

Cercidiphyllum and Fossil Allies: Morphological Interpretation and General Problems of Plant Evolution and Development

Valentin Krassilov



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Abstract

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Cercidiphyllum is a relict angiosperm bringing to us flavor of Cretaceous Period. Its reproductive morphology was interpreted, in the spirit of the dominant evolutionary paradigm, as pseudanthial inflorescences of reduced flowers represented by solitary pistils and groups of stamens. Phylogenetic significance of *Cercidiphyllum* has been long anticipated despite inconclusiveness of morphological interpretation and irrelevance of paleobotanical evidence.

This work was initially intended for paleobotanists who willingly compare their fossil material with the living *Cercidiphyllum*, using the overgeneralized descriptions and schematic illustrations of traditional plant morphology. My purpose was to provide an adequately illustrated material for such comparisons. Yet it turned out that there are more things in *Cercidiphyllum* and allies than are dreamed of in our traditional plant morphology.

It is found that the long shoot – short shoot system ramifies by new leafy shoots replacing the short-shoot reproductive structures. Such shoots produce elliptical foliage leaves. Otherwise the heteroblastic branching system is foliated by the short-shoot reniform leaves arising as prophylls by unequal dichotomy of the short-shoot axis, enfolded, together with the floral stalk, in the distal cataphyll. The renovation bud is sunken in a pit at the base of the short-shoot leaf. The scaly subtending bracts of floral receptacle can be replaced by miniature stipulate leaves. Multicellular marginal glands, consisting of columnar palisade cells on a basement of small-celled epithecum, are a prominent feature of all vernate leaves, including the leaf-like bracts. Mature leaves develop a system of hydathodes supplied by blind veinlets.

The androecia develop in two stages, the peripheral stamens separated before differentiation of the central (apical) group. The androecial bracts are not associated with particular groups of stamens except in the case of teratological developments. Staminate structures are more distinctly zygomorphic in *C. japonicum* than in *C. magnificum*, differing also in the number of stamens and subtending bracts (two and four, respectively), as well as in the size of the leaf stipules. Supernumerary bracts and hair-like processes may

develop in association with defective stamens. Pollen grains are triporate, with microverrucate – scabrate ornamentation and granulate pore membrane.

In the pistillate structures, the most common situation is three fully developed perophylls connate at base. The distal carpels are subtended by linear or hair-like bracts. A tendency of distal bract reduction is not extended to the carpels. There are occasional empty bracts. The carpels are peltate, with supervoluted margins. Placenta is formed by the fusion meristem of the carpel margins and is pectinate with meristematic lobes differentiated into free nucellus and two concentric collar-like integuments. It is intrusive into the narrow locule lined with a delicate endoderm. The ovules are distichous, orthotropous, acquiring hemitropous polarity later in development. The ripe seeds are samaras with a bilobed orbicular wing. The raphe strand forks in the chalazal lobe of the wing.

Morphological comparisons comply with Takhtajan (1969, 2009), Smith (1971), and Rao (1986) in placing this genus, together with the closely allied fossil forms, in a separate order *Cercidiphyllales*. supposedly one of several small satellite orders of ranunculid plexus.

Some of the morphological findings in *Cercidiphyllum* bear on general problems of angiosperm morphology and phylogeny. The naturally occurring conversions of floral structures to leafy shoots correspond to the experimentally obtained organ conversions in *Arabidopsis* and other model plants of the “evo – devo” research. When epigenetically transmitted, the mutant expressions of regulatory genes with the organ conversion/convergence morphological effects might have played a crucial role in plant evolution. In *Cercidiphyllum*, the floral structures, controversially interpreted as either incipient flowers or reduced inflorescences, seem to have been developmentally affected by the growth form morphogenesis, showing frequent floral bract to leaf conversion, rare carpel to leaf conversion and a supposed carpel to leaf convergence.

It is suggested that morphological peculiarities of *Cercidiphyllum* are evidence of a cyclic evolutionary development. Its reproductive structures are converted into leafy shoots, and the short-shoot leaves (floral prophylls) foliate most of the branching system. This means that the vegetative body is partly or mostly produced in the reproductive line, suggesting a neotenic ancestral form, in which the vegetative development was drastically reduced relative to reproductive domain. Later in evolutionary history, the vegetative body was rebuilt in the lineage on the way to arboreal forms, with foliation of the floral receptacles and the carpel – leaf convergence as side effects of the process. Therefore, the lineage represents a phylembryogenic cycle starting with neotenic transformation (acceleration of vegetative development) and proceeding in the prolongation (anaboly) mode.

At the neotenic stage, a shortening of internodes and verticillation of lateral organs, with subsequent functional differentiation of successive whorls, might have led to parallel development of ABC type regulation system in the cycadeoid bennettites, anthognetophytes and early angiosperms. In all these groups, phyllomes were either interspersed with floral organs or even proliferated in the central zone of receptacle, suggesting a less expressed apical dominance of the floral meristem identity genes than in modern

flowering plants. In a few conservative forms, like *Cercidiphyllum*, the ancestral conditions were fixed at the essentially pre-flower level of floral development.

A more flexible regulation in neotenic forms, with a dosage sensitive determination of meristem identities, as in the case of *LEAFY*, might have promoted developmental integration of foliar and floral structures, involving leaves in accessory reproductive functions, a precondition of new organs, flowers and carpels, rapidly appearing at this stage already. In the next round of morphological evolution, a size increase and rebuild of vegetative complexity have promoted the fertile structures – leafy shoot conversions, introducing a vegetative bias to the floral meristems and conferring leafy characters on reproductive organs.

A developmental machinery with ambivalent regulatory gene expressions in the foliar and floral primordia might have invoked two opposite evolutionary tendencies: (1) centripetal reduction and elimination of sterile organs from the apical zone and (2) secondary foliation of floral structures. The ambiguous floral morphology of *Cercidiphyllum* is here interpreted as a longstanding balance of these conflicting tendencies.

In regard of this model, the fossil record of *Cercidiphyllum*-like plants appears meaningful, although still incomplete. The weedy Early Cretaceous ranunculids, including forms with a few basal leaves, like in the Albian *Ternaricarpites* (Krassilov & Volynetz, 2008), represent the neotenic stage, also recognizable in evolution of their contemporaneous anthogonetophytes. Transitional floral morphologies link such forms to the later appearing cercidiphyllids, platanoids and trochodendrocarpoids, the vegetative features of which were formed at the next, size increasing stage, represented by the *Eocercidiphyllites* plant from the mid-Cretaceous of Negev, and were conserved in the later evolutionary developments

KEY WORDS: *Cercidiphyllum*, relict species, plant morphology, plant development, flower morphogenesis, early angiosperms, angiosperm evolution.

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1. INTRODUCTION

Cercidiphyllum Siebold et Zuccarini, 1846 is a charismatic genus of beautiful broadleaved trees growing in mountainous regions of central – eastern China and central Japan, locally descending to near sea-level on Hokkaido. The principal species, *C. japonicum* Siebold et Zuccarini is a tall canopy tree. A not unanimously recognized additional species, *C. magnificum* Nakai is found at higher elevations and differs in a lower stature, divaricate branches and larger leaves (a few differences in reproductive morphology are discussed later in the paper). Both species are widely cultivated over the temperate mid-latitudes.

The leafy shoot system of these trees is commonly characterized as heteroblastic, with the long and short shoots producing dimorphic – elliptical and reniform – leaves, respectively. The leaf stipules are prominent in development and were thought to be shed, but, on my observation, may persist at maturity. The trees are dioecious and wind pollinated, with floral organs developing on the short shoots in association with a solitary leaf (floral axis prophyll as here interpreted). The pistillate structures consist of two or occasionally more decussate pairs of free carpels, each subtended by a slender bract that is ambiguously interpreted (Endress, 1993; Yan et al., 2007). The staminate structures have numerous stamens, but only few bracts. The pollen grains have been described as tricolporate (Praglowski, 1974; Endress, 1993 and elsewhere), but here interpreted as triporate.

Cercidiphyllum is assigned to a presently monotypic family Cercidiphyllaceae Engler, 1907 that may include some fossil precursors discussed later in the paper. Its ordinal assignments are highly controversial varying from recognition of a monotypic order Cercidiphyllales to a membership in the Hamamelidales, Ranunculales (“Ranales”), Trochodendrales or Saxifragales, the opinions depending on morphological interpretation (Solereder, 1899; Harms, 1916; Swamy & Bailey, 1949; Hutchinson, 1973; Takhtajan, 1969, 1987, 2009; Thorne, 1976; Dahlgren, 1980; Cronquist, 1981; Endress, 1986) and, recently, on evidence of molecular phylogeny (Soltis et al., 2000, 2003; APG II, 2003; Judd & Olmstead, 2004; Sanderson, 2003; Anderson et al., 2005; Hermsen et al., 2006).

A discovery of *Cercidiphyllum*-like fossil angiosperms in the late mid-Cretaceous (Turonian) of Israel (Krassilov et al., 2005) and the long lasting controversy over the supposed fossil representatives of the Cercidiphyllaceae (Krassilov, 1976; Crane, 1984, 1989; Crane & Stockey, 1985; Krassilov & Fotyanova, 1995; Krassilov et al., 2005)

impelled a morphological revision of not only paleobotanical material, but also of extant *Cercidiphyllum*.

An additional incentive for this study came from molecular phylogeny, which assigned *Cercidiphyllum* a position in the system of flowering plants quite different from where we became accustomed to find it during the last century. The long-avowed place for this genus has been at or near the base of angiosperm phylogeny, whilst molecular evidence displaced it much higher in terms of phylogenetic advancement (APG II, 2003). Though allegedly new, the molecular phylogeny is suspiciously reminiscent of an arrangement that was fairly popular through the XIX century and was then abandoned in favor of modern morphological interpretations.

Phylogenetic pre-eminence of *Cercidiphyllum* has been long accepted despite the inconclusiveness of morphological interpretation and irrelevance of paleobotanical evidence. In the course of this study we found that credulity of nearly all commonly held opinions of *Cercidiphyllum* was overstated. Some of our findings seem to bear on general problems of angiosperm morphology and phylogeny. Here I am not attempting a comprehensive analysis of current situation in plant phylogeny, but touch upon general issues that seem pertinent to my interpretation of *Cercidiphyllum*.

Initially this work was addressed to paleobotanists who willingly compare their fossil material to the living *Cercidiphyllum*, using the overgeneralized descriptions and schematic illustrations of classical plant morphology. My purpose was to provide an adequately illustrated material for such comparisons. Yet it turned out in the course of this work that there are more things in *Cercidiphyllum* and allies than are dreamed of in our traditional plant morphology.

2. ACKNOWLEDGEMENTS

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3. HISTORICAL OVERVIEW

At anthesis, both pistillate and staminate structures look like somewhat unconventional flowers and this is how they were originally described (Siebold & Zuccarini, 1846). Their interpretation as pseudanthia was prompted by orientation of the carpels having their opening sutures turned outside and facing the subtending bracts. To Solereder (1899), such an unusual orientation was evidence of the carpels being originally born in pairs on a ramified axis with bicarpellate branches, their opening sutures facing each other. After reduction of the anterior carpel, the remaining posterior one was left with its suture to the outside (Fig. 1). Solereder advocated taxonomic affinities of *Cercidiphyllum* with the Hamamelidaceae.

Harms (1916) has abandoned his earlier opinion of solitary flower in *Cercidiphyllum* in favor of a modified Solereder's pseudanthial interpretation after finding 5 – 6-carpellate structures, with additional carpels situated above (inside) the two conventional pairs and subtended by reduced pherophylls (*Hochblätter*) that consequently "kein einheitliches, alle carpelle umfassendes und gemeinsam einschließendes Gebilde darstellen, da etwa als Perigon aufzufassen sein" (Harms, 1916, p. 279).

An additional argument for pseudanthium came from anomalous orientation of placental suture consistent with Solereder's idea of bicarpellate branches axillary to phe-

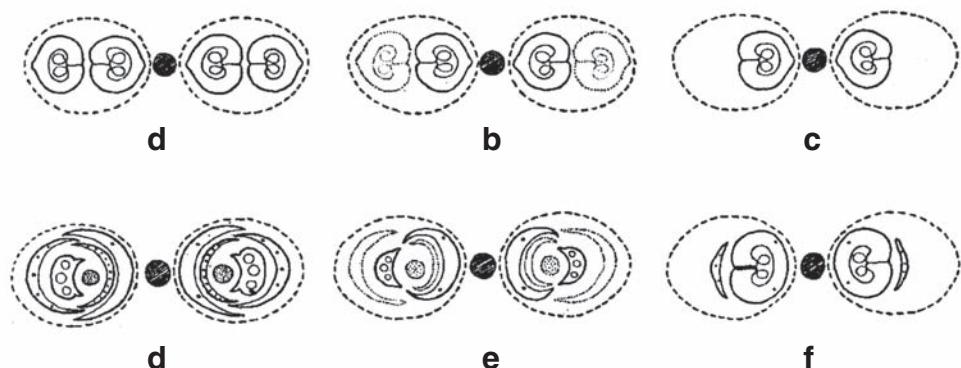


Fig. 1. Interpretations of the floral structure in *Cercidiphyllum* as reduced inflorescences: a – c, by Solereder (1899), d – f, by Harms (1916).

rophylls. Harms described the leaf – inflorescence system as sympodial, with the leaf terminal and with further elongation overtaken by an axillary growth point. He also noted a similarity between pherophylls and leaf stipules.

The pseudanthial interpretation was extended to staminate structures, although, admittedly, no direct evidence for their inflorescence origin has been ever obtained.

As a result of his interpretation, Harms considered the Cercidiphyllaceae to be an isolated family within the ranalean plexus related to the Trochodendraceae rather than the Hamamelidaceae. At the same time, *Cercidiphyllum* was compared with a monocotyledonous genus *Typha* (the Typhaceae) on account of the inverted orientation of carpels, while the leaf stipules clasping the axillary buds were believed to represent a typically monocotyledonous condition.

Swamy and Bailey (1949) in their comprehensive morphological study of *Cercidiphyllum japonicum* have stressed differences between the long-shoot and short-shoot leaves. They found that both leaf types are supplied by three vascular strands that arise from a unilacunal node in the short shoots, but from a trilacunal node in the long shoots. In the long-shoot leaves, primary veins depart from a single locus at the base, whereas in the short-shoots leaves they frequently depart in pairs at successive levels. Of the three short shoot cataphylls, the lower receives two primary veins, whilst the two subsequent cataphylls are supplied with five and seven to eleven veins, respectively. Reconstructed from serial sections, the eustele of reproductive axis has appeared to be formed of an arch of vascular bundles on the inner side of the upper cataphyll. The androecium was thought to consist of indistinctly segregated clusters of 8 – 13 stamens subtended by fewer membranous bracts, whereas each carpel seemed to have been subtended by a bract, although the inner bracts might have been underdeveloped and some unvascularized. Bracts were found to be supplied by three veins from the axial eustele. Above the floral bracts, vascular bundles of eustele are resolved into as many groups as there are carpels, giving rise to the ventral and median carpellary veins, the latter sometimes formed by fusion of two stellar bundles. Additional veins may occasionally enter the carpels.

The ovules are said to be arranged in two rows on the abaxial placentas and vascularized by a looping bundle that develops after fertility. Two integuments are differentiated, the inner one being resolved before maturity. The one-sided wing is formed as a chalazal extension, but becomes two-sided by flattening of integument in the plane of the wing.

