

Non-floral interpretation of male reproductive structures in *Cercidiphyllum* (Cercidiphyllaceae): evidence from vascular anatomy

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Summary: Male reproductive units of *Cercidiphyllum* are usually interpreted as highly reduced compact inflorescences of sessile perianthless multistaminate flowers, although exact boundaries between the uppermost flowers are difficult to distinguish. We use evidence from vascular anatomy to discuss flower identity in the male reproductive units of *Cercidiphyllum*. We show that difficulties in recognizing individual flowers in *Cercidiphyllum* are not due to insufficient knowledge of its reproductive morphology and development. Rather, the theoretically expected boundaries between putative flowers are non-existent. The stamens are not just segregated into flowers, at least not in the central part of the male reproductive unit. This phenomenon can be explained either as a secondary loss of flower identity or as a pre-flower condition ‘frozen’ on the way towards conventional flower. Fossils reportedly related to *Cercidiphyllum* are discussed. Their bearing on the problem of flower identity in the male reproductive units of extant *Cercidiphyllum* is inconclusive.

Keywords: angiosperms, Cercidiphyllaceae, evolution, flower, fossil record, inflorescence, vascular anatomy

Cercidiphyllum is a genus of dioecious broad-leaved trees of a temperate climate distributed in China and Japan. The genus contains two species, *C. japonicum* Siebold & Zucc. and *C. magnificum* (Nakai) Nakai and belongs to the monogeneric family Cercidiphyllaceae.

The morphological nature of both, male and female reproductive structures of *Cercidiphyllum*, has long been under intensive discussion. Male reproductive units of *Cercidiphyllum* represent a cluster of stamens surrounded by several (usually four) paired bracts. In female reproductive units their axis bears several bract pairs and each bract subtends a carpel. While most attention is paid to the female reproductive units with their ‘inverted’ carpels whose ventral sutures face the subtending bracts, less information is available about the male reproductive units.

Reproductive units of *Cercidiphyllum* were originally interpreted as flowers. Later the inflorescence interpretation of the reproductive organs has been proposed based mainly on the peculiar morphology of the female reproductive units. SOLEREDER (1900) and HARMS (1916) describe male reproductive units as inflorescences having a short stalk followed by one or two bract pairs and numerous free stamens. However, both authors agree that individual flowers cannot be delimited.

In their comprehensive morphological and anatomical study, SWAMY & BAILEY (1949) support the inflorescence nature of male and female reproductive units of *Cercidiphyllum* and provide their detailed descriptions. Authors note that bracts in male reproductive units correspond to those in female ones and are usually situated in two decussate pairs. Each bract subtends ‘an individual aggregation’ of 8–13 stamens. The association of a bract with corresponding stamen aggregation is better evident in the lower part of the inflorescence. In vasculature all stele bundles

are centrifugally distributed after giving off bract traces. Each stamen is supplied by single bundle. No direct association between traces of a bract and associated stamens is found. SWAMY & BAILEY (1949) describe anthers being latrorse at anthesis. The authors do not discuss in details the nature of male reproductive unit but note that by homology with reduced female inflorescence “each of the smaller aggregates of stamens with its subtending bract is the remains of a single male flower”.

Following SOLEREDER (1900) and HARMS (1916), ENDRESS (1986, 1993) indicates that male flowers are difficult to delimit. According to ENDRESS (1986), the inflorescence of *C. japonicum* consists of 25–32 free stamens and possesses either four or two bracts. He points out that if the homology between male and female inflorescences is established one should expect male flowers in similar positions as carpels in female inflorescences, i.e., two or several flowers in decussate pairs. Endress describes stamens being latrorse and having a collateral (or nearly collateral) bundle each. Since all stamen traces have a xylem facing the inflorescence centre all stamens are considered to be turned toward the inflorescence axis by their ventral side. If this interpretation is correct male flowers should be lateral and monosymmetric with stamens developed only on the abaxial side of the flower. Lower flowers have more stamens than upper ones. Another interpretation proposed by ENDRESS (1986) implies the presence of a terminal flower. In this case lower flowers associated with lower lateral bracts are represented by a row of about 7 stamens each, upper flowers developed in the axils of median bracts contain one to three stamens, and other stamens form a terminal flower. ENDRESS (1986) suggested that the second interpretation is perhaps less convincing than the former.

VAN HEEL (1987) studied the development of male reproductive units in *C. magnificum*. He compared them with female reproductive units, which he treats as inflorescences of unicarpellate flowers. According to VAN HEEL, bracts of male and female inflorescences are developed in a similar way and in the same position (a lower lateral pair plus an upper median pair) and thus are obviously homologous. Stamens in some inflorescences examined by the author form four presumably axillary groups. These stamen groups are more easily recognizable in inflorescences which bear more anthers. In inflorescences with less numerous stamens groups ‘cannot easily be distinguished’. Four stamen groups remain visible even if the upper median bracts are reduced. VAN HEEL (1987) notes that the four stamen groups are better recognizable when an inflorescence is viewed from above or on cross-sections. When viewed from the side, delimitation of stamen groups becomes difficult.

Some inflorescences in the material studied by VAN HEEL have three pairs of bracts. In such inflorescences the bracts of the lowermost pair look as vestigial foliage leaves with stipules, and often these bracts lack any stamens in their axils. Stamens associated with median bracts form two distinct groups. Within the median stamen groups the development of new primordia is acropetal (toward the centre of a group) and delayed on the side of the bract, i.e., adaxial stamen primordia are greater in size. The same phenomenon is found when lowermost bracts bear stamens in their axils. In the upper part of such inflorescences stamen groups are not clearly visible.

