

NOTE ON THE MORPHOLOGY OF THE MALE INFLORESCENCES IN *CERCIDIPHYLLUM* (CERCIDIPHYLLACEAE)

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SUMMARY

Male reproductive axes are described which have three pairs of decussate bracts, some with free axillary groups of stamens. The developmental stages are demonstrated by scanning electron microscopy (SEM). The view, earlier advanced for the female counterparts, that these reproductive axes are reduced polyaxial systems, is supported.

INTRODUCTION

The flowers or inflorescences of *Cercidiphyllum* have been discussed in morphological terms more than once recently. Curiously the discussion was mainly limited to the female organs, although Endress (1986) also considered the male organs. A certain homology between male and female structures should be expected beforehand. Recently important paleobotanical evidence was contributed by Crane and Stockey (1986). In the present paper a detailed description of the ontogeny of the male inflorescences in one treelet is given in order to reach a basis for comparison with the female structures. Together they should be compared with the reproductive organs of related genera.

MATERIALS AND METHODS

The material for this investigation was generously presented by Dr. P. Kooiman, who cultivates a male and a female treelet in his private garden at Delfgauw in the Netherlands. Both trees are young and vigorous, 2–3 m high. Dr. Kooiman has raised these trees from seeds which he acquired from the Botanic Garden of Seattle, U.S.A., in 1969. These seeds were sent to him as belonging to *Cercidiphyllum magnificum* Nakai. I will not discuss the taxonomic problem whether *C. magnificum* is a variety or species which is different from *C. japonicum* or not (see Spongberg, 1979). Certainly the inflorescence structure is identical.

The technique for SEM in this study was as described in Van Heel (1984). Also microtome sections were prepared, using standard procedures; the slides were stained with safranin and astrablue.