I quote Swamy and Bailey (1949) in some detail because their description is the most complete ever obtained. Yet their opinion on segregation of stamens into distinct clusters, each subtended by a bract, as well as on the development and vascularization of ovules are not confirmed by this study.

Although scarcely implied by their anatomical observations, interpretation of carpellate fascicles with their subtending bracts as derived from a highly reduced inflorescence was adopted by Swamy and Bailey (1949) on paleobotanical evidence (discussed below) of racemose inflorescences in fossil *Cercidiphyllum* (Brown, 1939), each carpel representing a reduced pistillate flower as postulated by Solereder (1899) and Harms (1913). Since

their developmental study provided no evidence of twisting or resupination, the abaxial orientation of ventral suture facing the subtending bract was explained, essentially after Solereder (1899), as resulting from a reduction of bicarpellate gynoecium, in which the anterior carpel was lost to reduction.

With accumulation of data on morphological diversity of carpel types in the “ranalean” angiosperms, the abaxial orientation of placental suture in *Cercidiphyllum* seemed less exceptional and scarcely a reason for inferring a branching inflorescence prototype for its floral structures. Yet interpretation of this feature remained controversial.

Notwithstanding the reductive interpretation of the floral structures, morphological evidence seemed supportive of a fairly isolated position of *Cercidiphyllum* among the orders of flowering plants. According to Swamy and Bailey (1949), assignment of this genus to the Ranales (Magnoliales) can only be validated upon recognition of the order as a useful repository for relic angiosperms that retained one or more archaic character states. Likewise, “*nothing is to be gained by transferring such genera as Trochodendron, Tetracentron, Euptelea, and Cercidiphyllum into close relationship with the Hamamelidaceae or Saxifragaceae*” (Swamy & Bailey, 1949, p. 208). Neither are these four genera closely related, differing from each other in the types of foliar idioblasts, stomatal configurations, pollen types, gynoecial structures and certain details of seed morphology. Earlier, Baillon (1871) came to a similar conclusion in regard of the Ranales – Saxifragales controversy.

Leroy (1980) emphasized a topological homology of the short-shoot leaf and the flower. He considered the dicliny in *Cercidiphyllum* to be primary rather than derived.

Van Heel (1986) in his developmental study of what he called “a deviating female flower” of *Cercidiphyllum japonicum*, asserted that carpels had their ventral sutures facing bracts in their early development already. This observation seemed to have ruled out Hutchinson’s (1964-1967) suggestion of twisting or torsion of carpels during development. An occasional growing point in the form of a minute knob reportedly occurred on the outside of the carpel primordium in the position of the supposedly lost anterior carpel according to the Solereder – Harms reduction model.

Van Heel (1986) refers to the paired carpels of fossil infructescences compared to *Cercidiphyllum* by Brown (1939) and Crane (1984) as giving indirect evidence in favor of the reduction model. He at the same time points out that unusual orientation of carpels, as in *Cercidiphyllum*, also occurs in *Drimys lanceolata* (Tucker & Gifford, 1986), in which it can be similarly explained by the loss of a bract-facing member. However, in another species, *D. piperata*, a solitary carpel is inconsistently orientated, with its opening suture either towards or away from the bract.

Van Heel (1987) proceeds with a series of SEM micrographs of primordial carpillary structures showing six carpels with three decussate pairs of subtending bracts appearing at slightly different levels over the receptacle, the upper bracts being considerably reduced. No additional growing points are reported this time, but a gap between a distal carpel and its vestigial subtending bract is considered to be the place for a lost structure like an inflorescence branch. Additional evidence of homology between the carpellate

and staminate structures is presented, the latter reportedly sometimes producing three decussate pairs of bracts, the lower ones with distinct axillary groups of stamens (considered as a teratological situation below).

Endress (1986) has described floral structures of *Cercidiphyllum* as heads or congested spikes, lacking both perianth and floral prophylls, and in this respect maintaining ultimate position in regard of the putative prophyll reduction series (*Trochodendron* – *Tetracentron* – *Euptelea* – *Cercidiphyllum*). His discussion of floral structures emphasizes their congruence with anemophilous syndrome. The pollen grains are characterized as 3-colporate like in the other trochodendrids. Later, Endress (1993) has interpreted Van Heel's (1986) observation as evidence of "distinct rudimentary floral axis between the carpel and the pherophylls". He gave full credit to paleobotanical findings in favor of the reduction model.

Recently, Yan et al. (2007) have studied floral morphogenesis in *Cercidiphyllum japonicum* with a focus on the leaf/bract relationships. They concluded that phyllomes traditionally described as bracts (pherophylls) are non-homologous to leaves, being different in the shapes of primordia, the presence/absence of glands and stipules, and in certain epidermal features. In their opinion, the "bracts" are tepals of floral units (flowers) that consist of a solitary carpel and a single tepal (a different interpretation is given below). It is claimed that carpels and bracts are correlated in their development: the reduced tepals constantly associate with underdeveloped carpels (which I failed to confirm). The carpels are described as consisting of a conduplicate fertile part and a planate stigmatic extension. However, Yan et al. (2007) found no developmental evidence in support of any vestigial floral parts that might justify the purported affinities to the racemose fossil forms (I applaud the latter conclusion, but disagree with the rest).

Summing up, the morphology of *Cercidiphyllum*, as it is currently interpreted, appears highly abnormal, defying recognition of its natural relationships. Despite the long history of morphological studies, interpretation of both vegetative and reproductive structures of *Cercidiphyllum* remains ambiguous or unpersuasive on such crucial issues as:

- (1) Branching mode in regard of shoot dimorphism;
- (2) Phyllotaxy;
- (3) Stomatal pattern in regard of the vein network and hydathodes;
- (4) Short shoot architecture: structural relationships of cataphylls, solitary foliage leaf, reproductive axis and renovation bud;
- (5) Flower/inflorescence dilemma of reproductive structures;
- (6) Subtending and intecarpellate/interstaminiate phyllomes: pherophylls, prophylls or tepals?
- (7) Floral structures lost to reduction: factual evidence or figments of interpretation?
- (8) Carpel morphology in relation to vernate leaf morphology;
- (9) Placentation type in regard of ovule development and vascularization;
- (10) Transformation of ovule polarity in the course of seed development;
- (11) Pollen apertural type: colporate or porate?
- (12) Phylogenetic prototypes in regard of paleobotanical evidence.

4. MATERIAL AND METHODS

Fresh material on two living species was courteously provided for this study by the Botanical Garden of Moscow State University (MSU), Main Botanical Garden of Russian Academy of Sciences (MBG), Botanical Garden of Botanical Institute, Russian Academy of Sciences, St-Petersburg (BIN), and Royal Botanical Gardens, Kew (Kew). The material consisted of leafy shoot systems and reproductive shoots in bud, at anthesis and at maturity, preserved as herbarium specimens or fixed in alcohol or formaldehyde.

A number of dormant buds were dismembered and all parts were immersed in alcohol or glycerin. Placentas with minute ovules were extracted from immature carpels by gently opening them along the ventral suture. Mature seeds were removed from open follicles. Pollen grains were released with fine needle from closed sporangia and removed from stigmas. Hand-cuttings were made by Krassilov and microtome sections by Remizova.

For microscopic studies, cleared organs and tissues were mounted under cover glass that was fastened with varnish. Transparencies were obtained by keeping the tissues in diluted nitric acid for several hours, washing with diluted alkali and decanting with distilled water. Floral structures with their subtending bracts, placentas with immature ovules, pollen grains and other small parts were mounted for SEM and covered with gold.

The paleobotanical material was collected during several field seasons by Valentin Krassilov, Natalia Silantieva and Julia Loven from the Institute of Evolution, University of Haifa joined by geologists Zeev Lewy and Shelomo Ashkenazi from the Geological Survey of Israel. The remains of leaves and fruiting structures come from the Late Cretaceous deposits of Arava, southern Negev. They are preserved as impressions coated with a subcutaneous ferruginous film (subcrustation). The impressions exposed on the bedding plains were cleared by removing bits of onlapping rock matrix with fine needles.

For microscopic studies, small pieces of cleared subcrustation were transferred onto varnish film by dissolving the underlying rock matrix in, sequentially, hydrochloric and hydrofluoric acids. The transfers were mounted on glass slides for light microscopy or on metallic stubs and covered with gold for scanning electron microscopy.

The micromorphological studies accompanied by microphotographic documentation were conducted under stereomicroscope Leica MZ6 with digital camera Leica DFC 320. Transparent slides were studied in transmitted light under Nikon Coolpix 4200. Scanning electron microscopy was done under CAMSCAN with digital camera Nikon Coolpix 8700.

5. MORPHOLOGICAL DESCRIPTION

SHOOT SYSTEM

The shoot system consists of branched long shoots bearing short shoots that produce three cataphylls, a solitary reniform foliage leaf and reproductive structures, as well as new long shoots. Our analysis show that all long ramifications of the system derive from short shoots. Therefore, the secular mode of branching is cyclic: long shoots produce short shoots that produce long shoots of the next cycle. In the branching long shoot – short shoot system like one shown in Plate I, fig. 1, all leaves are reniform short-shoot leaves. Slender ultimate long shoots arising in the position of a fruit stalk produce distichous elliptical leaves (Plate II, fig. 1).

On the older long shoots, epidermis is pilled off exposing a sinuously fissured periderm with hemispherical lenticels that are scattered or sometimes contiguous into short transverse files (Plate I, fig. 6). The young long shoots are ridged, with elongate lenticels in longitudinal files, brighter than the shoot surface (Plate III, fig. 5). Commonly, the long shoot branching nodes are spaced by internodes bearing 5 – 8 short shoots.

The branching is of diverse configurations, one of each is an apparent symmetrical division of a stout long shoot, in which two thinner arms are produced, diverging at about 45° (Plate III, fig. 5). The arms may appear as equal dichotomy, but actually they arise from a pair of short shoots at the branching node and are girdled by the short shoot cataphylls at the base. Coalescence of paired short shoots at the branching node is a frequent phenomenon (Plate III, fig. 3). Subsequent branching nodes up the shoot may appear in the same way. The angles of branching are preserved through the shoot system.

A somewhat different configuration arises when two nearly equal symmetrically diverging axes branch off not from the base, but from consecutive increments of the paired short shoots. In Plate III, fig. 1, short shoots of a nodal pair slightly diverge above the node, each producing two increments before giving off the sympodial long branches. Several short shoot increments are added after branching.

This mode may produce asymmetric branching when the nodal short shoots are unequally developed, which is commonly the case because their disposition is not strictly decussate, but transitional spiral – decussate. In such cases, a thicker short shoot produces a stronger long axis.

Another type of branching represents an apparent asymmetrical division, in which the stout arm takes in line with the main axis or only slightly deviates, whereas the slender arm embarks at acute angle (Plate III, fig. 3). The lenticels of the stout arm are hemispherical as on the main axis, but on the slender arm they are elongate elliptical. By these observations, the stout arm is an old branch, while the slender arm is a new branch. Plate III, fig. 2 represents the same branching mode, but with the short shoots brought to alternate arrangement by elongation of the main axis between them. A transverse girdle scar at the upper level is left by the previous year short-shoot bud, from which the long branch was produced.

A shoot in Plate III, fig. 4 is peculiar in the main axis being thicker above the short shoot node than below, showing the juvenile epidermis and lenticel characteristics. This situation may arise from fusion of the adjacent short-shoot growth points both contributing to elongation of the main axis.

As mentioned above, in the older shoot system all the leaves are the reniform short-shoot leaves. A shoot system with dimorphic, reniform and elliptical, leaves involves a slender long branch that emerges from a nodal short shoot at the position of a fruit stalk and is juxtaposed by a reniform leaf (Plate II, fig. 1). It has a long basal internode above which the first pair of opposite or subopposite leaves is produced followed by distichous alternate leaves over the internodes of irregular lengths. The leaves are spread in one plane, oblique to the axis and decurrent, swollen at base, with persistent 2-lobed or rarely 3-lobed stipules overhanging the axillary bud. One long shoot of the kind was found to be terminated by a fruit stalk overtopping the upper leaf (Plate II, fig. 3). This situation is interpreted below as an attempt at resuming reproductive development in a sterile shoot replacing a pistillate structure.

SHORT SHOOT DEVELOPMENT

In *Cercidiphyllum*, short shoots function as reproductive shoots producing either gynoecial or androecial structures (interpreted as flowers or pseudanthia), which can be replaced by a leafy shoot. Short shoots arise in decussate pairs or alternate on the long shoot axis. The pairs are always asymmetrical, not quite at the same level and one developmentally more advanced than the other, which is clearly seen on handcut sections perpendicular to the long axis (Plate IV, fig. 6).

Short shoots show well marked growth increments that develop from the apical dormant bud sunken in the base of petiole. Most dormant buds are floral buds, but some produce leafy long shoots. Irrespective of gender identity, each short shoot increment has three bud scales (cataphylls I – III) and a solitary petiolate leaf.

To give a general idea of the floral bud architecture, several closed male and female buds about 2 mm in diameter were handcut, showing in transverse sections a massive bicarinate cataphyll I on the adaxial side forming a trapezoid contour thickened at the

keels (Plate IV, figs. 1 – 5; Fig. 2). It closes around the bud wrapping the broadly involuted adaxial cataphyll III and clasping the conduplicately folded cataphyll II on the opposite side, which in turn enfolds the cataphyll III abaxially.

Cataphyll III subtends floral stalk that gives off a solitary leaf. Near the base, the leaf petiole and the floral stalk are nearly equal or the petiole is somewhat thicker (Plate IV, figs. 1 – 3). They are tightly appressed, separated by a minute stipule curving round the stalk. The petiole is rounded, slightly grooved on the side facing the stalk, which is elliptical, transversely elongated from the beginning, with an elliptical eustele. At the higher levels, the petiole and floral stalk gradually diverge with the membranous stipule becoming more prominent between them, flat with clasping margins. The petiole shows a slightly trilobed central trace. Peripheral bundles soon differentiate on the abaxial side. At the base of lamina, the leaf is crescent-shaped with circinately (doubly) involuted margins. The midrib trace is conspicuously thickened and the midrib protrudes on the back of the inrolled lamina.