On the basis of his developmental data VAN HEEL has concluded that the male reproductive unit is indeed a reduced polyaxial system – inflorescence – with variable node number and partial reduction of lateral branches represented by stamen groups. Toward the inflorescence top stamen groups gradually lose their individuality together with their subtending bracts. Noteworthy, VAN HEEL has not provided evidence to clarify what is the individual male flower in *Cercidiphyllum* and has not discussed this question.

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MEEUSE (1972) in order to support his anthocorm concept of polyaxial floral region against traditional anthostrobilar hypothesis treats reproductive units of *Cercidiphyllum* as primitive unisexual anthocormoids. According to MEEUSE (1972: 124) male reproductive units represent "... a perfect example of primitive androclad, the only advance in respect of the ancestral condition being a shortening of the axes of the polyandra and the axis of whole anthocorm to form a fertile brachyblast. The male anthocorm bears in the recent species a few androclad-bract units each consisting of a few monandra".

Since the evidences provided by different authors are controversial and floral boundaries are not clear we conducted a new study of male reproductive units in *Cercidiphyllum* to clarify their morphological nature. For our study, we selected *C. magnificum* as a species whose structure is less investigated than in *C. japonicum*.

Materials and methods

Plant material was collected at Royal Botanic Gardens, Kew and fixed in 70% ethanol. For scanning electron microscopy (SEM), material was dissected in 96% ethanol. The material was dehydrated through absolute acetone and critical-point dried using a Hitachi HCP-2 critical point dryer, then coated with gold and palladium using a Giko (Tokyo, Japan) IB-3 ion-coater, and observed using a JSM-6380LA SEM (JEOL, Tokyo, Japan) under 20kV at Moscow University. For light microscope observations the material was sectioned using standard methods of Paraplast or paraffin embedding and serial sectioning at 15–30µm thickness. Sections were stained in picroindigocarmine and carbolic fuchsine (AXENOV 1967) and mounted in BioMount or Euparal. Digital photomicrographs were taken using a Zeiss Axioplan photomicroscope.

Results

Male and female reproductive units of *Cercidiphyllum* develop on short shoots. The anthesis takes place in the spring. Each short shoot has three distichously arranged bud scales, a foliage leaf and a reproductive unit (Fig. 1). In the material studied stamens of male reproductive units start to expose before the foliage leaves. In reproductive units illustrated in Figure 1, the short shoot foliage leaf is either hidden by the second bud scale (Fig. 1 A, B), or only slightly exposed (Fig. 1 C, D). In Figure 1 C a droplet of secretion on the young foliage leaf is visible. The foliage leaf can be seen in dissected buds illustrated in Figure 2 A, B.

Male reproductive units of *Cercidiphyllum* have a short stalk and numerous stamens surrounded by the scale like bracts (Fig. 2). The bracts form (sub)opposite pairs. In our material of *C. magnificum* four bracts are usually developed in outer lateral and inner median pairs. Occasionally, three bract pairs are present. The stamens are basifixed, tetrasporangiate, rarely with five or three sacs (Fig. 3). A supraconnective is present. The stamens are clearly introrse in buds (Figs 5, 7). When examining the male reproductive units of *C. magnificum* carefully it becomes visible that stamens form several aggregations. Some stamens are associated with bracts (a group of stamens appear to be situated in the axil of a bract). Other stamens form a terminal cluster which is divided from stamen group-bract complexes by a short naked region of the main axis. Within the terminal aggregation a terminal stamen or terminal filament (a result of stamen reduction) is often found. In case illustrated in Figure 5 the terminal stamen has only two sporangia. In lateral aggregations stamens are usually inserted in a single row (Figs 4, 5). In a case shown in Figures 6 and 7 the