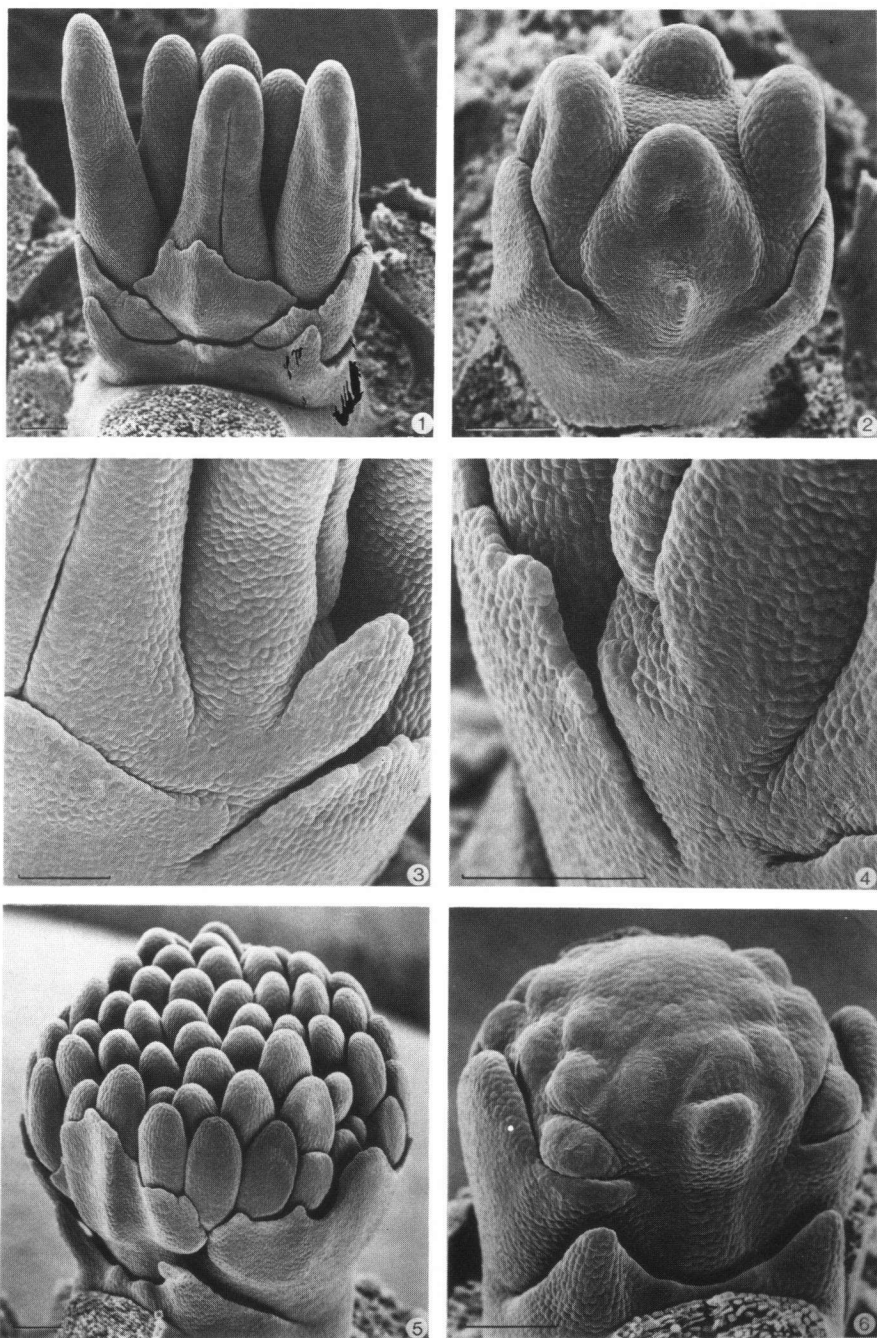


Plate 1. *Cercidiphyllum magnificum*. Bars represent 0.1 mm. — Photos 1–4: Female; 5–6: Male. Explanation in text.

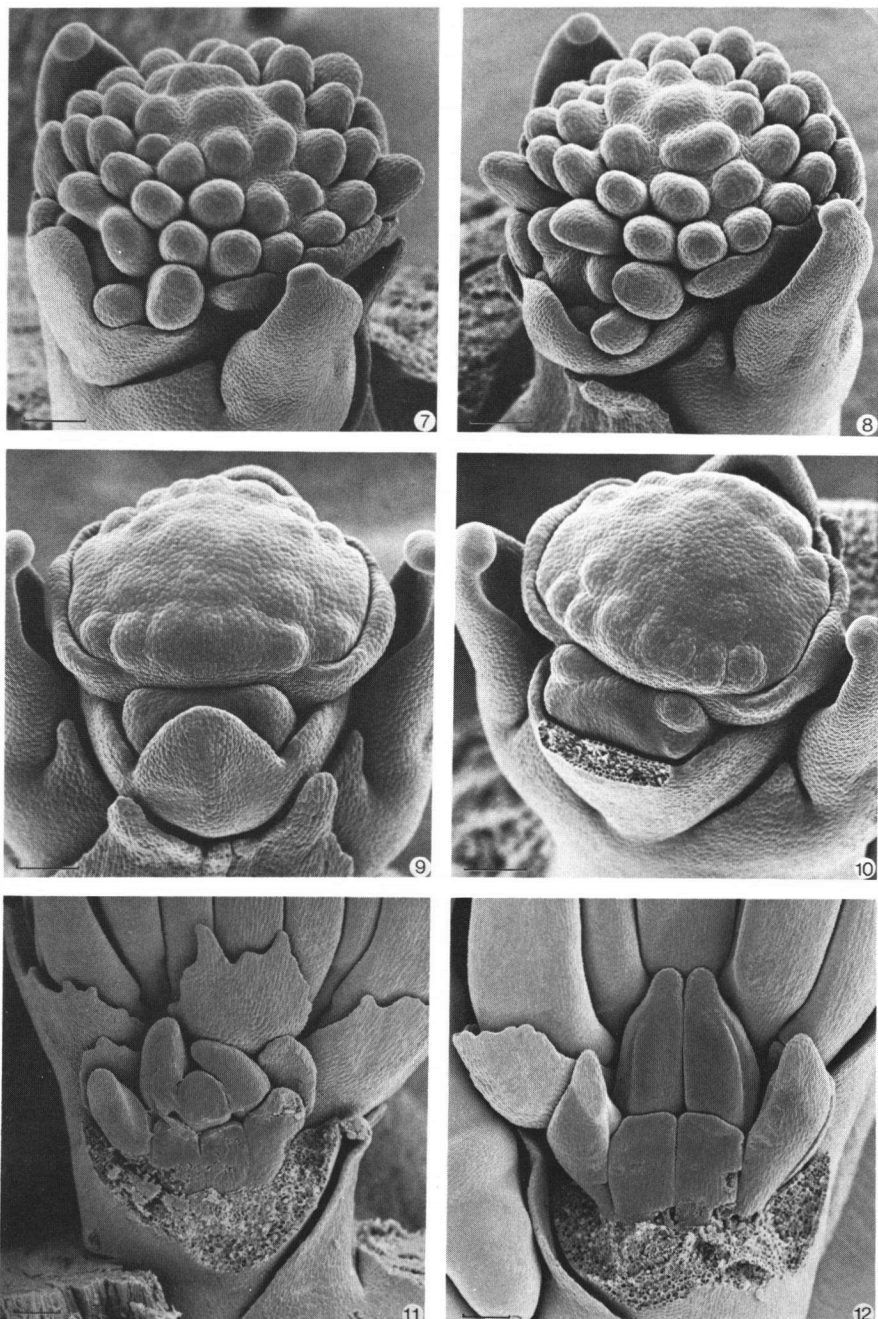


Plate 2. *Cercidiphyllum magnificum*. Bars represent 0.1 mm. – Photos 7–12: Male. Explanation in text.