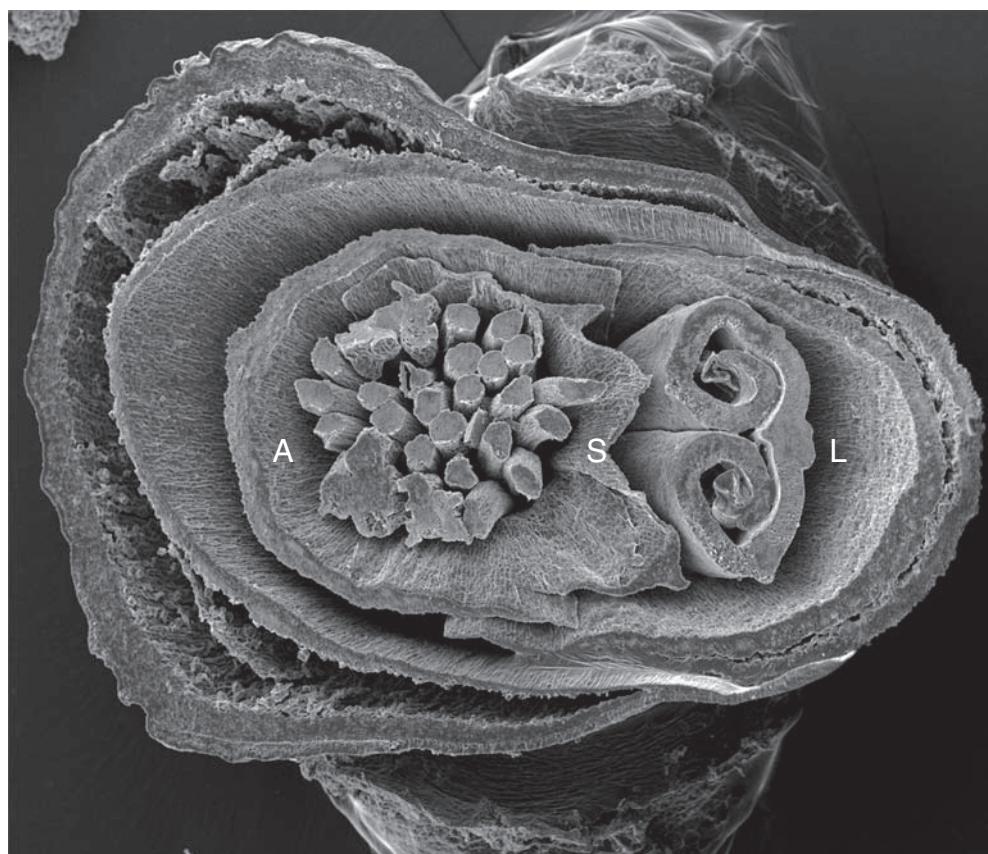


Fig. 2. *Cercidiphyllum japonicum* Sieb. Et Zuc., MSU: hand cut androecial bud (A, androecium, L, leaf, S, stipule), SEM.

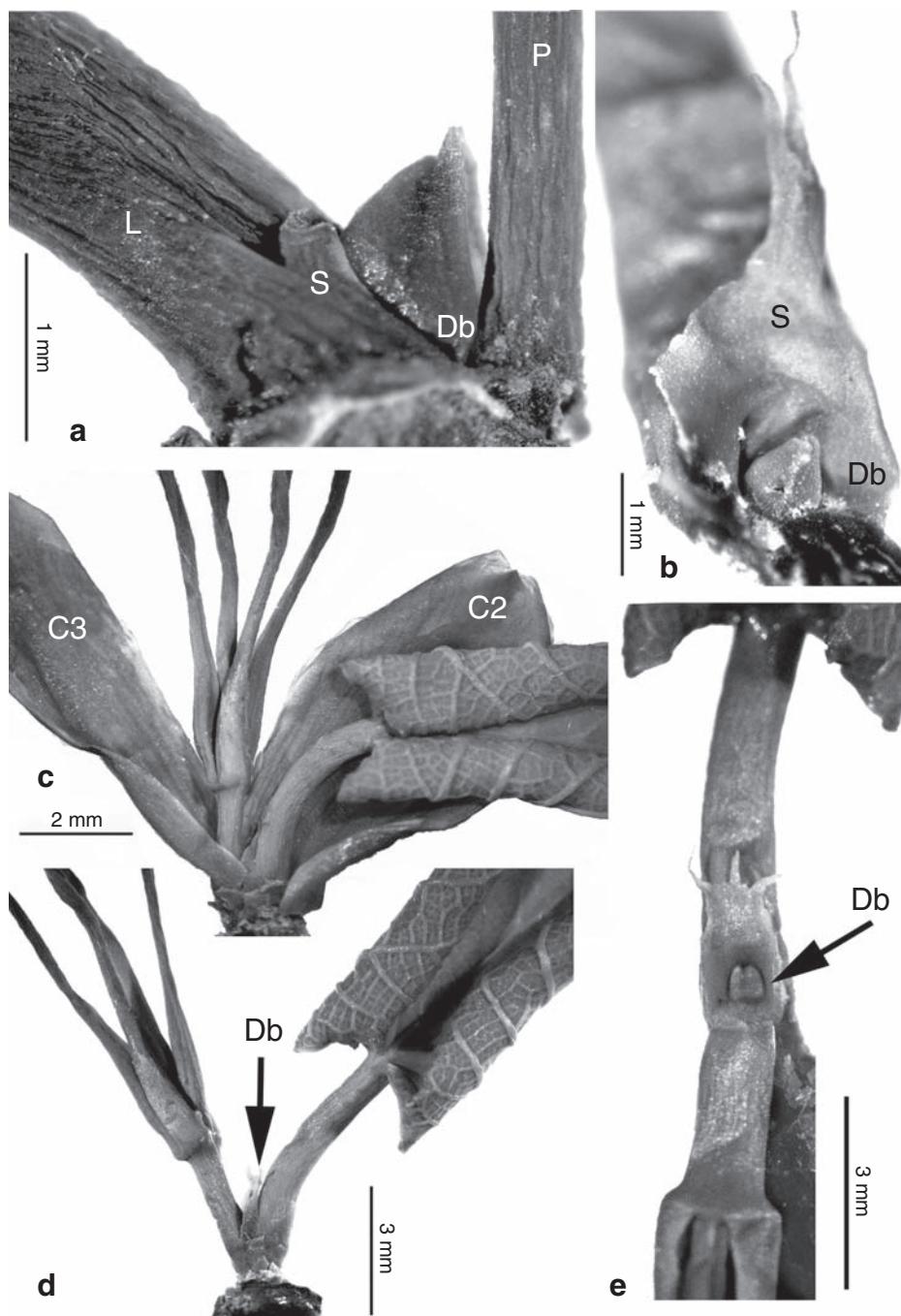


Fig. 3. *Cercidiphyllum magnificum* Nakai, BIN, dormant bud (Db) position: a, at mature leaf petiole (L) – gynoecial stalk (P) divergence (S, stump of stipule); and b – e, at anthesis, the leaf petiole and floral stalk drawn apart (C₂, C₃, cataphylls, S, stipule).

The renovation growth point appears as a flap of large-celled meristematic tissue between the leaf petiole and the floral stalk. It enlarges and becomes asymmetrically cleft at the apex before anthesis.

At anthesis, the floral organs and their associated leaf are still wrapped in three spirally arranged cataphylls that are identical in sterile, male and female buds. The leaf occurs next to the middle cataphyll II and the floral part next to the distal cataphyll III. By gently spreading the cataphylls one sees leaf petiole basally adnate to and bending away from the floral peduncle, with renovation growth point sunken in the base of petiole and clasped by the leaf stipule (Fig. 3a – e).

CATAPHYLLS

The cataphylls are sessile, arising in shallow spiral, imbricate – convolute at vernalization. The basal cataphyll (I) is thick, rigid, dark brown, dorsally bicarinate. The rest are much thinner, yellowish brown, dorsally striate. The middle one (cataphyll II) is broadly obovate with revolute margins. The number of vascular strands entering the base is 7 – 8, the midvein being appreciably thicker than the laterals. The distal cataphyll III is calyptrate, tightly wrapped around the floral structure and the leaf, apically screwed (Plate V, figs. 1 – 4). When spread, it is broadly ovate, truncate at base becoming spatulate, long tapering at base later in development. It is notched at apex, with irregularly incised membranous margins. Occasionally a small lobe develops at the end of midrib.

Before elongation, cataphyll III shows an irregular pattern of seven subparallel primary veins and a few slender interstitial veins traceable to 1/3 of blade length. The midrib is appreciable stronger than the laterals, straight, reaching to the apical notch, producing at different levels a steeply ascending secondary vein on each side and a few short looping branches distally. The laterals are gently bowed, converging toward the apex. Their secondary branches vary from pinnate to unequally dichotomous, diverging at acute angle, repeatedly branching on one or both sides, distally looping or approaching each other without actually connecting. The tertiary veins form a sparse scalariform or chevron network (Plate VI, fig. 2).

At the spatulate stage (Plate VI, fig. 3), the midrib is slightly if at all stronger than the laterals, which take nearly parallel courses toward the apex gradually diverging with expansion of the blade. Interstitial veins are vanishing midway up the blade. Each primary vein splits off a few slender long ascending branches that take parallel to it and connect the next branch or end blindly before the membranous fringe. In the middle part, this pattern appears monocot-like with alternate stronger and slender veins. Distally, the outer laterals are lost in splitting, while the inner ones converge to the apex, giving off to the outside a set of dense repeatedly forking secondary branches that produce a loose reticulate pattern.

Cataphylls never produce marginal glands and do not exhibit epidermal leaf blade characters. Cataphyll epidermis consists of longitudinally filed cells with transverse or oblique cross walls. Mesophyll wedges out in a saw-teeth line before the membranous fringe (Fig. 4).

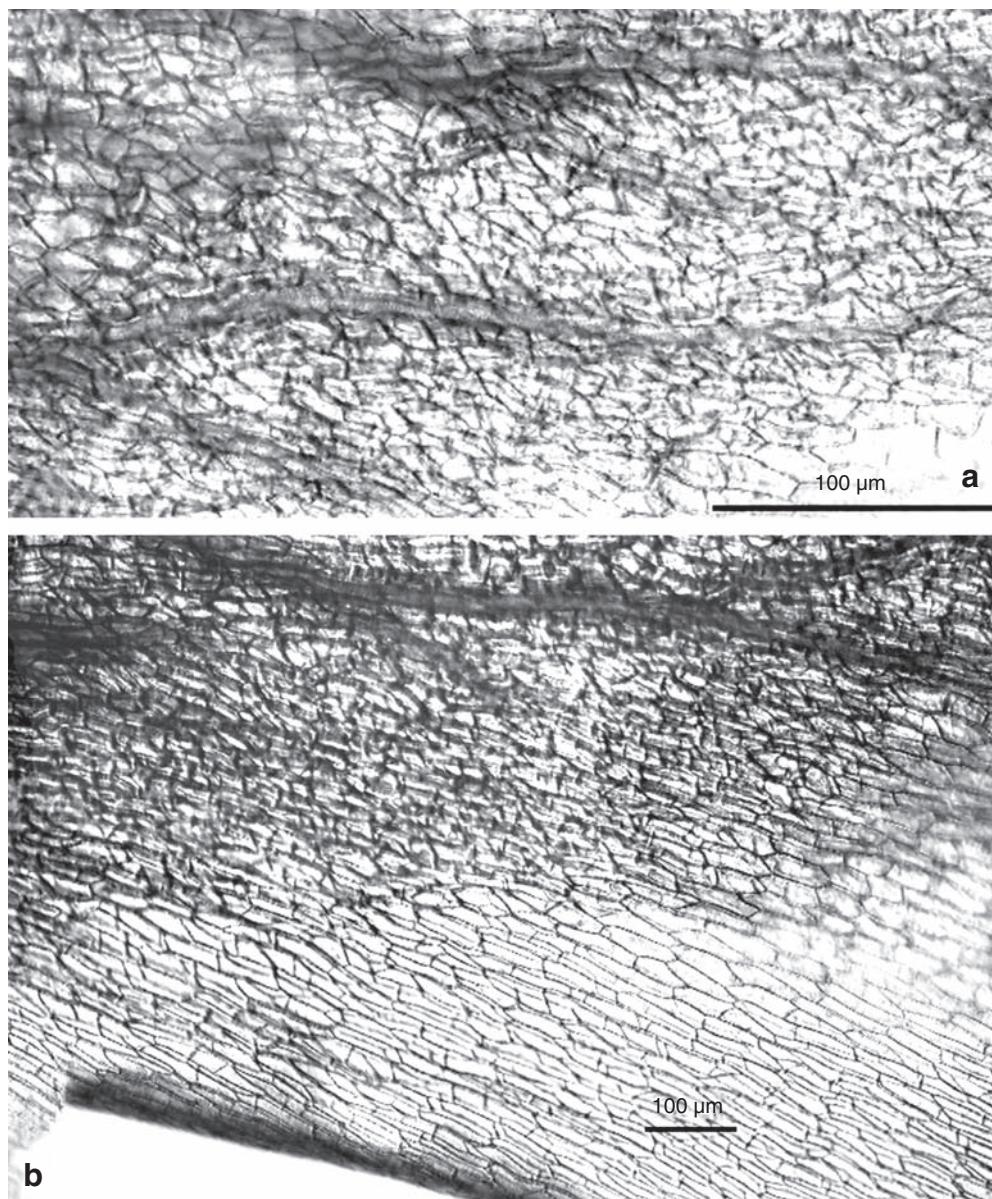


Fig. 4. *Cercidiphyllum japonicum* Sieb. Et Zuc., MSU, cleared cataphyll III, showing veins with anastomoses and the pattern of epidermal cells, mesophyll wedging out before the marginal fringe.

SHORT-SHOOT LEAF (PROPHYLL)

A solitary short-shoot leaf divides from the floral stalk opposite its subtending cataphyll III. Therefore it is not a continuation of the spiral phyllotaxy of imbricate cataphylls. The floral stalk – leaf petiole separation appears to be an unequal dichotomy producing two stem-like axes, one circular and the other elliptical in cross section (Plate IV, figs. 1 – 3). The leaf stipule is a bilobed (bipartite) membranous structure with irregular additional teeth (Plate V, figs. 5, 6) that may grow faster than the leaf blade itself. In bud, the stipule clasps the floral receptacle, whilst the leaf – floral axis assemblage as a whole is enclosed in the calyptrate cataphyll III, to be released the blade forth (Plate V, figs. 1 – 3).

Approaching anthesis, cataphyll III opens, delivering leaf blade first, then stipule and finally the floral stalk. On account of their topology and close association in development, the leaf is a part of reproductive shoot as its solitary prophyll. It functions as a foliage leaf at maturity (described under “Leaves”).

LONG SHOOT DEVELOPMENT

Long shoots are produced from the short-shoot renovation buds or by conversion of reproductive structure at the position of the androecial or gynoecial stalks. Otherwise such buds do not differ from those producing fertile organs, having identical sets of cataphylls and the terminally diverging leaf petiole with cylindrical eustele and the peduncle-like flattened stalk with elliptical eustele. Several situations were encountered, grading from an occasional leafy shoot production from a solitary sterile bud among the male or female floral buds or an occasional short shoot pair, in which one bud is sterile to about 1/5 of all short shoots sterile. Predominant sterile short shoot production occurs as a rare phenomenon (e.g., in *C. japonicum* from Kew), perhaps induced by climatic conditions.

Two developmental types of long shoots are distinguished. Long shoots developing from renovation buds in the axil of prophyll at the position of a short shoot increment appear as hemispherical primordia of large spreading cells, with inconspicuous basal – lateral prominences a few cells thick (Fig. 5). The primordium rapidly elongates into a club-shaped axial structure before the development of leaves (Fig. 6a, b). At the next stage (Fig. 6c) the axis is somewhat flattened and the leaf primordia are better defined. The axis elongates without producing more leaf primordia, and the lateral pair of leaves develop into somewhat asymmetrical stalk-like structures with disproportionately large peltate apical glands, converging over the protruding axis. Stipules arise as minute knobs becoming slender elongate appendages onlapping the axis (Fig. 7a – f). In the young shoots emerging from the first year short-shoot increments (Plate III, figs. 8, 9), the basal internode extends to 0.5 – 1.5 cm long before producing a terminal pair of short-shoot

buds. Later growth can be overtaken by one of the short shoots or both produce nearly equal or unequal branches as described above.