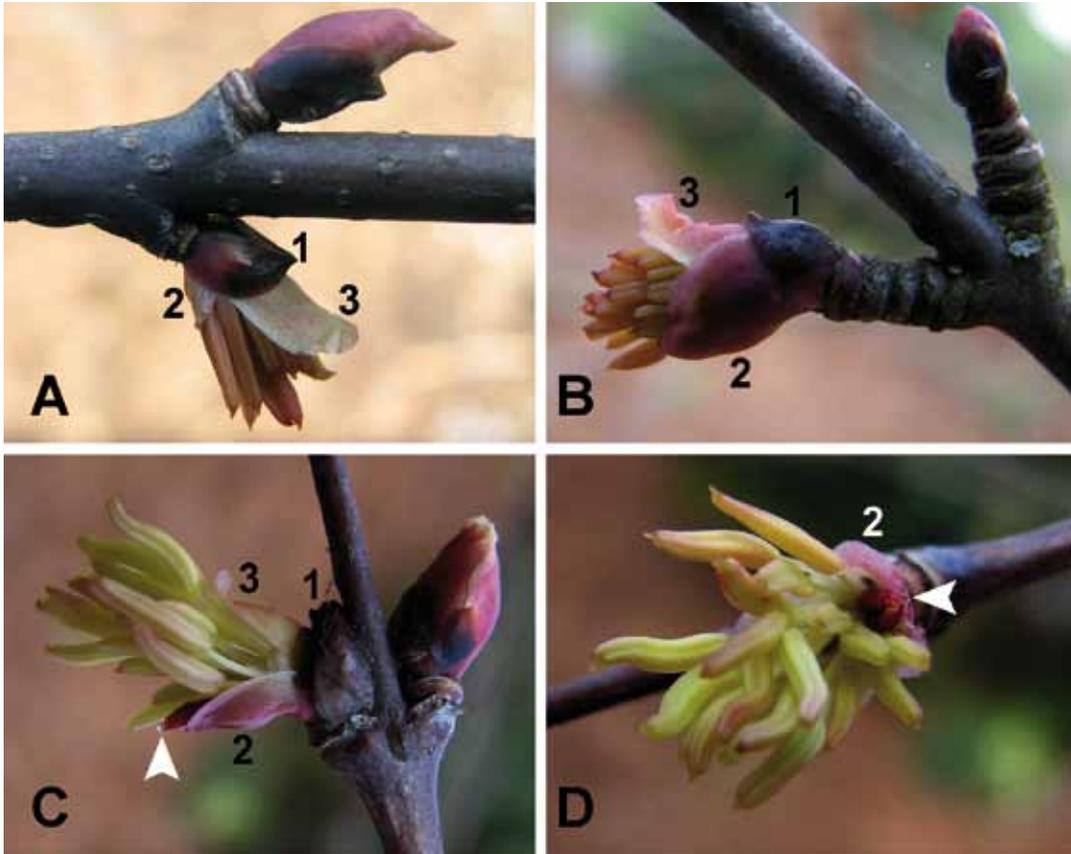


Figure 1. Male reproductive units of *Cercidiphyllum magnificum*. 1, 2, 3 = bud scales numbered consequently; arrowhead = foliage leaf. In A and B, the foliage leaf is yet hidden by bud scales. In C and D the foliage leaf is just slightly exposed; a droplet of secretion is visible on its tip.

stamens associated with each bract of the lower pair form a compressed, but complete whorl. Stamens of this whorl look each to other, thus some stamens appear inverted with respect to the centre of the reproductive unit.

Bracts are typically vascularized by three bundles (a median and two laterals) and the bract node is trilacunar. In upper bracts the vein number is often reduced up to two or even one vascular strand per bract. Stamen trace consists of a single bundle. Stamen and bract traces enter the reproductive unit axis and gradually form a ring of vascular strands (Figs 4–7). Making anastomoses the bundles of the ring enter the reproductive unit stalk and continue further down toward the stalk base. The trace of a terminal stamen enters the axis centre where it divides into several strands. Some strands migrate toward the periphery and fuse with other stamen traces. A small trace left in the centre continues further down and terminates in the reproductive unit stalk.

Figure 2. Male reproductive units of *Cercidiphyllum magnificum* just before anthesis (SEM). Arrowheads = lower bracts situated in transversal position. A, B – reproductive units seen from the side of the foliage leaf, which is visible in the centre of each figure. Foliage leaves bear conspicuous glands at the top. C – a reproductive unit seen from the side opposite the foliage leaf. Only one of the two inner whorl median bracts is visible (in the centre). D – a reproductive unit dissected longitudinally along the median symmetry plane. A filamentous structure can be seen in the centre of the reproductive unit. Scale bars = 1 mm. >>>

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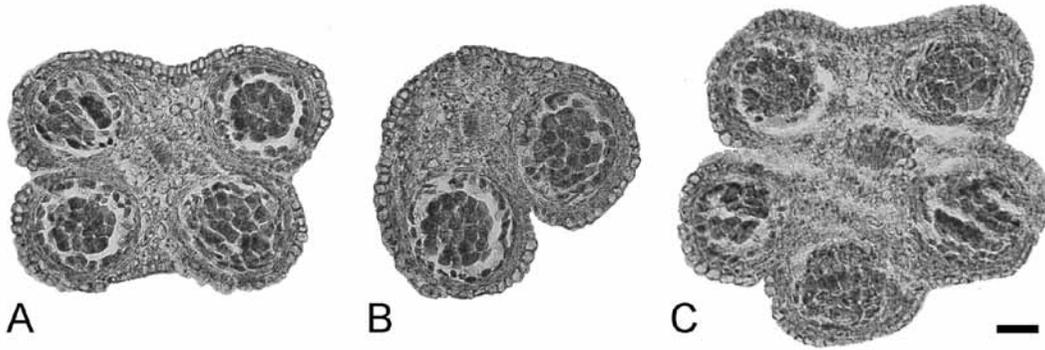


Figure 3. Anthers of *Cercidiphyllum magnificum* in transverse sections (LM). A – tetrasporangiate anther typical to *Cercidiphyllum*. B – bisporangiate anther. C – pentasporangiate anther. Scale bar = 50 μ m.

Discussion

Our anatomical data are complementary and congruent with those of VAN HEEL (1987), who studied early developmental stages of male reproductive structures in *Cercidiphyllum magnificum*, but did not examine vascular anatomy of mature reproductive units. Like in this study, VAN HEEL found groups of stamens clearly associated with lower bracts and admitted some difficulties in recognizing boundaries between the two stamen groups that hypothetically should occur in the axils of the two upper bracts. VAN HEEL (1987) did not pay attention to the occasional presence of a terminal stamen. However, it is illustrated in his figures 7 and 8.

