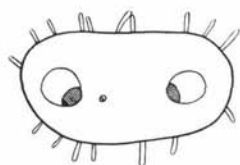


Fig. 3

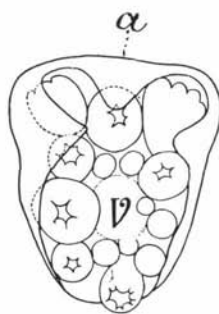


Fig. 4

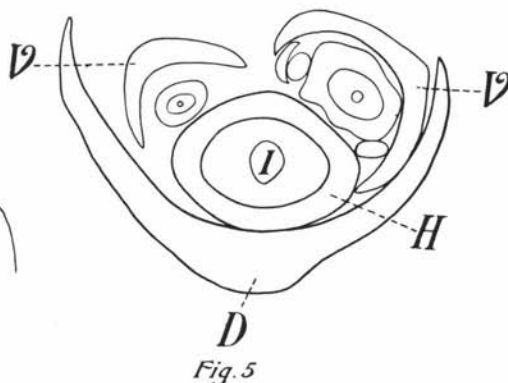


Fig. 5

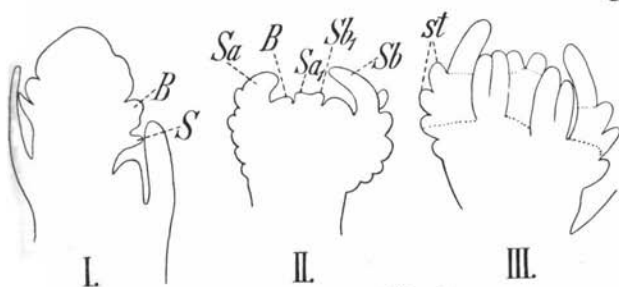


Fig. 6

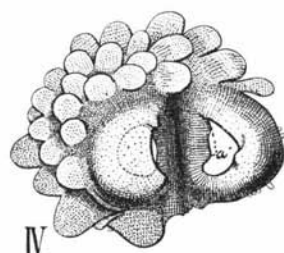


Fig. 7

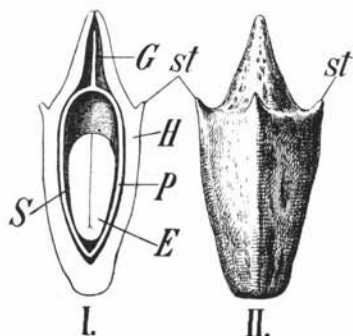


Fig. 8