In the second type, leafy shoot arises in the position of floral stalk and is here considered as vicarious of the latter. The leaves develop in a tight cluster of three decussate pairs before elongation of the axis.. The leaves are born in not quite symmetrical,

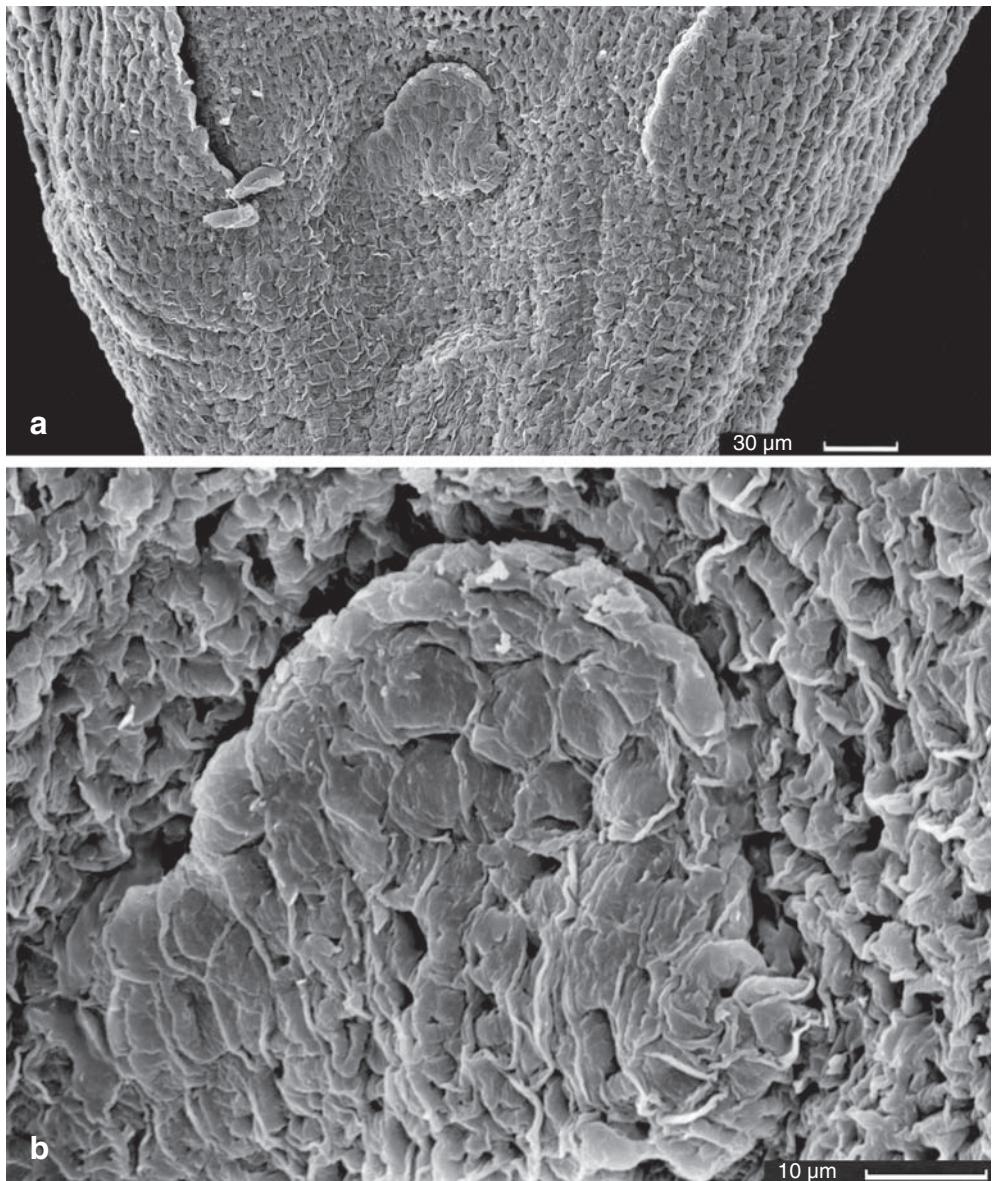


Fig. 5. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, leafy shoot primordium developing from the short-shoot renovation bud, with leaf primordia as lateral prominences few cells thick, SEM.

irregularly decussate pairs, like the carpels, and are involuted their lower surface outside, showing a prominent midvein. The apical glands are immediately followed by smaller marginal glands (Figs. 8, 9).

In Plate VII, fig. 1, the leaves of the first pair transverse to the bowed short-shoot leaf are unequal, their involute faces meeting over the shoot apex, showing dispropor-

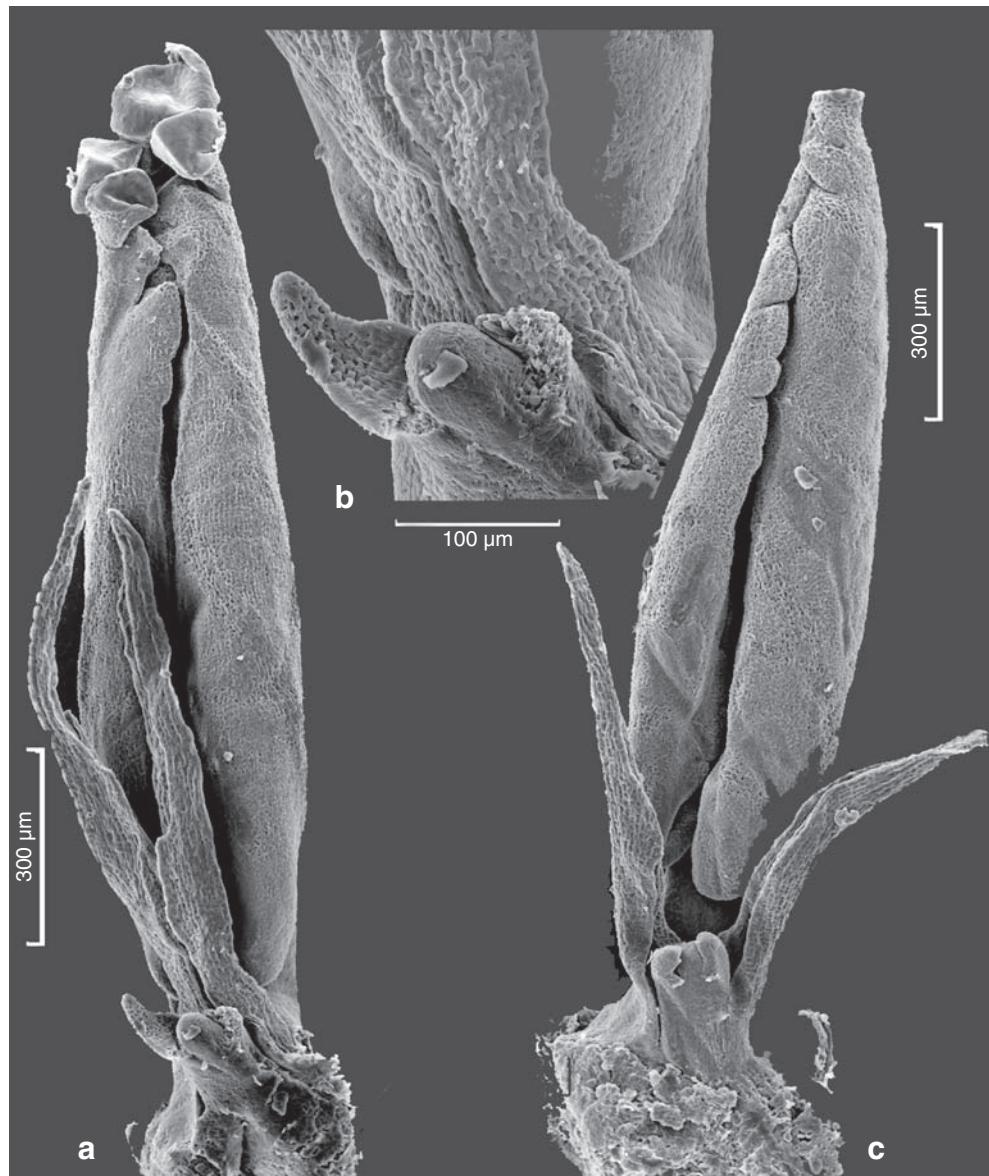


Fig. 6. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, leafy shoot primordium developing from the short-shoot renovation bud: a, b, as a club-shaped axis with the first pair leaf primordia scarcely protruding (c), SEM.

tionably large glands. Stipules are discernible in only one leaf of the pair. In Plate VII, fig. 2, there are three primordial leaves in the position of primordial carpels that also may arise in trios. The lateral leaves are somewhat crescent-shaped, both with minute



Fig. 7. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, leafy shoot primordium developing from the short-shoot renovation bud: a – f, developmental stages of the first leaf pair primordia, stalk-like with incipient stipules and the disproportionately large apical glands, SEM.

stipules, the smaller median one is straight, with shoulders at the sites of would-be stipules. In Plate VII, fig. 3, two decussate leaf pairs are nearly equally developed, with large apical and smaller subapical glands. The lateral leaves show hair-like stipules onlapping the median leaves. The lateral leaves show rows of marginal glands, the median leaves are endowed with distinct stipules and the third pair appears inside the fascicle. The leaf shoot becomes bushy, as in Plate VII, fig. 4. An exposed leaf of the third pair is strikingly similar to the leaf-like perophylls (below).

Plate VIII, figs. 1 – 3 illustrates increase in leaf size without considerable elongation of the axis that suddenly accelerates before emergence from the bud (Plate VIII, fig. 4). Only basal internode elongates, bearing a tight cluster of juvenile leaves. The axis shows lenticels like in the exposed long shoots. Further, the primordial long shoots with clusters of decussate leaf pairs develop by elongation of leaf internodes into a long shoot with distichous leaves, like in Plate II, fig. 1.



Fig. 8. *Cercidiphyllum japonicum* Sieb. et Zuc., Kew, leafy shoot with 3 leaf pairs replacing floral stalk in the short-shoot bud development (see also Fig. 38), SEM.

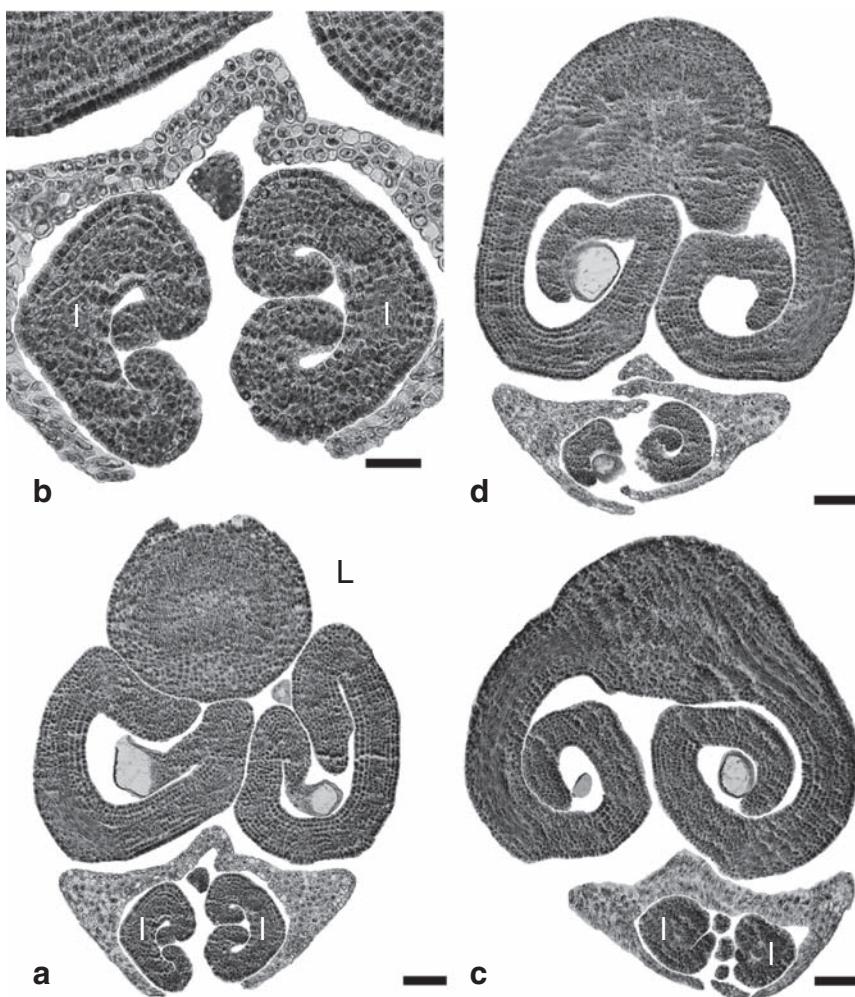


Fig. 9. *Cercidiphyllum japonicum* Sieb. et Zuc., Kew, leafy shoot replacing floral stalk in the short-shoot bud development: transverse sections showing homeomorphy of the larger short-shoot leaf (L) and the tiny first pair leaves of the vicarious leafy shoot (I); Scale bar = 100 µm.

FOLIAGE LEAVES

In *Cercidiphyllum*, the dimorphic, reniform and elliptical, foliage leaves are commonly described as belonging to the long shoots and short shoots respectively. As discussed above, in the main shoot system all leaves are the monomorphic short-shoot leaves produced in association with reproductive organs and here considered to be prophylls that assumed the function of foliage leaves. The elliptical leaves belong in the long shoots produced from the short-shoot buds instead of fertile structures.

In bud, a solitary short shoot leaf is coiled in a tube with supervolted (double coiled) margins, so that large marginal glands occur in two adjacent subparallel rows inside the tube (Table V1, fig. 4). A midrib and two basal veins enter the blade from a short disproportionately stout petiole, their secondary branches supplying the glands. The leaf emerges from the calyprate cataphyll III at anthesis, still involuted, showing prominent abaxial venation that tightens the coil.

When spread, the leaf blade is elliptical reniform, cordate at base. The margin is irregularly serrate, the prominent teeth alternating with one to several smaller serrations. The teeth spacing also varies and a few teeth are contiguous. Such irregularities are more evident in juvenile than in mature leaves and are most conspicuous in the basal part (Figs. 10). Near the apex, the teeth are longer and stronger forwarded. The apical tooth is symmetrical and about twice as broad as the rest (Fig. 11).