Detailed data on development and vascular anatomy of male reproductive structures in another species, *Cercidiphyllum japonicum*, are presented by ENDRESS (1986); they are congruent with anatomical data of SWAMY & BAILEY (1949). The following differences with *C. magnificum* can be noticed: (1) ENDRESS (1986) highlighted that all stamens of *C. japonicum* have the thecae in a lateral position relative to the inflorescence axis. This is different from our data on *C. magnificum* where stamens are usually introrse, at least when studied before anthesis. (2) In *C. magnificum* stamens associated with each lower bract form either a complete whorl or a single row of stamens. Within each group of stamens the anthers tend to be introrse relative to the centre of such a group. In *C. japonicum* stamens associated with lower bracts reportedly always form single rows (ENDRESS 1986). (3) Stamen initiation is continuously centripetal in *C. japonicum* (ENDRESS 1986). In the male reproductive unit of *C. magnificum* clear centripetal pattern was found only within the distal group of stamens, whereas stamens associated with lower bracts initiate in a centrifugal pattern relative to the centre of the male reproductive unit (VAN HEEL 1987). (4) Terminal stamens with central vascular traces are not reported from *C. japonicum*. Because only a limited number of accessions of both species was studied by various researchers, it is possible that the differences found characterize accessions rather than species.

Most authors consider reproductive units of *Cercidiphyllum* to be highly compact inflorescences (pseudanthia). Strong similarity in patterns of arrangement of all phyllomes, including bracts, in reproductive short shoots of male and female individuals suggests that male and female inflorescences likely have the same architecture (SWAMY & BAILEY 1949; ENDRESS 1986; VAN HEEL 1987). Female reproductive units of *Cercidiphyllum* are interpreted as head-like open inflorescences with each bract subtending a lateral flower, though the uppermost bracts are

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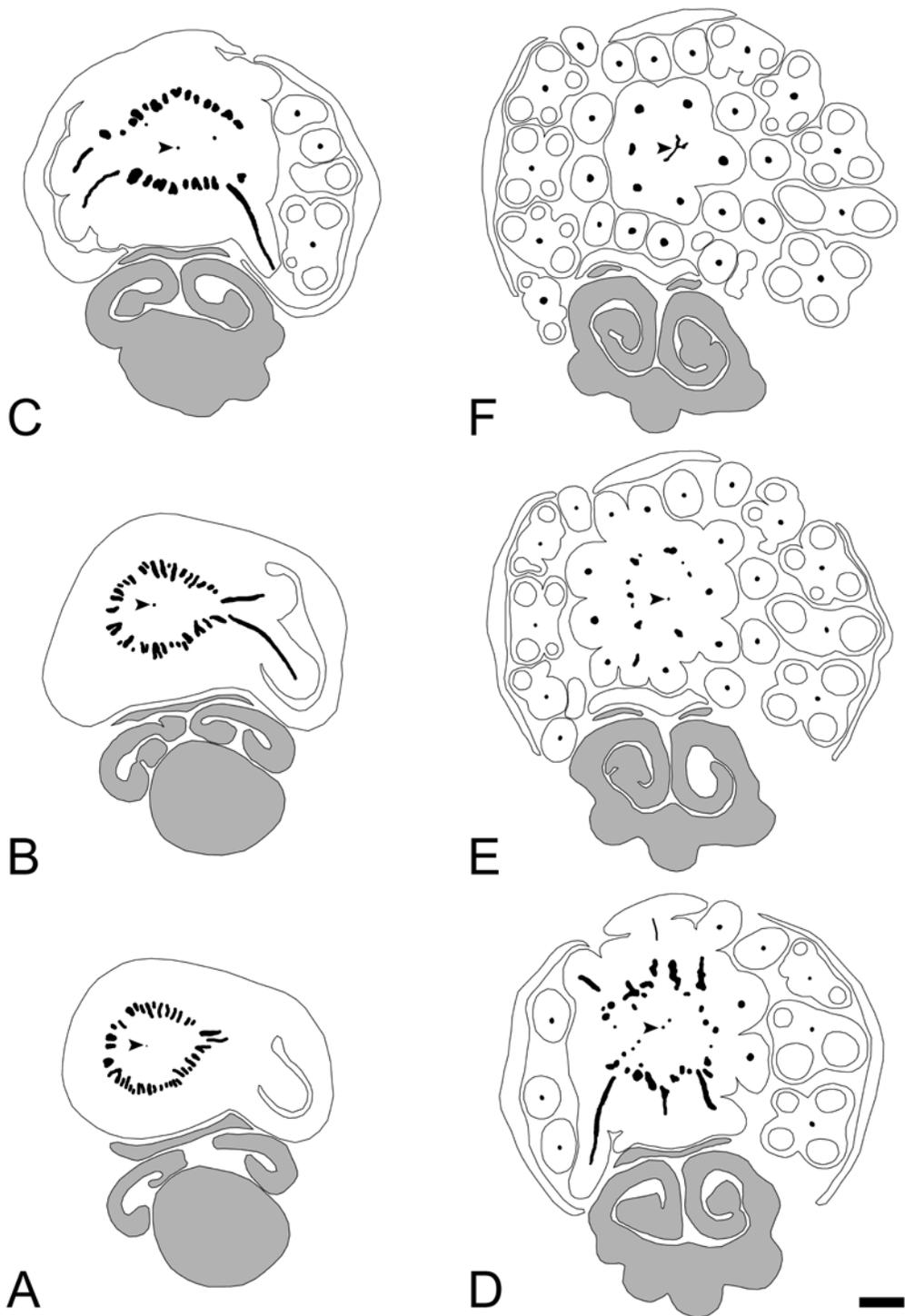


Figure 4. Serial cross-sections of a male reproductive unit of *Cercidiphyllum magnificum*. Bud scales removed. Vascular bundles (xylem) are given in black, foliage leaf and its stipule are grey. Vascular bundles of the foliage leaf and bracts are not shown. Arrowhead = vascular trace of the central stamen. Scale bar = 100 μ m.

