Contributions to the Morphology of the Mistletoe (Viscum album, L.).

BY

SELMAR SCHÖNLAND, Ph.D.

With Plate XVII.

DURING the past few years I have repeatedly had opportunities of observing a large number of abnormalities in the structure and arrangement of the organs of the mistletoe, many of which have been noticed before, while others are apparently new. They have led me to give interpretations to some morphological characters of this plant different from those hitherto given, and I therefore think they are worth describing.

In the present paper I propose to deal chiefly with the morphology of the flowering shoots, including both the arrangement and the general structure of the flowers. In order to make my remarks more intelligible, I have included almost all that has been said on the subject by Wydler[1] and Eichler[2].

The mistletoe is dioecious[3]. The plants of the two sexes have on the whole the same structure. The axis of the seedling produces two cotyledons and a pair of foliage-leaves alternating with these. It then ceases to grow any further, but in the axils of the foliage-leaves buds are produced which develop into branches the next year. Each branch bears at its base two minute opposite scale-leaves, the prophylls of the new shoot (p, p in the diagrams); they are at right angles to the bract of the shoot (B in the diagrams). Near the top of

[1] Flora, 1860, p. 443.

[2] Blüthendiagramme, ii. p. 552.

[3] Only a single case in which a male plant had also produced some female flowers and fruits is mentioned by Masters in his Vegetable Teratology, p. 509.

a branch two foliage-leaves (*L*, *L*, Figs. 1, 2, etc.) are usually found, which alternate with the prophylls, and are therefore median. During the first years the apex of each shoot is either naked, or it bears two more scale-leaves, which again alternate with the foliage-leaves, but the growth is always continued by buds springing from the axils of the latter, and thus the well-known pseudo-dichotomous structure of the mistletoe is produced. The foliage-leaves normally last only one season, while the prophylls may remain for a period of eight or more years. In about the fourth or fifth year of the life of the plant a small capitate inflorescence is produced at the top of each shoot.

It commonly happens that foliage-leaves or shoots are not developed in places where the general plan of the plant would lead us to expect them. The shoots especially may remain dormant for several years. If only one shoot is developed, it often appears as the direct prolongation of its mother axis. If this goes on for several years a sympodium is produced which is frequently of considerable length. It also happens sometimes that new shoots are produced in the axils of the prophylls, and thus false whorls of three to six shoots are formed. As this may be repeated in the case of the accessory shoots, their number may be increased still more, and Wydler[1] found as many as twelve in one case; he also saw prophylls developed into foliage-leaves. Shoots bearing a whorl of three foliage-leaves are not rare, whereas whorls of four foliage-leaves[2] are uncommon, but I found them in both male and female plants. The increase in the number of foliage-leaves seems on the whole to be more frequent in the male plants. As a rule, this is due to the substitution of a trimerous or tetramerous whorl for the normal dimerous whorl, as is shown by the fact that each of them may

[1] Flora, 1860, p. 445.

[2] In one case I found five foliage-leaves in a rather irregular whorl. This was due to the fasciation of two shoots, one bearing two, the other three leaves. The true nature of this abnormality was clearly shown by the internode being groved, etc., also by the structure of the two inflorescences which terminated this double shoot.

bear an axillary bud, and thus true whorls of three or four branches may also be produced. I have actually observed such true whorls of three and four branches. The structure of the inflorescence, moreover, corresponds usually to the number of foliage-leaves, as we shall see later. In one case only, where three foliage-leaves occurred, they seemed to have arisen from the normal two leaves. One of the three leaves was rather broad, and showed beginning of splitting at the apex, while two others were about the normal size; but neither one nor the other of these had, like the third, a bud in its axil, there was, however, a bud between them, which served, as it were, as a common axillary bud for the two together (Fig. 3). It is probable, therefore, that they owed their origin to the splitting of one of the normal leaves. The odd leaf of the true trimerous whorls of foliage-leaves is always turned towards the axis (Figs. 4, 5 I), whereas the leaves of the tetramerous whorls are placed diagonally (Fig. 5 II, 6).