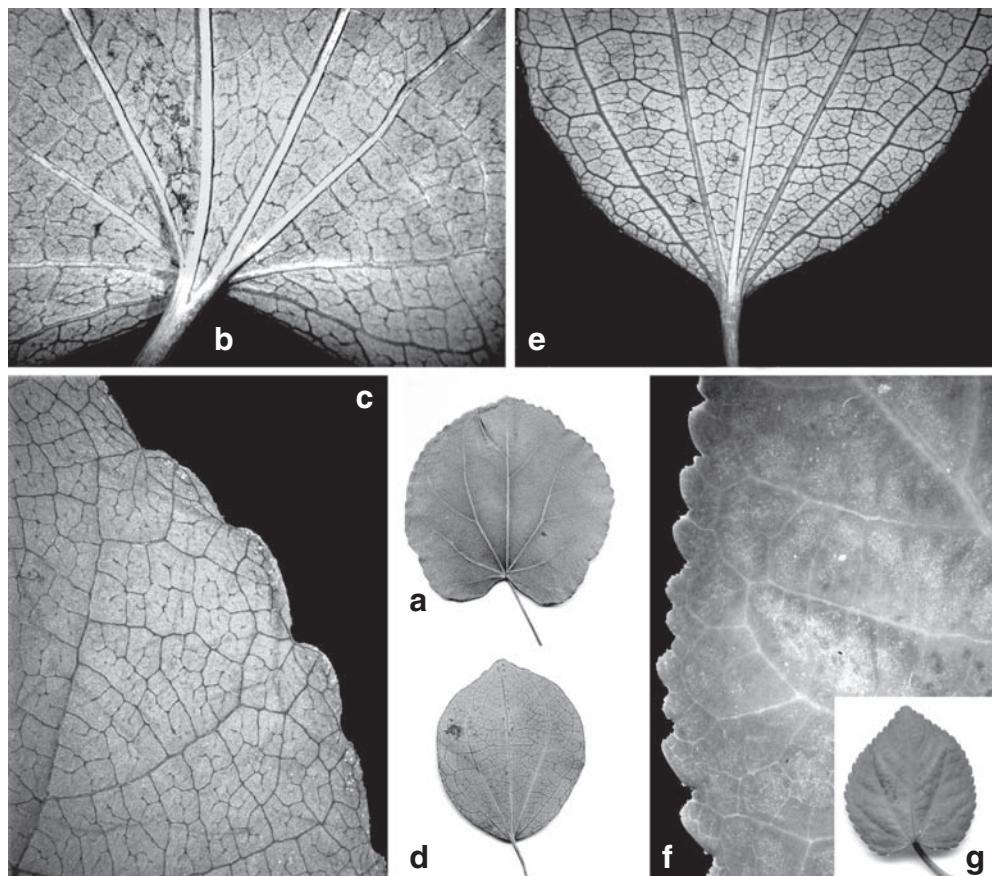


Fig. 10. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, leaves: a – c, reniform leaf, basal veins, and crenulate margin; d, e, elliptical leaf, basal veins; f, g, underdeveloped reniform leaf, irregularly biserrate margin.

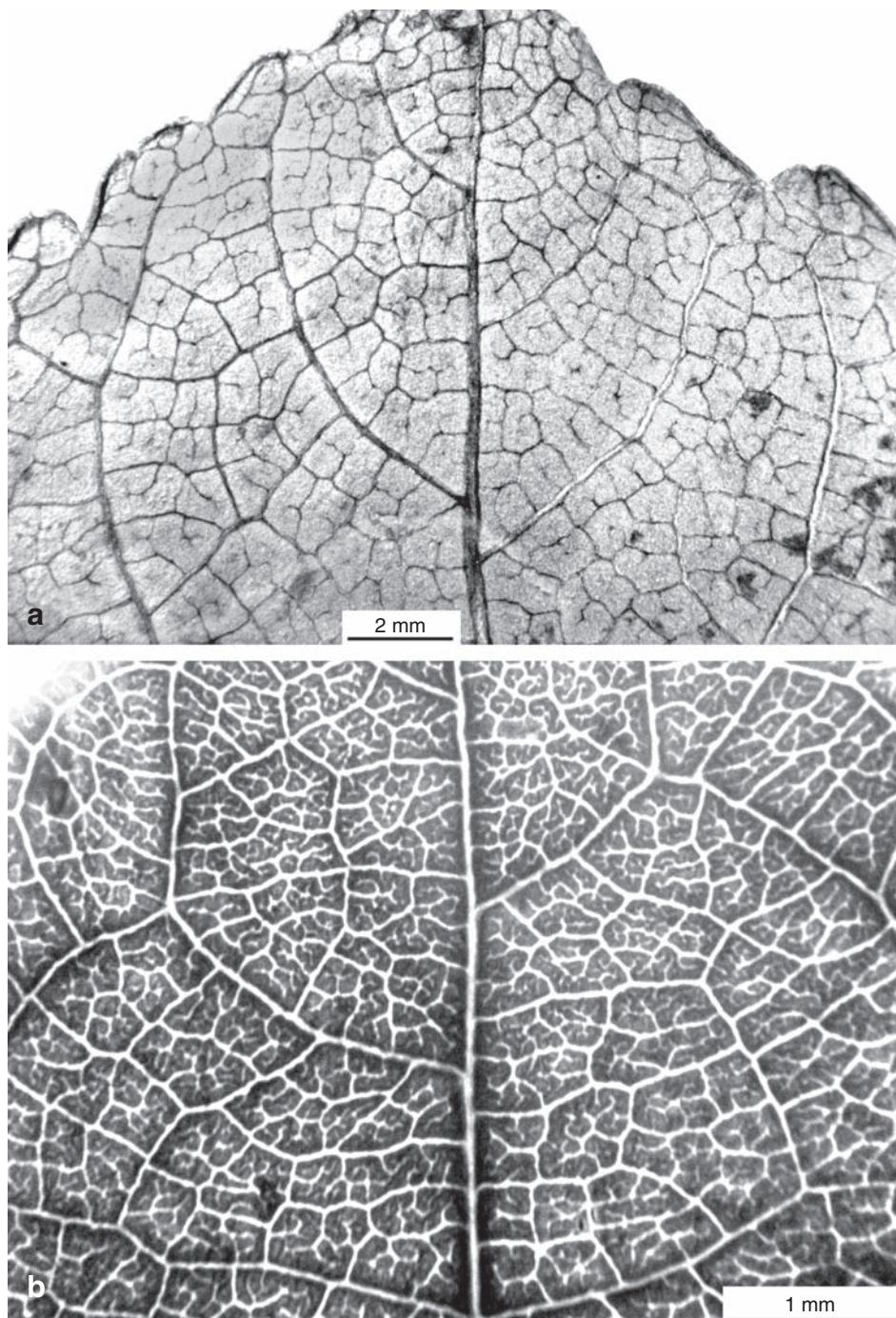


Fig. 11. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, reniform leaf: a, irregular marginal teeth near apex, some with additional serration; b – venation in transmitted light.

The venation of juvenile leaf is a coarser and simplified version of the mature one. The petiolar bundle is split shortly before entering the leaf blade, as in some mature variants, producing six primary veins in a dichopodial sequence. However, in distinction from mature leaves (below), the primary veins are radially spreading and their behavior before the margin can be described as semicraspedodromous rather than acrodromous (Plate VI, fig. 1). Their outside branches either enter marginal teeth or loop at a very short distance from the margin giving short offshoots to the glands. No difference was found between juvenile and mature leaves in regard of minor venation pattern, except that the 5th order areoles are feebly marked in the former, and the blind veinlets are less conspicuously if at all developed.

The mature reniform leaves are long petiolate, shortly pointed, cordate and somewhat peltate at base, the blade being upcurved on end of petiole. The leaf margin is proximally entire for 1/5 of blade length, serrate above. The marginal teeth are low, forwarded, dorsally smoothly rounded, bluntly pointed, each with a small resinous gland (or notched at the scar of a shed gland). Near apex, serration is less regular, with occasional reduced teeth or crenulations. A few teeth show an additional dorsal point. Apex appears as a symmetrical tooth. The venation is acrodromous, prominent on both sides, but more so abaxially. The petiole bundle splits into six primary veins. The first unequal division commonly occurs before entering the blade (Fig. 10b). The midvein is segregated among the basal group, running straight to the apex. Strong laterals are produced by a sequential sympodial splitting of the basal strands, decreasing away from the midvein. The angle of departure increases in the same direction and the veins respectively ascend to 3/4, 1/2 and 1/3 of the blade length. A pair of slender intrabasal veins follows downcurved margins of the basal indentation.

Secondary veins depart in alternate order on both sides of the midrib and run parallel to the laterals, which in turn branch on the outside. All veins decrease after branching and the secondary branches are broadly looping before the margin, sending short offshoots to the glands. Minor veins of the marginal zone converge toward the small knots at the bottom of the sinuses (Fig. 11a). Tertiary veins are scalariform, irregularly ramified, strongly arcuate on flanks of the midvein, gently arcuate or nearly straight between the laterals, not percurrent or only occasionally so. The 4th and 5th order veins are of a slightly different prominence abaxially, but indistinguishable adaxially. Their ramification is a miniature copy of the tertiary network, forming irregular rectangular or trapezoid areoles. Blind veinlets are well developed (Fig. 11b).

The elliptical leaves appear in decussate pairs, but become distichous at maturity. They are short-petiolate, bluntly pointed, broadly cuneate at base (Fig. 10d). The leaf margin is entire with slightly protruding glands or minutely serrate, sometimes more conspicuously serrate near the apex. The veins are patterned in the same mode as in reniform leaves, but the midvein is more obviously stronger than the laterals, which arise at slightly disparate levels. The inner pair of laterals extends nearly to the apex marking off an obovate central area. The outer laterals are appreciably weaker ascending to about

2/3 of blade length, their numerous outside branches regularly looping along the margin. Intrabasal veins are very short or inconspicuous. Since the 5th order veins are barely discernible, the network of minor veins may seem coarser than in the reniform leaves.

LEAF EPIDERMIS

The reniform and elliptical leaves do not differ in their epidermal structures. The leaves are hypostomatic, with all orders of veins represented by well-marked costal zones of elongate cells. The last order areoles are bordered by the intercostal ridges of 3–4 rows of fusiform cells fringed with irregular bulging cells that extend to the blind veins (Fig. 12). On the lower epidermis, the blind veins are marked by irregularly filed thick-walled

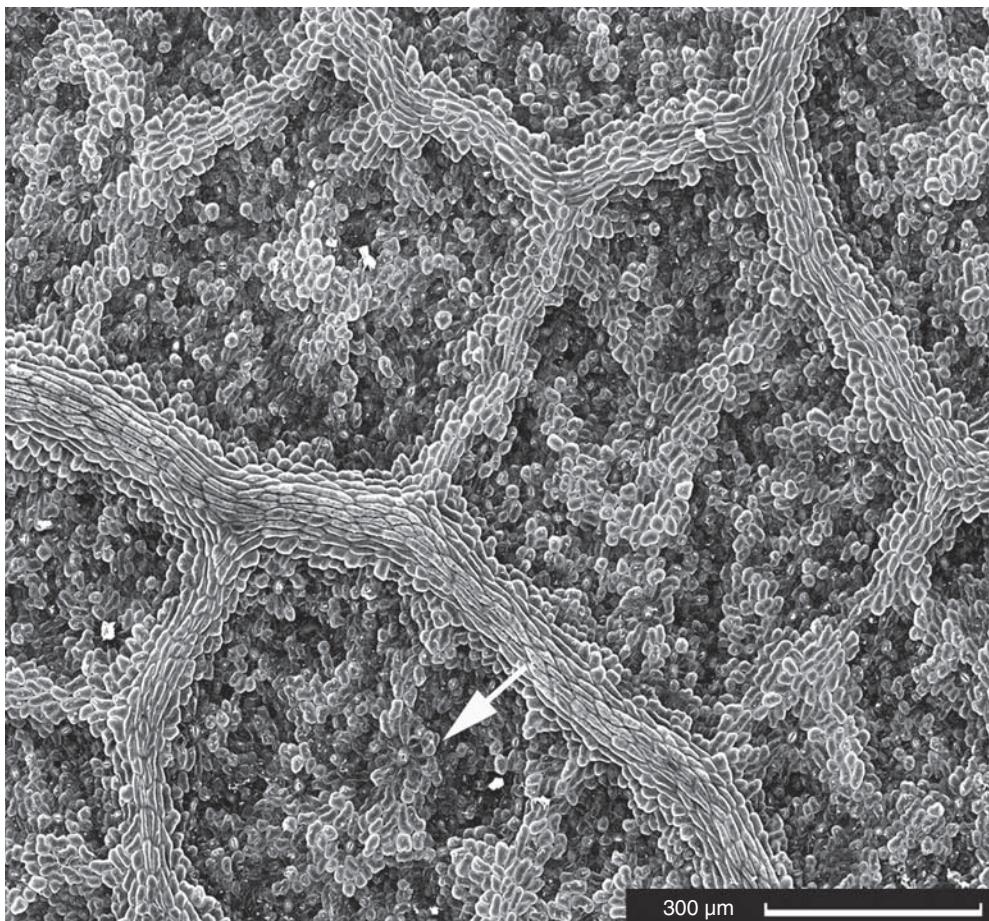


Fig. 12. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU: last order areoles intruded by the blind veins, some supporting hydathodes and hydathode-like stomata (one at arrow is shown in Fig. 35), SEM.

tabloid cells that occasionally have sinuous anticlinal walls. The endodermal sheath cells show fine striation on the inner periclinal wall (Fig. 13).

Inside the areoles, the cells are irregular isometric, chaotically orientated. The blind veins are conspicuous in cleared leaves owing to their excessively developed endodermal sheaths. They are vigorously twisted and ramified with pinnate, sympodial or flabellate, simple or forked, occasionally anastomosing branches (Fig. 14a, b). The bundle sheath is expanded at the blind end, forming a funnel-shaped hydathode (usually colorless, but some showing a yellowish secretory substance, therefore glandular).

In surface view, the hydathodes may appear as irregular thin areas with or without a central pore. The pore, when present, is an elliptical opening surrounded by a thick raised border, with accessory cells feebly if at all developed, suspended on the epithem and surrounded by the radially arranged tabloid cells. Or it is more stomata-like, with

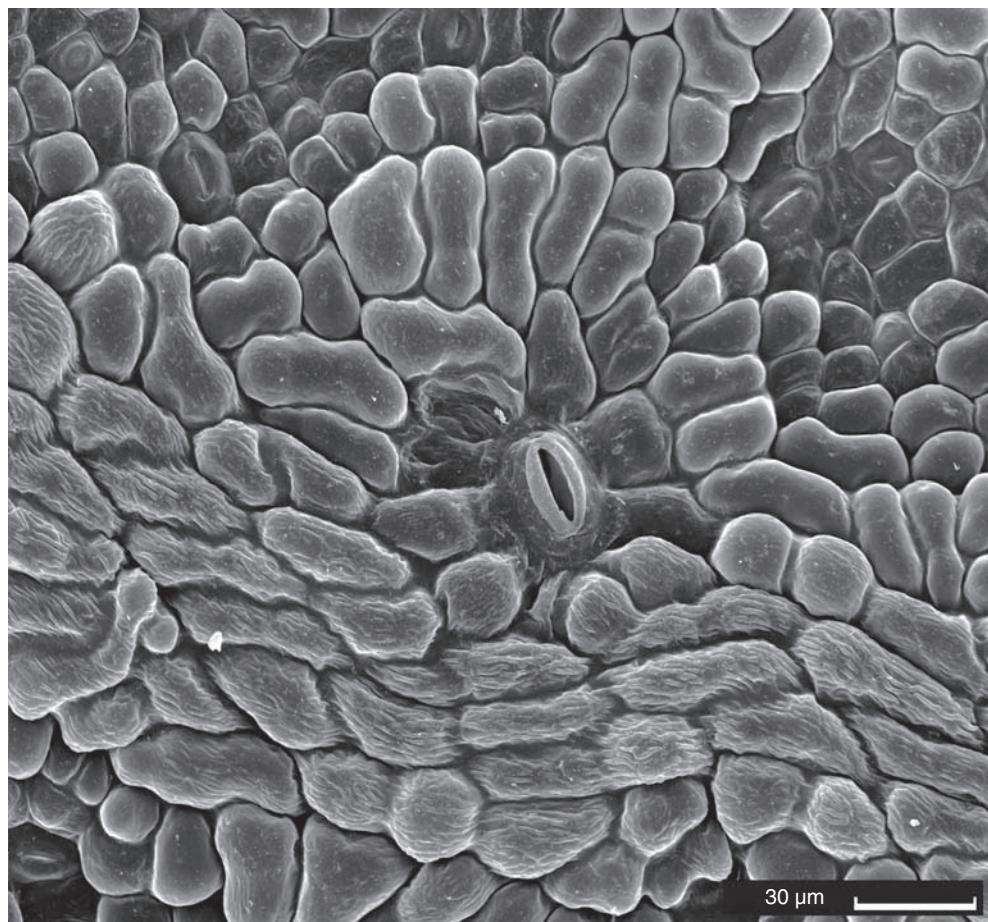


Fig. 13. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, stoma-like hydathode opening on the border of a blind vein; the sheath cells are finely striate on the inner wall, SEM.

numerous radial accessory cells. When on the border of a coastal zone, such hydathodal stomata may involve a few striated vein sheath cells as its accessory cells (Fig. 13). The stomata are confined to the areoles, occasionally intervening the costal zones, scattered and irregularly orientated, with a weak tendency to align the bordering costal cells (Fig. 14c, d). Contiguous stomata are infrequent, found near the veins and usually transverse to the costal cell files.