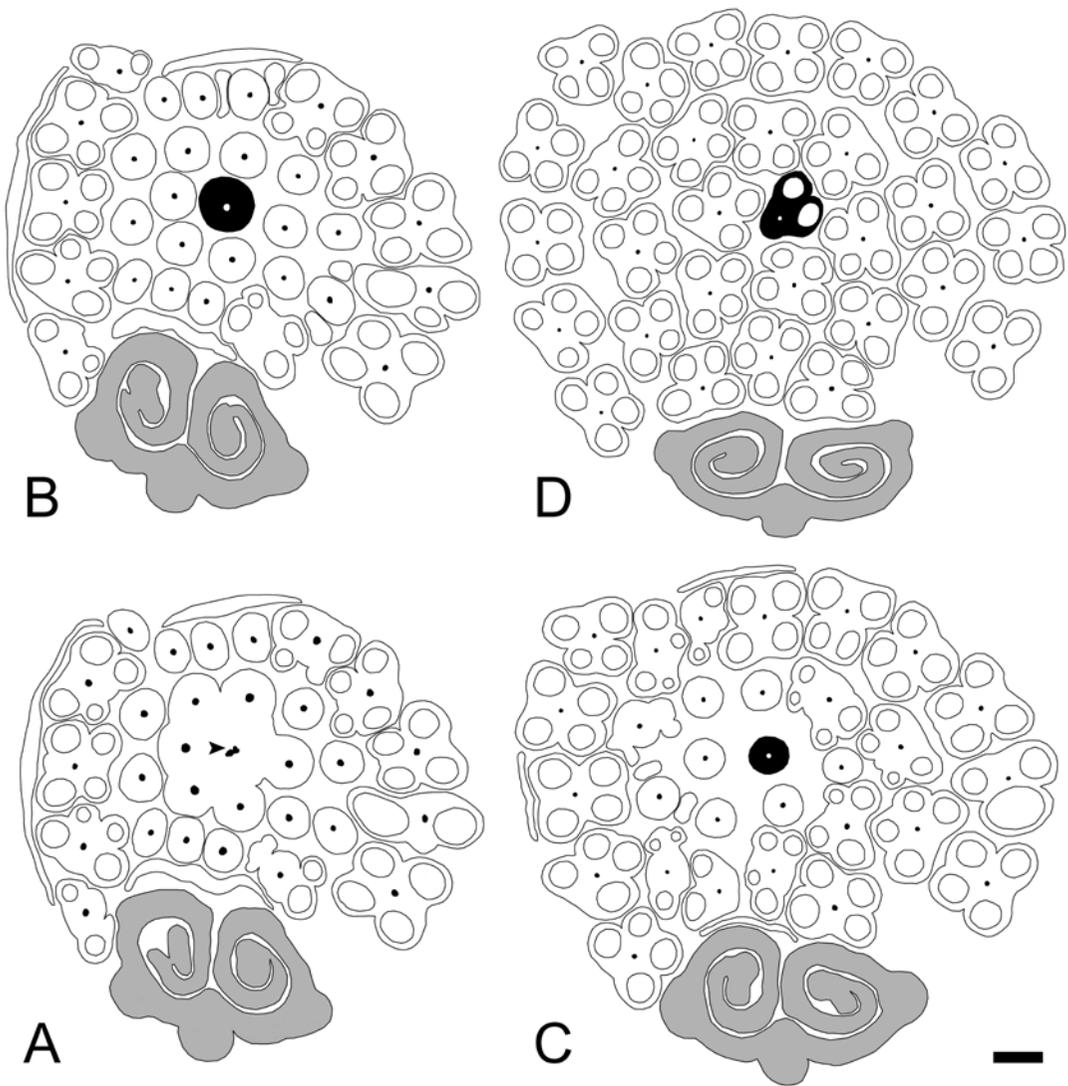


Figure 5. Continuation of a series given in Figure 4. Note that almost all stamens are slightly introrse and looking to the centre of the entire reproductive unit. Vascular bundles (xylem) are given in black, foliage leaf is grey. Central stamen is given in inverted colour (parenchyma black, vascular bundle white). Arrowhead in A = vascular trace of the central stamen. Scale bar = 100 μm .

sometimes reduced. The same concept is usually applied to male reproductive units, but difficulties in delimiting flowers have been admitted. These difficulties are most prominent at the top of male reproductive units. According to ENDRESS (1986), a possibility that the distal group of stamens represents a terminal flower cannot be ruled out.

ENDRESS (1986, 1993) suggested that lateral male flowers of *Cercidiphyllum* are highly monosymmetric with stamens seemingly present only on the abaxial side. Indeed, in *C. japonicum* stamens appear to form a single row in the axil of each outer bract (ENDRESS 1986). This row can be then interpreted as an incomplete whorl with stamens developed on its abaxial side only. Our data on *C. magnificum* allow hypothesizing that flowers in axils of lower bracts at least sometimes possess a complete whorl of stamens with both, adaxial and abaxial stamens differentiated.