The inflorescences are usually found between the two foliage-leaves, and normally consist of two lateral flowers at right angles to these leaves, and a terminal flower. Each of the former stands in the axil of a small scale-leaf, the two together thus forming a third whorl of leaves (*s*, *s*, Figs. 1, 2). No more leaves are borne directly by the primary axis of each shoot in the male plants, but in the female plants the terminal flower is usually preceded by a fourth pair of leaves, which is like the one preceding it, and continues the regular decussate arrangement of leaves[1] (s^1, s^1, Fig. 1). Where three or four foliage-leaves are borne by a shoot, the number of the upper scale-leaves is increased at the same rate; this is often also the case with the lateral flowers, but frequently their full number is not developed (Figs. 5 I and 5 II). Very often scale-leaves are only developed where foliage-leaves ought to be, either in the place of one or of both of a pair. This occurs chiefly in shoots which have been dormant one or more years. Very commonly these additional scale-leaves also bear flowers in their axils,

[1] From a remark made by Wydler, Flora, 1860, p. 443, I conclude they may also bear flowers in their axils.

and thus we get an inflorescence of five flowers, as represented in Fig. 7. Such an inflorescence has usually a short stalk, and is like the ordinary shoots provided with two prophylls at the base. Whole inflorescences or single flowers may also be formed in the axils of the prophylls of ordinary shoots.

The terminal flower of the male inflorescence is, as a rule, not preceded by scale-leaves, as indicated above. But Hofmeister[1] has stated that they are present here, as in the female inflorescences. This is really often the case, although not observed by Eichler, but still the structure of the inflorescences in which it occurs is not the same as that of the female inflorescences. I only observed this apparent abnormality in inflorescences developed from dormant buds. I have represented it in Fig. 8 I. It is shown there that in the abnormal cases the shoots of male plants have only three pairs of decussate leaves, as in the normal cases. The abnormality is at once understood by comparing it with a case such as is represented in Fig. 7, and which I have explained already. If in such a case the two lateral flowers are not developed, as frequently happens, a three-flowered inflorescence is produced which, it is true, agrees in its general structure with the normal female inflorescences, but there is one difference (quite apart from the number of leaves) by means of which its true nature may be at once detected. A normal female inflorescence is always transverse (Fig. 1), whereas these inflorescences are always median, which must be the case, as two out of the three flowers composing it are seated in the axils of the equivalents (*l*, *l*) of the two foliage-leaves, which are always median. The uppermost pair of leaves preceding the terminal flowers (*s*, *s*) in such cases is therefore not equivalent to the uppermost sterile pair of leaves (s^1, s^1, Fig. 1) in the female inflorescence. If, again, both the lateral flowers and their bracts are suppressed (Fig. 8 II), the resulting inflorescence is exactly like the normal male inflorescence, differing only in its relative position to the mother-axis and the bract of the shoot.

[1] Neue Beiträge, i. p. 553. I am quoting here from Eichler, Blüthendiagramme, p. 553.

In the female flowers the perianth[1] consists usually of two dimerous alternating whorls of scale-leaves, which cohere, more or less, at the base. Their position will be readily understood by a glance at Fig. 1, which has been copied from Eichler[2]. The two carpels which compose the ovary continue the regular alternation. No exception has come under my observation with regard to the number of parts composing the lateral flowers, whereas in the terminal flowers of shoots bearing three foliage-leaves only one whorl of perianth-leaves, alternating with the three scale-leaves which precede the flowers, was observed (Fig. 4). Wydler mentions a case in which a female terminal flower, preceded by two scale-leaves, had also a trimerous perianth. An increase in the number of perianth-leaves beyond four has also been described by the same author, and is very likely to be explained in the same way as a similar increase of the organs composing the male flowers, which will be treated of later. Whether any variation in the number of carpels takes place I am unable to say.

The male flowers are, on the whole, built on the same plan as the female ones, but every trace of an ovary is absent in their centre. Each perianth-leaf bears six to twenty pollen-sacs. Hofmeister[3] and van Tieghem[4] consider each of these structures (taken as a whole) as a single leaf. The former bases his view on the development, which shows that it arises apparently as one organ; while the latter bases his view chiefly on anatomical grounds, but he is careful to call them simply polliniferous sepals ('sépales pollinifères'); he does not call them stamens, as one would expect. Eichler, on the other hand, who based his view on a comparison between the structure of the flower of the mistletoe and that of nearly allied forms, came to the conclusion that each consists of two parts, namely of

[1] I have never seen the so-called 'calyculus' of the flowers. It is frequently mentioned that it does not occur regularly, and it seems to be certain that it is only an outgrowth of the axis without leafy character. Compare Hofmeister in Flora, 1854, p. 644 (note); Wydler, in Flora, 1860, p. 445; Eichler, Blüthendiagramme, p. 553.