The stomata vary in size and configuration of accessory cells, forming two not always clearly delimited types: (1) the ordinary stomata, confined to the intercostals areas, and (2) the giant stomata associated with the blind veins and hydathodes. The ordinary stomata are anomocytic, with guard cell about 25 – 30 μm long. They tend to be slightly sunken, with thick pavement cells bulging over stomatal pits that are somewhat angular, exposing about six small irregular thin-walled subsidiary cells. Most ordinary stomata are monocyclic, but in few cases there are two or more encircling cells of the same aspect. The giant stomata are 1.5 – 2 times larger, amphicyclic, with irregular number of small subsidiary cells, some of which are occasionally paracytic, and a greater number of radial encircling cells of unequal length, sometimes arranged in two circles. The giant stomata developing over blind veins acquire hydathode characteristics.

Hydathodes strongly affect the patterning of ordinary stomata, which encircle the opening or spread in radial files away from it, an arrangement probably inflicted by the auxin maxima associated with hydathode formation (more on this in the discussion below).

LEAF GLANDS

A remarkable feature of *Cercidiphyllum* leaves is constant presence of marginal glands that are less conspicuous in mature leaves than in vernate leaves, including the leafy pherophylls. The excessively developed mushroom-like apical glands appear on leaf primordia and are soon followed by somewhat smaller subapical glands. The juvenile clusters of decussate leaves are ornamented by garlands of lustrous glands that appear shortly stalked. At anthesis, the leaves are serrate, with glands sessile on marginal teeth.

The well-developed glands are hemispherical or low dome-shaped, smoothly rounded, some with a central knob (Plate IX, figs. 1 – 3). They consist of an opaque collar-like basal part composed of small polygonal epitem cells supporting the transparent globular to conical gland body, which is formed of long vertically aligned or somewhat spreading thin-walled columnar cells, some with dark content. The roof is paved by polygonal end walls of columnar cells, with small intercellular spaces at three cell joints (Plate IX, fig. 1).

Each gland is supplied by a short offshoot of intramarginal vein. The vascular bundle enters the basal collar ascending through the mass of small cells toward the base of the gland body (Plate IX, fig. 2).

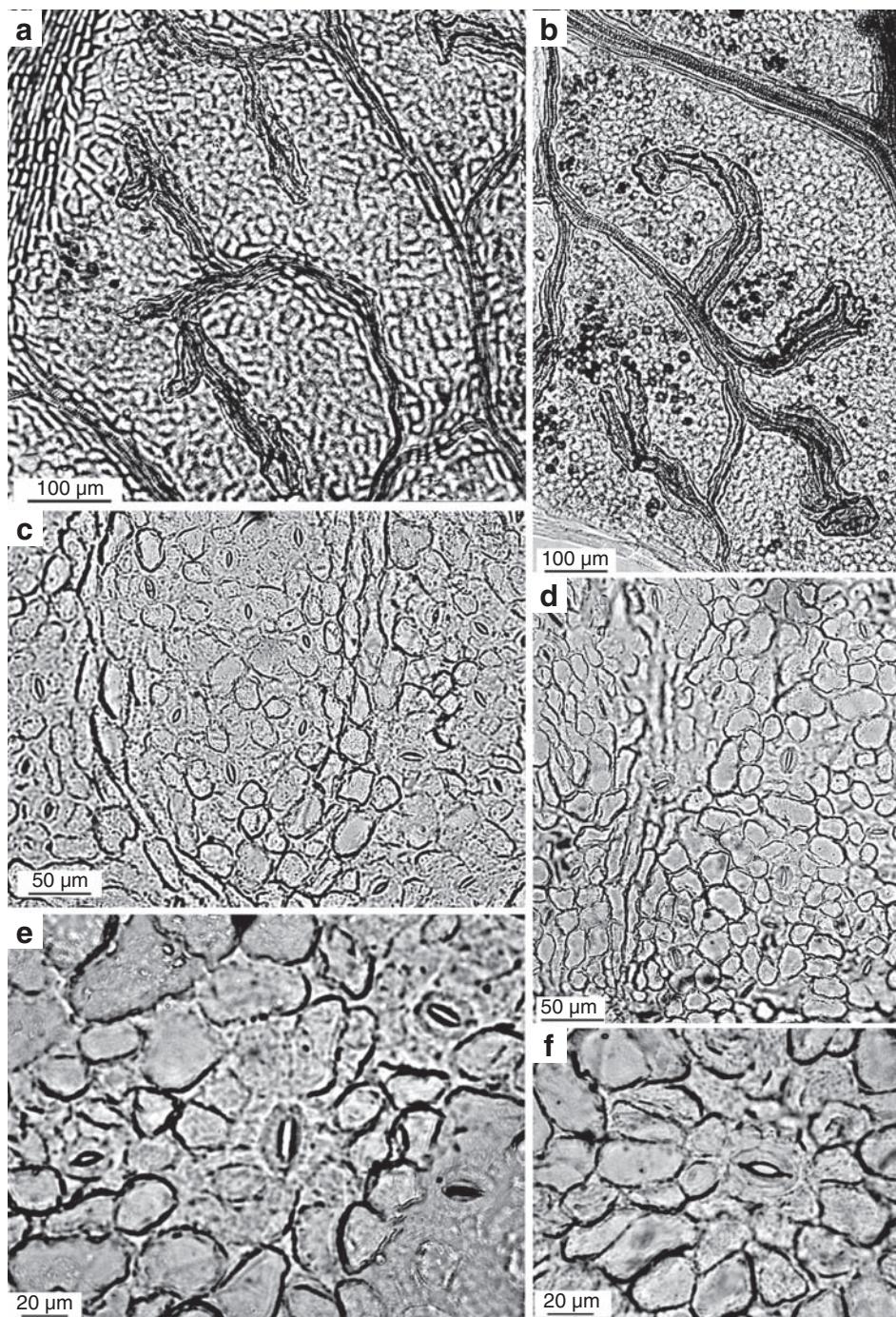


Fig. 14. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU: a, blind vein network; b, blind veins with hydathodes on ends; c, d, stomatal patterns relative to small veins; 5, 6, stomata-like hydathode openings.

FLORAL STRUCTURES

In view of their controversial interpretations in *Cercidiphyllum*, “flower” and “inflorescence” are here avoided as descriptive terms, and a neutral designation “floral structure” is used for the pistillate and staminate fascicles with their subtending bracts. Both species of *Cercidiphyllum* are dioecious, having staminate and pistillate floral structures on different trees. Yet these structures are similarly produced on reproductive short shoots with identical sets of cataphylls and are associated with a solitary leaf (prophyll) that differs in minor details between the genders. Both staminate and pistillate shoots can be replaced by leafy shoots. Despite these morphological and developmental similarities, the androecia and gynoecia are fairly dissimilar, with no conversions or vestiges of opposite gender ever observed in the material at hand or reported in the literature.

The subtending bracts are very much alike in both genders, but in pistillate structures they support individual carpels, whereas in staminate structures their assignment to distinct groups of stamens is questionable. They are arranged in decussate pair, with a tendency of forming a perianth-like whorl and the opposite tendency of the median bracts being reduced. Staminate structures of *C. japonicum* with only two lateral bracts appear distinctly zygomorphic. At anthesis, the anthers are pending outside on their slender filament, but only the twisted whip-like stigmas are produced from the female bud.

A peculiar hitherto unknown phenomenon of floral bracts being replaced by tiny leaves differentiated into leaf blade and stipule is observed in both genders, but is more frequent in pistillate structures. These leaf-like pherophylls are noticeable owing to their apical (sometimes also lateral) glands and differs from the short-shoot leaf in size alone. They are seen at the bud stage, but are scarcely recognizable at anthesis. Intermediate structures show that regular bracts are mainly formed of stipules that are expanded, while the blade is reduced and eventually lost to fusion with stipules, being microscopically discernible as a median thickening of the bract. Less frequently, a reduction of stipules results in a linear or hair-like bract consisting of the primordial leaf blade alone.

STAMINATE STRUCTURES

In androecial buds, the bicarinate cataphyll I is sometimes naturally cleft nearly to the base. The convoluted cataphyll III is seen through the cleft forming a solid calyptra enfolding the androecium as well as the leaf (Plate V, fig. 4). It is tightly wrapped and screwed at the apex or the margins are slightly apart at the base exposing the base of petiole.

In *C. japonicum*, the prophyll is relatively short, reaching to about 2/3 of androecium, but its bilobed stipule is considerably longer, equal to or even exceeding the stamens (Plate X, figs. 1, 2; Plate XI, fig. 3). The androecium is typically subtended by two lateral bracts accentuating zygomorphy of staminate structures. The pherophylls are membra-

nous, decurrent, with a flabellate and irregularly dentate free portion (Plate X, fig. 1b). The eustele of androecial stalk is concentric or slightly horse-shoe shaped, resolved into distinct traces of individual stamens (Plate IV, fig. 4). The most common number of stamens at the bud stage is 10 to 14. Stamens arise in centripetal order and are irregularly clustered in pairs or trios. The filaments are stout and slightly angular at this stage, much shorter than anthers that are fully developed before elongation of filaments, showing a protruding connective that is longer relative to the thecae than in mature stamens. Some anthers are laterally slit in bud already. Aberrant 2, 3 and 5-sporangiate stamens occur in both peripheral and central groups.

A few hair-like processes of various lengths protrude between the bracts (Plate XI, figs. 1 --3). Topologically they correspond to stamen filaments, but some arise at the level of the lateral bracts.

In *C. magnificum*, the androecial buds of about the same developmental stage differ in smaller leaf stipules with hair-like tips. The androecia are considerably longer than the prophyll. The stamens are at least twice more numerous than in *C. japonicum* of a comparable androecial age. Four bracts are as common as two bracts, and all may be nearly equally developed, but the lateral are at least slightly larger. They arise at somewhat different levels, which does not prevent from forming a perianth-like whorl (Plate XII, figs. 1, 2). Yet occasionally the internodes between the lateral and median bracts are as long as the androecial stalk itself (Plate XII, fig. 3). It was also noticed that an occasional stamen may arise from the bract whorl at the level of the lateral bracts.

Abnormal bracts and sterile appendages. Abnormal bracts and hair-like processes are often associated with defective stamens. Occasional stamens or groups of stamens show developmental abnormalities, such as reduced filaments or undifferentiated anthers, perhaps inflicted by bacterial infection or arthropod damage.

Defective stamens dry out or the anthers are abscised leaving filament stumps callous on ends (Plate XIII, figs. 1, 2). There is a tendency of such pruned stamens being wrapped by a subtending bract. Alternatively, additional bracts and sometimes hair-like processes develop in association with pruned stamens. (Fig. 15).

Leaf-like bracts. In occasional staminate structures, the androecial bracts appear as tiny leaves differentiated into leaf blade and stipules. Such leaf-like bracts may associate with abnormal stamens. Plate XIV, fig. 3 shows a peripheral group of stamens that are conspicuously shorter than the rest. They are subtended by a leaf-like bract, with a prominent apical gland and with relatively large stipules enfolding short stamens. In another aberrant staminate structure (Fig. 15), the bract enfolding a group of short stamens looks much like the rest, but the median tooth is more prominent and bears a vestigial gland. In another example (Plate XIV, figs. 1, 2), a bract associated with a group of short stamens is not so strikingly different from the rest, but still have a more prominent median tooth with a vestigial gland on it.

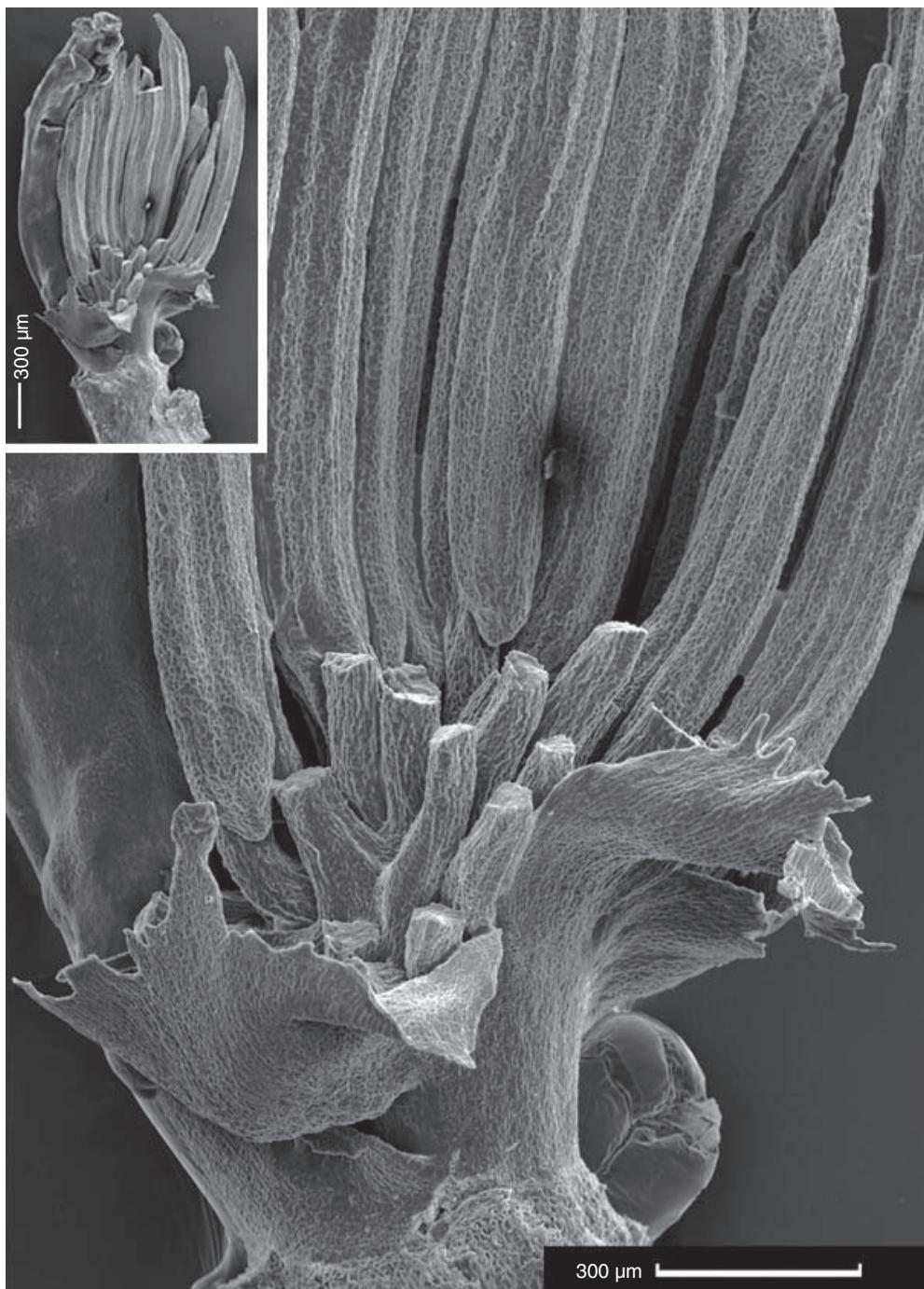


Fig. 15. *Cercidiphyllum magnificum* Nakai, Kew, androecium with a group of pruned stamens enfolded by a leaf-like bract with a reduced apical gland, SEM.