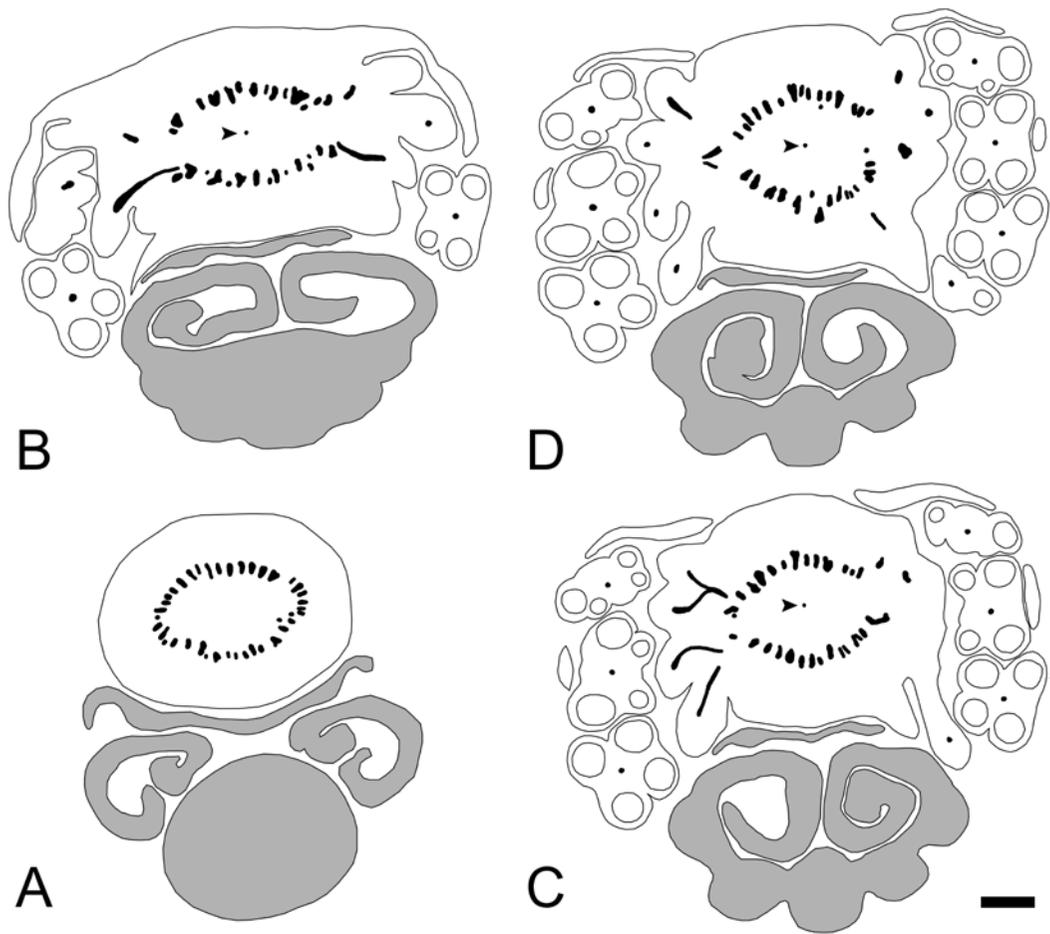
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Figure 6. Serial cross-sections of a male reproductive unit of *Cercidiphyllum magnificum*. Bud scales removed. Vascular bundles (xylem) are given in black, foliage leaf and its stipule are grey. Vascular bundles of the foliage leaf and bracts are not shown. Arrowheads in B–D = vascular trace of the central stamen. Scale bar = 200 μ m.

Developmental data of VAN HEEL (1987) suggest that adaxial stamens appear earlier than abaxial in *C. magnificum*.

Our data confirm earlier observations that stamens in the distal part of the male reproductive unit cannot be easily assigned to two lateral flowers. Some stamens with equal probability can belong to either one or another flower. Occurrence of a central stamen in reproductive units of *C. magnificum* is of special interest. Its vascular supply shows that the central stamen occupies a purely terminal position on the axis of a reproductive unit. Therefore, it definitely cannot be assigned to either of the two uppermost lateral flowers whose presence is hypothesized by most authors. Therefore, the difficulties in delimitation of these flowers are not because of our insufficient knowledge. The boundary is just absent. Since a clear boundary is absent, one may argue the distal group of stamens forms a terminal flower, according to the second hypothesis of ENDRESS (1986). However, in that case we should accept presence of a terminal stamen in a multistaminate flower. It is commonly considered that all stamens of multistaminate androecia must be lateral. In euanthial interpretation of angiosperm flower stamens are considered to be microsporophyll homologues. Since sporophylls are lateral organs, stamens also must be lateral.