[2] l. c., Fig. 236, B.

[3] l. c., p. 539.

[4] Ann. d. Sc. Nat. série 5, Tome xii. p. 101.

a perianth-leaf and an anther. I am inclined to think that his view is right, although I cannot offer much additional evidence to support it. But I may mention that I have often seen the posterior perianth-leaf of lateral flowers forming a compact body with the adjoining perianth-leaf of the terminal flower, both of them bearing their pollen-sacs in their proper places. Now, when we thus see that leaves of different flowers frequently coalesce to form a single structure, we are certainly justified from a morphological point of view to assume that such a coalescence may constantly take place in the leaves of the same flower, if there are other reasons to support such an assumption. Eichler adduces as an argument in support of his view the fact that in other species of *Viscum*, as also in the nearly allied genera *Eremolepis*, *Phoradendron*, and others, the two leaves, which are only hypothetical in our species, may actually become nearly separate; and, further, that it also happens exceptionally in these genera that the flowers possess three perianth-leaves and two anthers, one of the latter being then placed between two of the former, 'certainly the best evidence against Hofmeister's view [1].'

Eichler says that the male lateral flowers are 'always' tetramerous, but I found them frequently to be trimerous or even pentamerous. In the trimerous flowers there was apparently a single whorl of perianth-leaves [2] substituted for the normal two dimerous whorls, whereas in the pentamerous flowers evidently a splitting of a perianth-leaf with the adnate stamen had taken place (compare the diagrams of the lateral flowers in Fig. 6). The terminal flowers of shoots with a dimerous (and I may add also those with a tetramerous) whorl

[1] See also Schumann in Pringsheim's Jahrbücher, 1887, Bd. xviii. p. 133, where questions of this kind are treated of in a more general way; the case of *Viscum* is mentioned on p. 170. My paper was in the hands of the editors before No. VI. of the Annals of Botany was published. I have noticed with satisfaction that Mr. T. Johnson in his paper in that number, on '*Arceuthobium Oxycedri*,' brings forward very strong arguments in support of Eichler's view (cf. Annals of Botany, Vol. II. No. VI. pp. 155 and 156).

[2] For shortness' sake I am only speaking of perianth-leaves here and in the following passages. It will be understood that I always mean the structures composed of a perianth-leaf and an anther.

of foliage-leaves are usually tetramerous, the outer whorl of perianth-leaves being median, and, therefore, differing in this respect from the terminal female flowers, as will be seen when Fig. 1 and Fig. 2 are compared. It will also be seen that the outer whorl of perianth-leaves of the male flowers has the same relative position as the uppermost pair of scale-leaves in the female ones. The terminal male flowers of shoots with three foliage-leaves usually possess two trimerous whorls of perianth-leaves, the outer one having also the relative position of the three scale-leaves in the corresponding female flowers. Eichler is of opinion that in the common male terminal flowers the two scale-leaves which precede the female flowers are made use of ('werden einbezogen'[1]) in the formation of the perianth. Although at first sight this appears obvious, I cannot agree with such an interpretation. First of all it may be argued, from a general point of view, that the outer and first formed perianth-leaves take a median position, simply because there is room for them to develop in this position on account of the scale-leaves being absent. If we adopt Eichler's view we must further admit that the male terminal flower is constantly without the inner dimerous whorl of perianth-leaves which the corresponding female flower always possesses. But there is, thirdly, one reason which directly compels us to give up the view brought forward by Eichler. I have already mentioned that dormant buds often produce inflorescences composed of a various number of flowers. I have described the three cases which are the most frequent. Let us compare the two cases represented in Fig. 8 I and II. These two inflorescences were found side by side. It will be admitted that in these two cases the terminal flowers are absolutely equivalent, and yet, if we examine the relative position of their parts, we notice the actual difference which exists between the normal male and female terminal flowers. If, as in Fig. 8 I, the terminal flower is preceded by two sterile scale-leaves, the outer whorl of perianth-leaves is median, and thus alternates with them; but if it is not preceded by them,

[1] It must be said that the German expression is rather vague.

as in Fig. 8 II, this whorl is placed transversely, assuming the position of the scale-leaves which are wanting. I have tested this fact in many cases, and always with the same result. I am thus led to believe that the difference between the terminal male and female flowers, with regard to the position of their parts, is simply caused by the complete suppression in the former of the uppermost (fourth) pair of leaves.