Bracts at anthesis. At anthesis, the androecium grows faster than the leaf and is fully exposed when the leaf is still partly wrapped in cataphylls (Plate XV, fig. 1). In *C. japonicum*, the androecium is raised on a very short stalk with a pair of membranous decurrent bracts spreading in transverse plane (Fig. 16). The bracts arise at the slightly different levels and, although both laminar, are somewhat asymmetrically developed, one flabellate and dentate, the other ovate and entire. There are minute stipule-like basal prominences and a semicircular adaxially concave area between them representing a residual leaf blade of a vestigial leaf-like bract. It is traversed by a median vascular bundle that splits into one-tracheid thick strands (Fig. 17).

The filaments are coalescent and distally divided into two unequal arms, but this is due to their stickiness (although similar drawings can be found in literature suggesting to their authors separate “male flowers”).

In another staminate structure from the same tree, the stamens are pending from inside the cataphyll III, their filaments still interwoven, but some are separated. Twenty eight stamens are counted. The anthers are basifixated with the thecae separated at the attachment point as prominent basal auricles. The connective is apically produced. Some anthers are latrrosely opened as is typical of the genus.

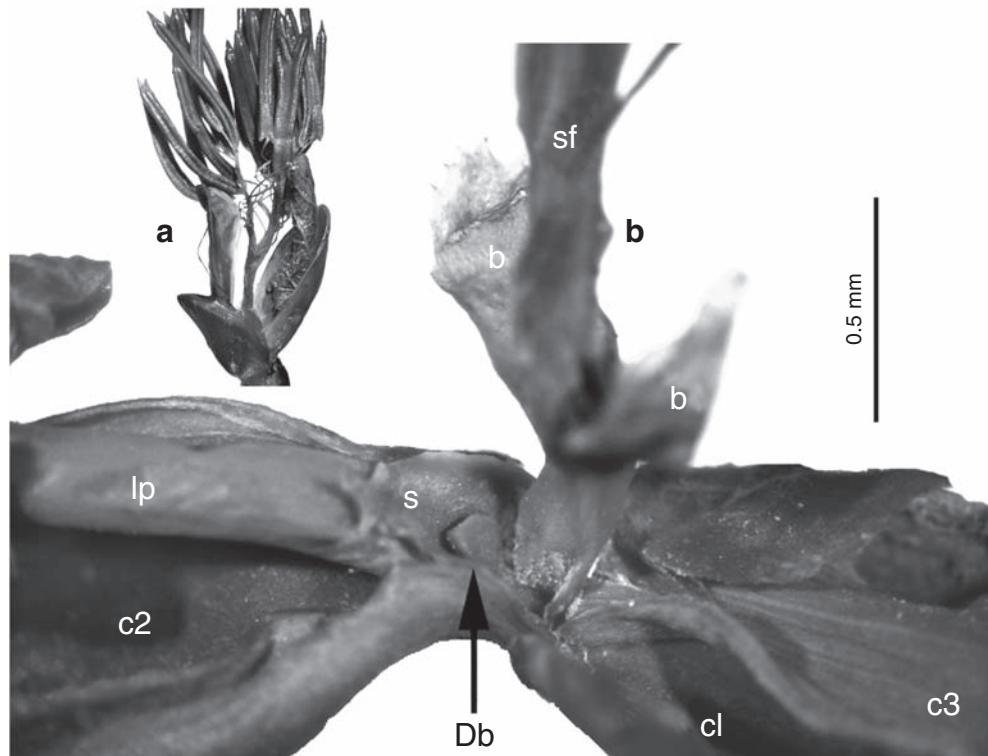


Fig. 16. *Cercidiphyllum magnificum* Nakai, BIN: a, b, staminate structure at anthesis, raised on a short pedicel with subtending bracts at different levels; stamens divided into two clusters by their interwoven filaments (b, bracts, c1 – c3, cataphylls, Db, dormant bud, lp, leaf petiole, sf, floral stalk).

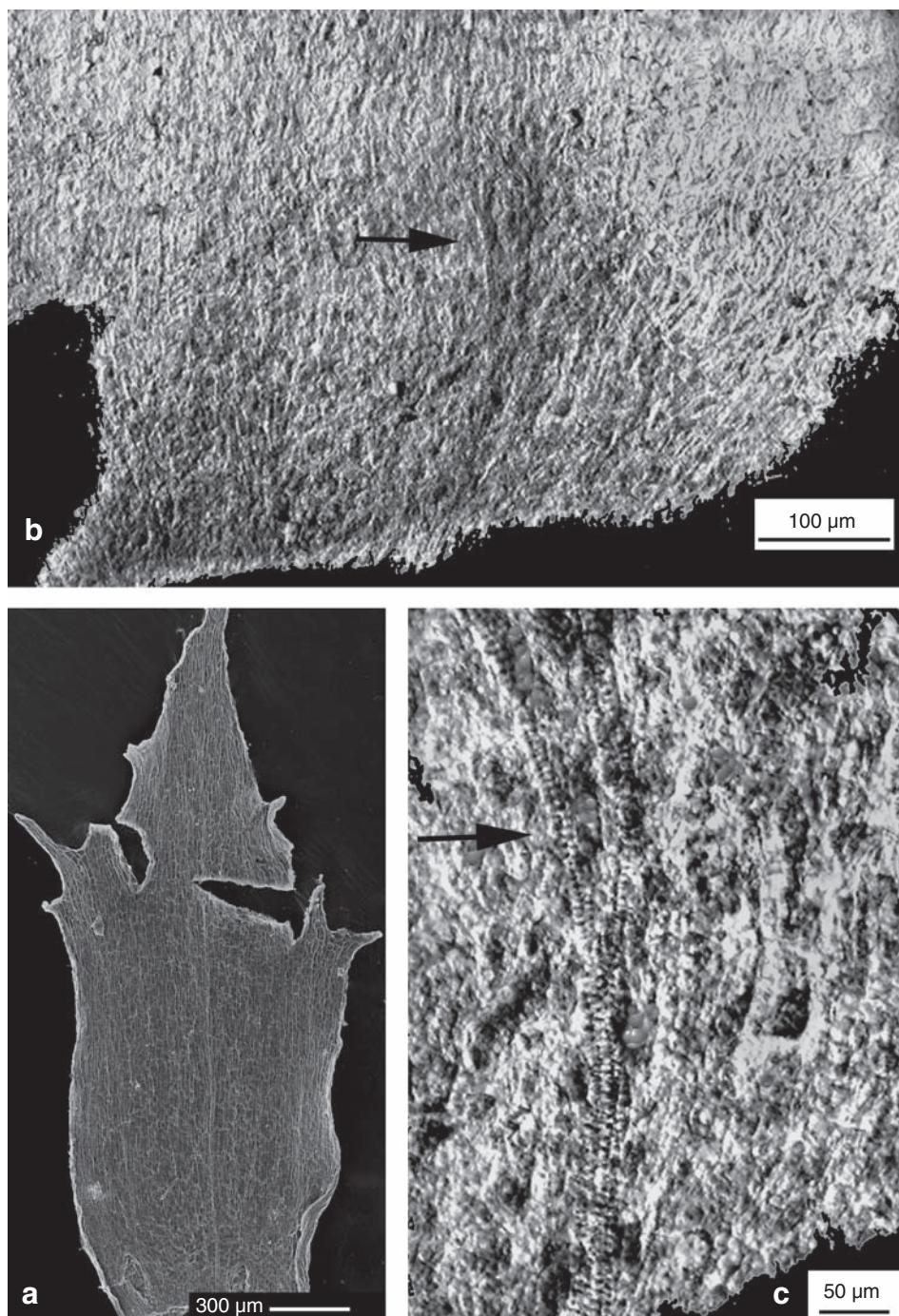


Fig. 17. *Cercidiphyllum magnificum* Nakai, BIN, pistillate bracts: (a) bract shape, SEM, b, cleared bract with a thickened area and small lobes at base; c, median vascular bundle of spiral tracheids.

POLLEN GRAINS

The pollen grains of *Cercidiphyllum* (Praglovsky, 1974; Endress, 1993) are traditionally described as tricolpate, but are in fact triporate. Under SEM, the unacetolized grains are globose, about 17 – 19 µm in diameter, with three symmetrically arranged equatorial pores. No significant difference was found between naturally and point dried grains, although the latter may appear slightly larger. The polar aspect is broadly trilete, smooth or irregularly folded. The arms of mesoporum extending between the pores are transversely plicate. The pores occupy most of the lateral facet, prominent, hemispherical in profile, circular in outline, about 6 – 7 µm in diameter, or somewhat lalongate, about 6 – 6.5 x 7 – 7.5 µm wide, bordered by a shallow groove, which is traversed by the plicae of the mesoporial exine (Fig. 18).

The sculpture of mesoporial exine is indistinctly verrucate – scabrate, with minute perforations. The porous membrane is protruding, microgranulate. Orbicules are occasionally present.

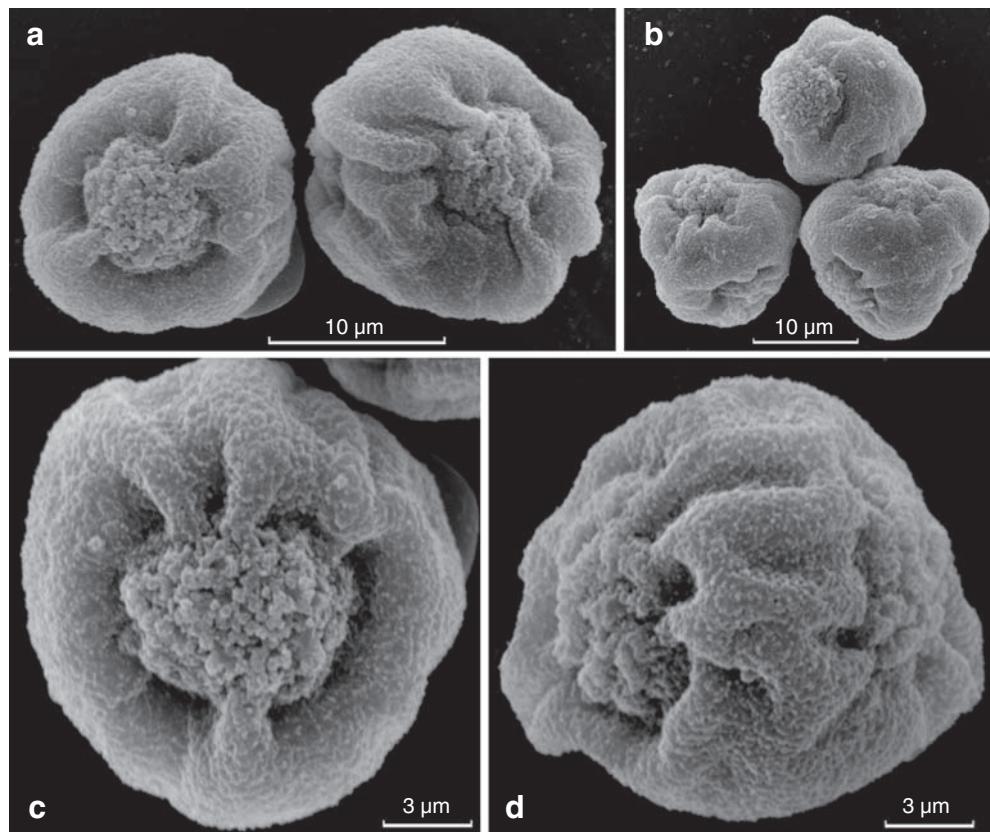


Fig. 18. *Cercidiphyllum magnificum* Nakai, BIN, triporate pollen grains: a – d, microgranulate pore membranes and the coarsely plicate mesoporial areas, SEM.

Transmission electron microscopy of pollen wall (sections and photographs by Maria Tekleva) shows four exinal layers (Fig. 19). The tectum is massive, with short conical prominences, perforated by the widely spaced slender canals. The infratectal layer is slightly thicker than tectum, formed by irregularly spaced bacula, the massive heads of which coalesce, forming the tectum. The bacula are variably strong, rooted in the foot layer, rarely unrooted, pending from the tectum, some with a slender stalk or otherwise reduced to a low knob. Spaces between the bacula are partly filled with an electronically sparse material. The foot layer is nearly as thick and as dense as the tectum, uniformly

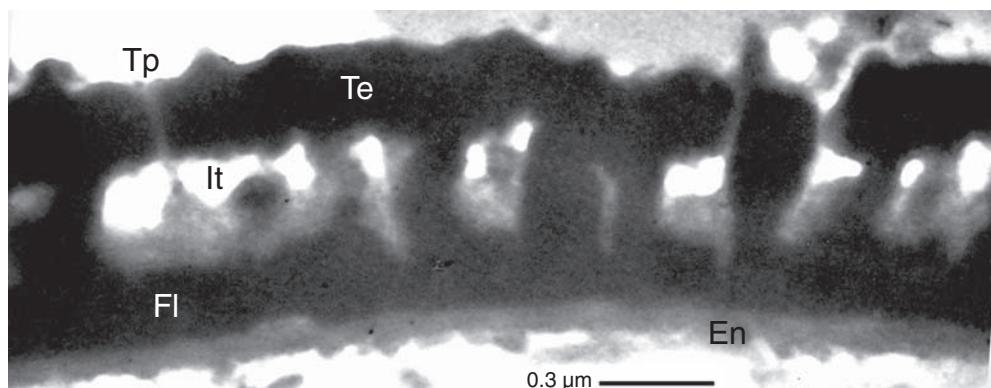


Fig. 19. *Cercidiphyllum magnificum* Nakai, BIN, pollen grain ultrastructure, mesoporum (T, tectum, Tp, tectum pore, It, infratectum, Fl, foot layer, En, endexine), TEM.