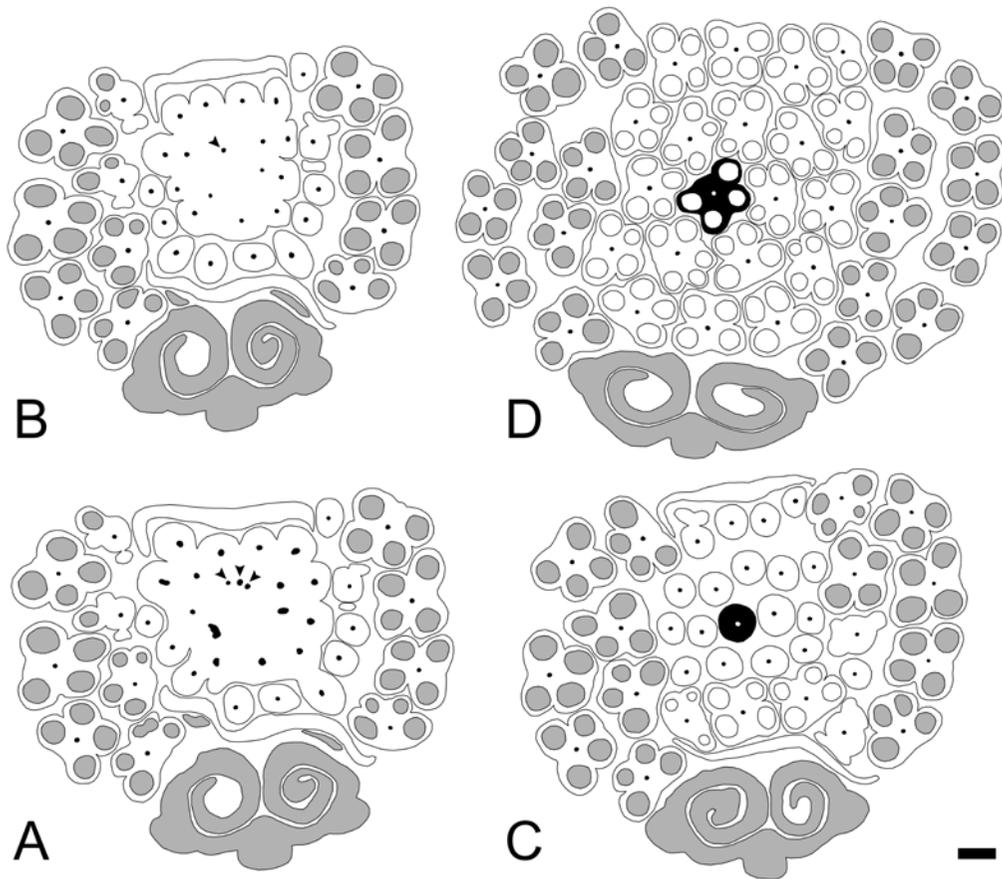


Figure 7. Continuation of a series given in Figure 6. Vascular bundles (xylem) are given in black, foliage leaf is grey. Central stamen is given in inverted colour (parenchyma black, vascular bundle white). Microsporangia of stamens associated with outer whorl bracts are coloured grey. Arrowheads in A and B = vascular traces of the central stamen. Scale bar = 200 μm .

If a stamen is observed in the centre of a multistaminate androecium, it is interpreted as a lateral stamen shifted in a pseudoterminal position, e.g., in *Theligonum*, Rubiaceae (RUTISHAUSER et al. 1988)¹. Our anatomical data on *Cercidiphyllum magnificum* show that the central stamens examined are purely terminal and not shifted. Therefore, it appears to be unnatural to describe the whole distal group of stamens as a multistaminate terminal flower.

Occurrence of a terminal stamen might indicate that flowers of *Cercidiphyllum* are actually unistaminate. Each stamen then represents a male flower of its own, like each carpel represents a female flower of its own. To our knowledge, this option was not previously discussed for *Cercidiphyllum*. It is very difficult to either prove or disprove such a hypothesis. We think the concept of unistaminate flowers can be applied when a reduction series from more typical flower to unistaminate condition is available or when certain rudiments of other floral organs are visible

1) Situation can be more problematic in male flowers with a solitary central stamen, like in *Najas* (POSLUSZNY & SÄTTLER 1976) or Zannichelliaceae (POSLUSZNY & TOMLINSON 1977). Any structural evidence of its pseudoterminal position can be lost due to strong reduction of the whole flower. Also, such a stamen might be a fusion product of several lateral stamens.

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apart from the single stamen. Since this is not the case for *Cercidiphyllum*, we do not follow the concept of unistaminate flower. In our opinion it is easier to describe the situation as is: at least distal stamens in reproductive units of *Cercidiphyllum* are not organized in flowers.

RUDALL et al. (2009) made a similar speculation regarding reproductive units in Hydatellaceae. They suggested that nonfloral organization of reproductive structures in Hydatellaceae can be evolutionary interpreted in two different ways. The reproductive units of Hydatellaceae could be preflowers, i.e., a step toward true flowers. Alternatively, the morphological organization of extant Hydatellaceae might be a result of a secondary loss of flower identity. The same two possibilities can be discussed for *Cercidiphyllum*.

The idea that *Cercidiphyllum* has prefloral organization of reproductive organs has been discussed, for example, by MEEUSE (1972). This view probably requires an assumption that *bona fide* flowers evolved many times in course of angiosperm evolution. Multiple origins of angiosperm flower have been suggested by many authors, including MELVILLE (1963), CROIZAT (1964), MEEUSE (1972), KRASSILOV (1977). One of us (V. K.) supports the interpretation of reproductive structures in *Cercidiphyllum* as flowers in formation. Two of us (M. R. and D. S.) consider that it is plausible that *Cercidiphyllum* has undergone a secondary loss of flower identity, at least in the distal part of male reproductive units. Loss or partial loss of flower identity is observed in terminal structures that can be occasionally found in racemose inflorescences (reviewed in SOKOLOFF et al. 2006). Terminal flower-like structures (peloria) could be interpreted as pseudanthia or united uppermost lateral flowers. However, this is that type of pseudanthia where (partial) loss of flower identity occurs and boundaries between individual flowers cannot be recognized (SOKOLOFF et al. 2006). In course of evolution, elaborated terminal structures could give rise what we might call typical flowers. Therefore, the fact that male reproductive structures of *Cercidiphyllum* resemble flowers *in statu nascendi* does not contradict the view that floral identity was once lost in this evolutionary lineage. Molecular phylogenetic placement of Cercidiphyllaceae in Saxifragales, i.e., far above the root of angiosperms (e.g., APG II 2003), supports the idea on secondary loss of flower identity in male reproductive units of *Cercidiphyllum*.