An increase in the number of parts composing the male terminal flowers is not rare. Eichler only knew of pentamerous and hexamerous flowers besides the normal ones; but I have also observed one heptamerous and one decamerous flower[1]. Eichler explained the abnormal cases known to him by assuming that in the hexamerous flowers the inner dimerous whorl of normal flowers was replaced by a whorl of four members, and in the pentamerous flowers by a whorl of three; but his own figure, which I have copied (Fig. 9), suggests at once the idea that the increase is simply due to the splitting of the two normal members composing the inner whorl[2]. I have already adopted such an explanation in the case of the pentamerous lateral flowers, where I usually found it to agree extremely well with the position of the parts of the flowers. In the terminal flowers a regular arrangement of the parts cannot always be recognised when their number has been increased, but it is easy to find all intermediate stages between perianth-leaves only slightly divided at the top, and others which are divided down to the base. My explanation covers also the cases in which seven and ten perianth-leaves were found, whereas those adopting Eichler's view would find difficulty in explaining them. The view that the increase is due to splitting may perhaps be strengthened still more when I restate the fact, which I hope has been distinctly proved, that splitting of foliage-leaves also occurs in the mistletoe.

[1] The hexamerous flowers of shoots with three foliage-leaves were also apparently unknown to him, but these must be left out of account here, as in a certain sense they have to be considered as normal.

[2] I may here call attention to the similarity between our case and the interpretation of the androecium of Cruciferae, regarding which Eichler holds exactly the view I take of it in *Viscum*.

EXPLANATION OF FIGURES IN PLATE XVII.

Illustrating Dr. Schönland's paper on the Morphology of the Mistletoe (*Viscum album*, L.).

[All figures represent diagrams of flowering shoots as actually observed by the author, with the exception of Fig. 9.]

[A = mother axis of each shoot; B = bract; p = prophyll; L = foliage-leaf; b = axillary bud; l = scale-leaf corresponding to L; s and s' = scale-leaves in inflorescences.]

Fig. 1. Normal female shoot (after Eichler).

Fig. 2. Normal male shoot.

Fig. 3. Male shoot in which the posterior foliage-leaf has split into two; the anterior leaf shows beginning of splitting; the terminal inflorescence is also abnormal.

Fig. 4. Trimerous female shoot.

Fig. 5. I. Trimerous male shoot; one lateral flower is not developed. II. Tetramerous male shoot; one lateral flower and the terminal flower are not developed. The two median lateral flowers are trimerous, and occupy the apex of the shoot.

Fig. 6. Tetramerous male shoot; one lateral flower is trimerous, another pentamerous.

Fig. 7. Male shoot with five flowers developed from a dormant bud. In the place of the two foliage-leaves, scale-leaves are developed which also bear flowers in their axils.

Fig. 8. I. A similar case as represented in Fig. 7, only the two lateral flowers are suppressed. II. Case similar to the preceding one; a further reduction has taken place by the suppression of the uppermost pair of scale-leaves.

Fig. 9. Male shoot with hexamerous terminal flower (after Eichler).

Fig. 1.

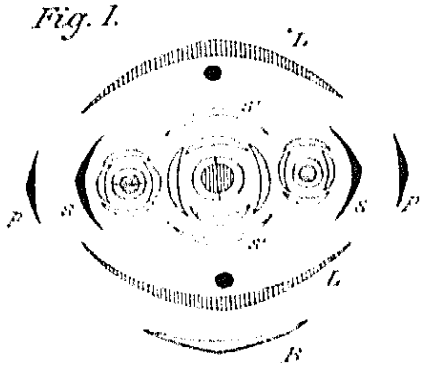


Fig. 2.

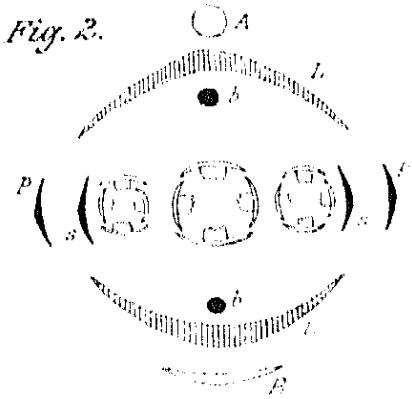


Fig. 3.