DEVELOPMENT OF THE FEMALE INFLORESCENCES

First it is necessary to return to the morphology of the female inflorescences. Reviews of the arguments for the inflorescence theory as opposed to the flower theory can be found in Leroy (1980) and Van Heel (1986). Female units are arranged in one to three decussate pairs on a short shoot, and each is in principle supported by one bract. This arrangement was presented clearly in a diagram by Swamy and Bailey (1949). The units themselves consist each of a single carpel that has its suture facing the bract. Because of this position an additional hypothesis is necessary to uphold the theoretical construction. This hypothesis implies that a reduced lateral axis, or one that is lost in evolution, is located in the axil of each bract. This axis would carry one lateral carpel posteriorly, that is on the side of the primary axis of the inflorescence. In this manner the suture of the carpel would be oriented toward this reduced lateral axis as normally. Some uncertain fossil evidence was offered to sustain this hypothesis. There is also a report of a growing point on one female unit of one inflorescence which was found in the position as required by the hypothesis (Van Heel, 1986).

The present investigation supports the above hypothesis. Photo 1 presents a young stage of a normal female inflorescence consisting of a succession of one lateral pair of carpels, one median pair, and another lateral pair. The lateral pairs are situated somewhat forwards or backwards. The cut-off primordial foliage leaf of the next year is seen in front, provided with its two medianly fused stipules. Then two pairs of bracts follow, the lateral pair overlapping the median pair. Again it is noticed that the carpels originate with their sutures towards the outside as such; later twisting does not occur. This means that twisting cannot be adduced as an alternative hypothesis, which would lead to the mono-axial flower theory.

Photo 2 shows a smaller and younger stage consisting of two pairs of carpels, one lateral, lower and one median, upper pair. The bracts of the upper pair are reduced. This reduction of the bracts of the upper carpels occurs generally. In this case, moreover, the median bract and its carpel both seem to be inserted on an individual bulge, laterally on the apex of the inflorescence. The bract seems to be carried by a reduced axis proximally. Possibly this phenomenon could be compared with the concaulescent bracts as shown in a scheme of the fossil *Joffrea speirsii* by Crane and Stockey (1986: fig. 20).

Photos 3 and 4 show two inflorescences consisting of three pairs of bract-carpel units. In fact photo 4 shows the same inflorescence as shown in photo 1 but viewed from the other side. In both inflorescences the upper pair of units have reduced bracts, and in addition a stretch of the apex is evident between bract and carpel that has remained unoccupied. A similar stretch could be postulated in photo 2. Thus the female units in these cases consist of a bract, a carpel, and an unused part of the apex in between the two. I think that it is this region of the inflorescence that gave rise to the growing point between bract and carpel described in my paper of 1986, because there is homotopy. Therefore the hypothesis of the existence of reduced lateral bracteated axes each carrying one carpel on the side of the primary axis receives considerable support. Likewise the concept of the inflorescence as a decussate arrangement of several of these reduced, but fertile, axes is supported.

DEVELOPMENT OF THE MALE INFLORESCENCES

Photo 5 presents a diagonal view on a young male inflorescence as found in a lateral short shoot. Each short shoot bears three prophylls, one foliage leaf and the inflorescence. In both male and female trees, after the flowering period in spring, the development of next year's inflorescence proceeds quickly in June. Later, in August, an axillary bud develops in the axil of next year's leaf primordium, which will continue the short shoot sympodially in yet another year to come. In this way in August the primordia for two later years are already present, albeit in different stages.

By comparison of photos 1 and 5 the homology of the primary structure of female and male inflorescences is at once evident; two pairs of decussate bracts, one lower lateral and one median upper pair, occur in both. This was found by Swamy and Bailey (1949) and by Endress (1986). However, the subdivision of the glomerule of anthers into four (axillary) groups cannot be made at first sight.

The male inflorescence shown in photo 5 has many anthers; it was thought that the greater number of anthers would permit an easier subdivision. Commonly the number of anthers is less. I have received male material from the Botanic Gardens of Strassbourg, Zürich, and Tokyo. In all this material the number of anthers of one inflorescence is not high, and groups cannot easily be distinguished. At best there is a bulging of the periphery of the glomerule suggestive of groups. As Endress remarked, research should be extended to more specimens.