Fossil record is crucial in understanding evolutionary origin of reproductive structures of extant *Cercidiphyllum*, especially because of the large morphological gap between *Cercidiphyllum* and other extant angiosperms.

All fossils reportedly related to extant *Cercidiphyllum* possess unisexual reproductive units. Male and female structures were never found in organic connection. The plants were seemingly dioecious. Female reproductive structures and leaves of extinct *Cercidiphyllum*-like plants are better known than male reproductive units. Male structures are not traced for several important fossils, e.g., for *Eocercidianthus* (KRASSILOV et al. 2005). So far, male reproductive structures are described for two groups of fossils.

The first group comprises *Trochodendroides* leaves and female reproductive structures known as *Nyssidium*, *Trochodendrocarpus* and *Joffrea* from Late Cretaceous and Paleogene deposits of the Northern Hemisphere. Male structures that seemingly belong to these plants are reviewed by GOLOVNEVA (2006) who formally described them as a morphogenus *Alasia*. They represent axes with helically arranged 10–20 coriaceous bracts and numerous stamens in their axils (GOLOVNEVA 2006). In many specimens the stamens are hidden by bracts and the whole structure resembles a

conifer shoot, so that some species of *Alasia* were initially described within the genus *Araucarites*. Most authors support the idea that *Trochodendroides-Nyssidium/Trochodendrocarpus/Joffrea-Alasia* plants are evolutionary related to the extant *Cercidiphyllum* (CRANE & STOCKEY 1985; GOLOVNEVA 2006 and references cited therein). KRASSILOV & KODRUL (2008) agreed that *Alasia* inflorescences can be linked with *Trochodendroides* leaves, but did not support the idea on close affinity to extant *Cercidiphyllum*. KRASSILOV & KODRUL (2008) highlighted several differences between *Alasia* and extant *Cercidiphyllum*. In particular, *in situ* pollen grains of *Alasia* are tricolpate with very long colpi, whereas *Cercidiphyllum* has very short apertures and its pollen grains can be characterized as triporate (KRASSILOV & KODRUL 2008). KRASSILOV & FOTYANOVA (1995) and KRASSILOV (1997) emphasized differences between female reproductive units of these fossils and of the extant *Cercidiphyllum*. They think *Joffrea*, *Nyssidium* and *Trochodendrocarpus* are much closer to Hamamelidaceae than to Cercidiphyllaceae. KRASSILOV & KODRUL (2008) also suggested hamamelid affinity of *Alasia*. Even if *Alasia* is indeed closely related to *Cercidiphyllum*, evidence from this fossil is equivocal. Those who support the pre-floral interpretation of *Cercidiphyllum* would consider *Alasia* 'inflorescences' as structures comparable to MEEUSE's (1972) anthocorms. Those who support the opposite view would consider that each stamen group in the bract axil of *Alasia* represents a reduced angiosperm flower, implying that flower reduction took place earlier in this evolutionary lineage.

The second group of fossils include those that possess leaves, fruits and – where known – shoot systems closely approaching extant *Cercidiphyllum*. Among fossils of this group associating male structures are described for *Cercidiphyllum crenatum* from Miocene of Bohemia (KVAČEK & KONZALOVÁ 1996; KVAČEK 2008). The staminate structures are interpreted as consisting of about four long pedicellate male flowers, each flower with about five perianth members. The flowers developed on short shoots with numerous cataphylls, some of which are interpreted as flower-subtending bracts. If this interpretation is correct and if the fossil is related to extant *Cercidiphyllum*, this supports secondary loss of flower identity in male reproductive units of *Cercidiphyllum*. There is, however, a large morphological gap between the fossil male structures and those of extant *Cercidiphyllum*. A foliage leaf typical for reproductive short shoots of extant *Cercidiphyllum* is not recognizable on figures in KVAČEK (2008) and KVAČEK & KONZALOVÁ (1996). Our Figure 1 shows that it is also not visible at early anthesis in *C. magnificum*. However, illustrations of fossils show later stages of anthesis than our Figure 1. Therefore, the absence of a foliage leaf is problematic for interpretation of the fossil as a close relative of extant *Cercidiphyllum*. Besides, anthers of the fossil lack connective appendages typical to extant *Cercidiphyllum* and anther dehiscence is not the same. Finally, *in situ* pollen of the fossil illustrated in KVAČEK & KONZALOVÁ (1996) differs from the pollen of extant *Cercidiphyllum* (KRASSILOV & KODRUL 2008; M. Tekleva, pers. comm.; our unpubl. data).

Acknowledgements

We are indebted to Gerhard Prenner and Irina Belyaeva for help with collecting plant material of *Cercidiphyllum* and to Natalia Maslova and Maria Tekleva for helpful discussion. Valentin Krassilov was supported in this work by the German – Israeli Foundation of Scientific Research and Development, Grant No. 1-888-159.8/2005. Margarita Remizowa and Dmitry Sokoloff were supported by Russian Foundation for Basic Research (project # 09-04-01155) and President of Russia grant No. MD-2644.2009.4.

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