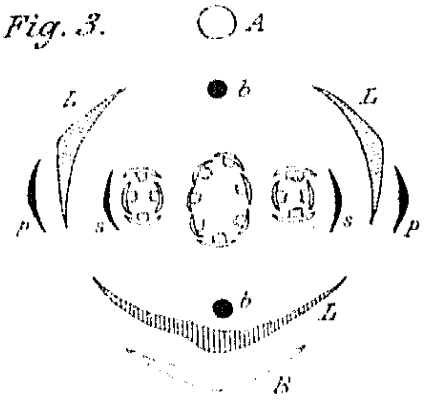


Fig. 4.

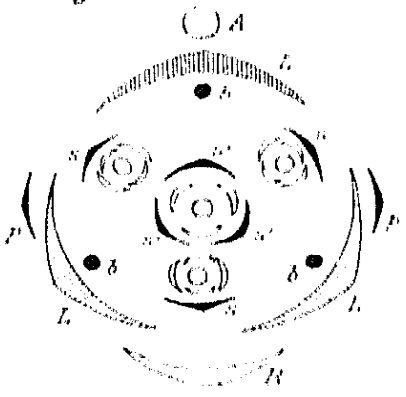


Fig. 6.

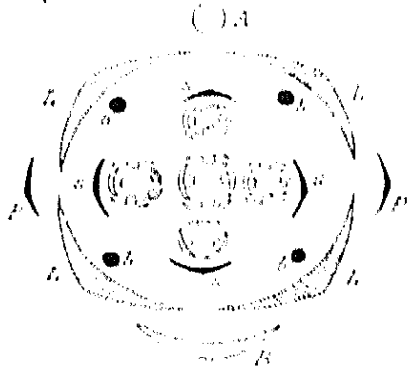


Fig. 7.

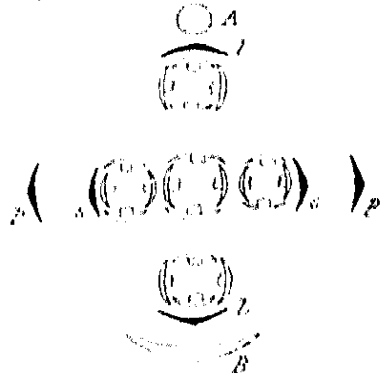


Fig. 8.

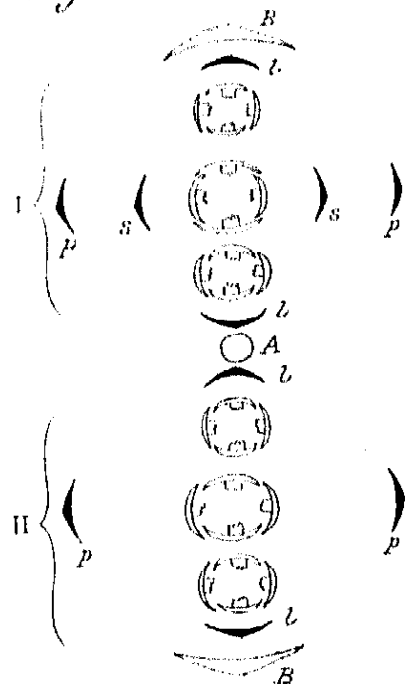


Fig. 9.

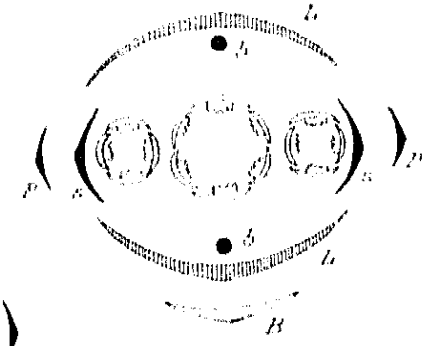
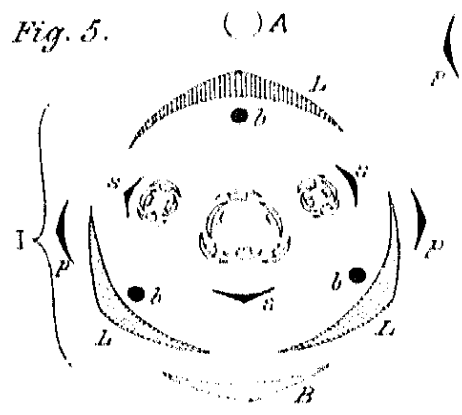


Fig. 5.



Schönland del.

University Press, Oxford.