Also Swamy and Bailey suggested that there might be a relation between decussate pairs of bracts and opposite pairs of aggregations of stamens. However, their figures of cross sections (of mature stages) show that, viewed along the axis of the inflorescence, the stretches of stamens are overlapping and laterally contiguous where they overlap. (The same is true for my material as will be shown.)

Photo 6 shows an inflorescence comparable with the one of photo 5, but younger. (Next year's foliage leaf has been cut off, but its median stipule is still there.) It is evident that the main direction of development of the (groups in the) inflorescence is acropetal. The delimitation of groups of stamen primordia remains difficult. It is interesting to note that the median bracts are reduced, just as they are in the female counterpart shown in photo 2. In both cases a median group of primordial stamens belonging to the reduced bract could possibly be suggested.

If an homology between male and female inflorescences exists on the primary level, then inflorescences with a succession of three, instead of two, decussate pairs of bracts should occur in male trees as well. Such cases which I indeed discovered are shown in plate 2.

In all cases the bracts become more bract-like upwards, or are even reduced. The lower bracts look more like primordial stipuled foliage leaves, and they may be without stamens in their axil, like prophylls. In all these cases the lowest pair of bracts is placed laterally.

Photos 7 and 8 present two opposite diagonal views on the same inflorescence. The stipule of next year's foliage leaf can be seen at the base laterally (right in photo 7, left in photo 8). No stamens occur in the axils of the lower bracts. However, pri-

mordial stamens do occur in the axils of the median bracts, which can be distinguished as groups separate from the other stamens. The direction of development of the stamen primordia in such a group is away from the main axis towards the bract centre (centrifugal). The top stamens of a lateral group are single (photo 8), or paired (photo 7). The succeeding distal primordial stamens cannot be subdivided into groups; however, their main direction of development in this stage is acropetal, as clearly shown.

Photos 9 and 10 present an abaxial and adaxial view on an inflorescence, which is constructed like the one shown in photos 7 and 8, but is younger. Again the lowest pair of bracts is without axillary stamen primordia. However, separate primordial stamen groups are placed in the axil of the next higher pair of median bracts. Their development is centrifugal and seems to begin with two paired stamens. Groups cannot be delimited with certainty in the upper part of the inflorescence though its quadrangular shape suggests a prolongation of a decussate arrangement. Tangential series of primordia may be observed, similarly as noticed by Endress (1986). Anyhow the acropetal primary development is again evident.

Photos 11 and 12 show separate groups of primordial stamens in the axil of the lowest lateral bracts (cut-off) of two different inflorescences. The direction of development is clearly centrifugal. Moreover, the groups show two lateral leafy appendages on the side of the main axis, which in one case are connected by a basal ridge, looking like a set of prophylls. The groups as a whole lag behind in development. The distal stamens, based by two successive decussate pairs of bracts, cannot be subdivided into groups except on the argument that their median parts are inserted lower than their lateral parts, in correspondence with the position of the bracts.

CONCLUSION

The discovery of three pairs of decussate bracts each subtending a single carpel has produced the decisive argument for the concept of – female – bracteated inflorescences (Harms, 1916). The associated assumption of reduced axillary axes each carrying a single posterior carpel receives support by the fact that unused meristematic regions or a growing point sometimes occur in the axil of a bract. Moreover, a second anterior carpel is shown to be present on that lateral axis in the systematically related fossils *Joffrea*, *Nyssidium* and *Trochodendrocarpus* (Crane & Stockey, 1986). In such a case the sutures of the carpels may face one another. Thus an evolutionary reduction of the lateral axis to its single resulting carpel is indicated.

In the present paper it is shown that also in the male short shoots a succession of three pairs of decussate bracts may occur. Therefore the primary construction of the male and female inflorescences is homologous. Groups of stamens may be present in the axils of the lower or middle bracts, which are either entirely separate, or are contiguous as groups with the aggregate of distal stamens. The distal mass of stamens cannot be subdivided into individual groups so easily. However, from general – tetramerous – configuration as well as by the different level of insertion, a composite nature seems probable. Upwards in the acropetalous inflorescence – rather the reduced polyaxial system – the centrifugal stamen groups would seem to lose

gradually their separateness, and their bracts. This phenomenon could be of general interest in Dicotyledons for flowers with a centrifugally developing – complex – androecium, in connection with the theory that these flowers are, or once were, polyaxial systems.

If the homology between male and female structure is valid for the lateral axes also, then the female unit – reduced axis plus posterior carpel – should in some way be linked with a lateral group of centrifugal stamens (possibly including two posteriorly united prophylls). However, present evidence does not favour a possible theoretical explanation. A closer comparison is needed of the ontogeny and variation of the reproductive assemblages of the Trochodendrales.

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