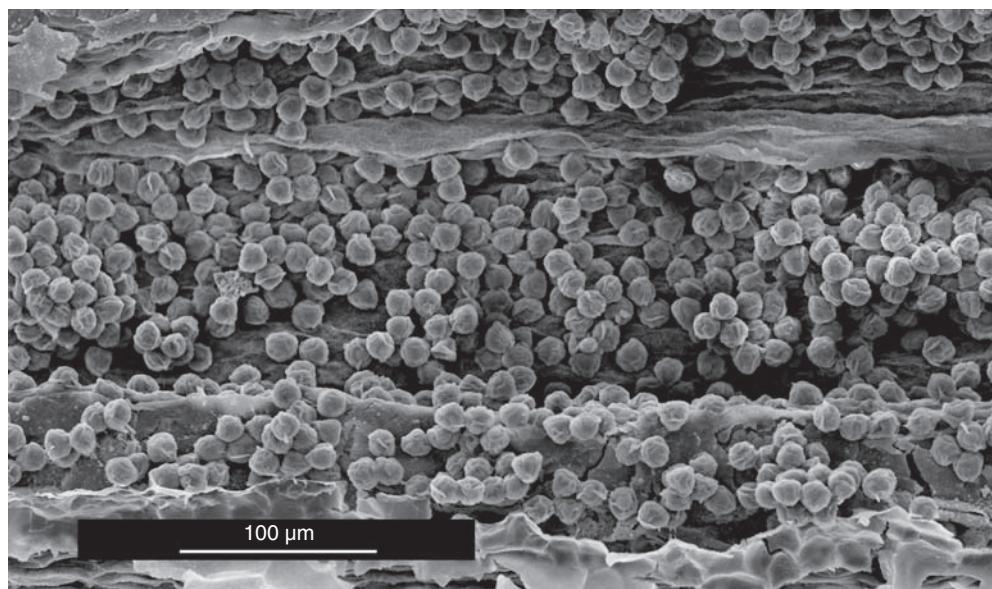


Fig. 20. *Cercidiphyllum magnificum* Nakai, BIN, pollen *in situ*, SEM.

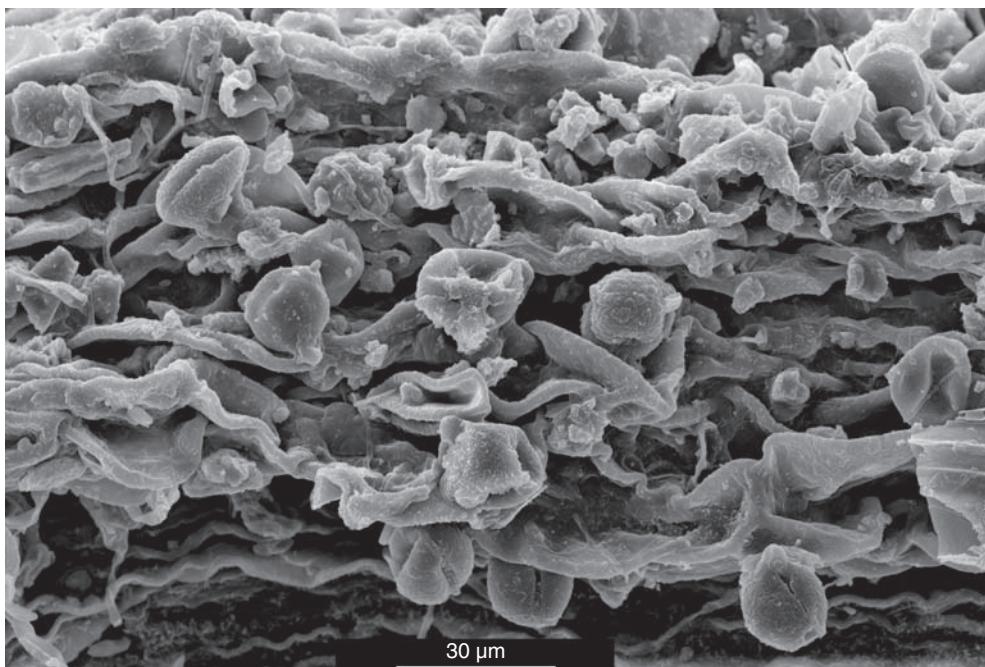


Fig. 21. *Cercidiphyllum magnificum* Nakai, BIN, pollen on stigma, SEM.

developed over the non-apertural regions. The sexual layers gradually wedge out toward the aperture. The endexine is appreciably thinner and less dense than foot layer, its interior border is irregularly indented.

The anthers dissected shortly before anthesis contain masses of well separated pollen grains, none of which germinate, but many showing prominent radial folds at which the exine would split at germination (Fig. 20). On stigmas, pollen tubes grow amidst the sinuous cuticular ridges covered with minute warts (Fig. 21). Pollen walls of germinate pollen grains often show longitudinal slits over the radial folds that may look like germination colpi, and the empty exines are irregularly infolded.

PISTILLATE STRUCTURES

The pistillate structures of *Cercidiphyllum* are commonly interpreted as consisting of two or seldom three decussate pairs of carpels subtended by membranous bracts that in the distal pairs are more or less reduced. However, the assumed pair wise disposition of the bracts is compromised by the arrangement of their attachment scars that are all at the slightly different levels, suggesting a compressed spiral rather than decussate phyllotaxy.

The numbers of carpels vary between geographical populations (and possibly between individual trees, but this was not checked in this study). Thus, in *Cercidiphyllum japonicum* from the Moscow University Botanical Garden, 2 – 3- carpellate gynoecia are fairly frequent, as are the cases of incongruous numbers of carpels and bracts, such as of bicarpellate gynoecia with three bracts or tricarpellate gynoecia with two bracts (Fig. 22). Such relationships occur at the primordial level already. In *C. japonicum* from the Main Botanical Garden, Moscow, 5 – 6-carpellate gynoecia are more frequent than the 4-carpellate, but only four bracts are normally developed (Plate XVI, figs. 4, 5). The distal carpels either lack bracts or are associated with a minute hair-like appendage (Fig. 23).

In *C. magnificum* from the Botanical Garden, St. Petersburg, four-carpellate gynoecia are a statistical norm. Each carpel is subtended by a bract, if but reduced to a hair-like process. Typically there is no more than one such reduced bract per gynoecium (Fig. 24). Exceptional gynoecia have fully developed empty intrafloral bracts. In *C. magnificum* from Kew Botanical Garden, 5-carpellate gynoecia are the most common.

Carpels are arranged in a whorled cluster, showing a transitional spiral – decussate disposition characteristic of all metamerous organs of the genus. Normally, all carpels of a fascicle are equally developed. In bud, they are already differentiated into a conical



Fig. 22. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, pistillate structures in bud: a – c, two and three-carpellate gynoecia with unequal number of subtending bracts, SEM.

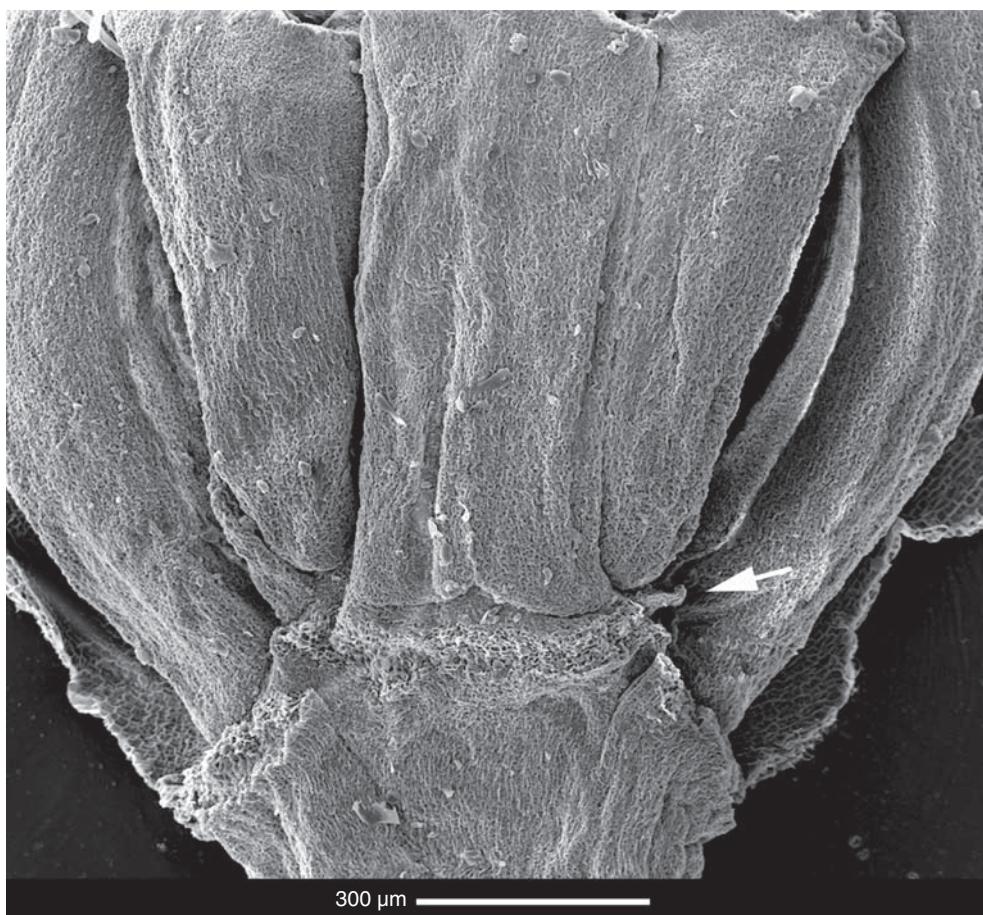


Fig. 23. *Cercidiphyllum japonicum* Sieb. et Zuc., MBG, 6-carpellate gynoecium at anthesis, outer bracts removed, showing a hair-like process at the base of a distal carpel (arrow).

ovary and a somewhat longer stigmatic blade, with a constriction between them, which is extended into an elongate stylodium later in development. The stigmatic part is long pointed, strongly contorted before anthesis, later exserted as a whip-like stigma. Both adaxial and abaxial suture ridges extend whole length of the ovary and the latter continues into the stigmatic blade. Sectioned carpels appear adaxially keeled, abaxially strongly convex and cleft, revolved towards the abaxial side, with supervoluted (doubly coiled) margins forming an intrusive placenta. The ovules are spreading to both sides of the placental ridge, slightly reflexed (further considered below, see Fig. 28).

In 4-carpellate gynoecia of *C. magnificum* from the Botanical Garden, St. Petersburg, the carpels may seem to be arranged in decussate pairs, but actually all arise at somewhat different levels. In 6-carpellate gynoecia of *C. japonicum* from the Main Botanical Garden, Moscow all carpels are nearly equally developed forming a radial fascicle, in which the



Fig. 24. *Cercidiphyllum magnificum* Nakai, BIN: 4-carpellate gynoecia at anthesis, with median bracts represented by a short (a, d) or long (c) process or reduced to cushion (b).

lateral and median pairs are not clearly differentiated (Plate XVI, figs. 4, 5). This disposition agrees with a compressed spiral rather than decussate arrangement. The carpels are not uniformly orientated, their ventral side facing the bract or turned toward the adjacent carpel. Despite the repeated claims to the contrary, torsion must have occurred during development.

Carpels at anthesis appear sessile or indistinctly stipitate, elongate-ovate, recurved, adaxially grooved, abaxially convex, laterally somewhat compressed. Placenta is marked by a low longitudinal ridge on the abaxial side. The fertile portion of the carpel is much shorter than its stigmatic extension. The latter is shallowly plicate, with a strong median ridge decurrent upon the placental side of the ovary facing the subtending bract, but on many occasions carpels are turned their lateral facet toward the bract. Cleared carpels show a double vascular strand opposite the placental ridge and a pair of slender lateral strands of spiral tracheids at a short distance from the ridge (Fig. 25).

Leaf-like carpelodes. Fig. 26 represents a 3-carpellate gynoecium of two lateral and one median carpels. One lateral carpel is subtended by a broad scaly bract, the other by a leaf-like bract with an apical gland. The median bracts are smaller than the lateral. The missing second median carpel of a pair is replaced by a bulky tubular structure crowned with a massive, excessively developed apical gland. In its shape and size, this leaf-like



Fig. 25. *Cercidiphyllum magnificum* Nakai, BIN: cleared carpel wall with a ventro-lateral vascular bundle.

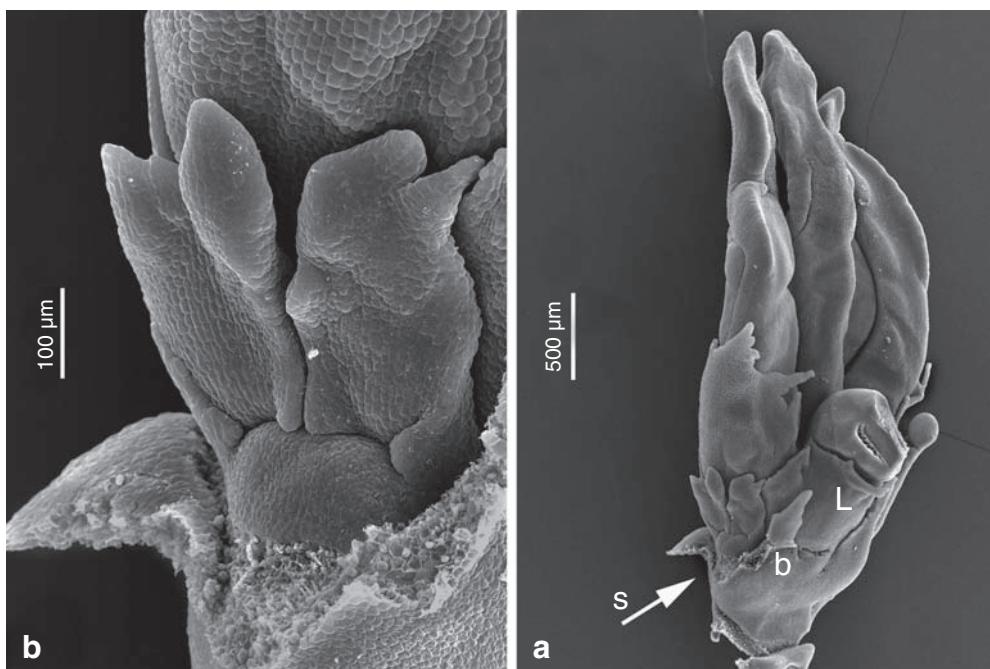


Fig. 26. *Cercidiphyllum magnificum* Nakai, Kew: a, 4-carpellate gynoecium with one carpel transformed into a leaf-like structure (L) with two bilobed stipules (arrow), subtended by a small bract (b); b, carpellode stipules with a hemispherical protrusion (blind bud) at base, SEM.

structure corresponds to a vernate short-shoot leaf, being much larger than the leaf-like bract. Moreover, it is subtended by a normal, if but somewhat reduced, scaly bract. At the base of the massive tube, there are two stipules appearing as slightly concave scales, basally auriculate, apically bifid, with thickened conical points. A knob beneath the stipules may represent a blind renovation bud. Thus, the leaf-like structure replacing the anterior median carpel of a pair, is situated opposite the short-shoot leaf and is symmetrical to the latter on account of stipules and renovation bud.

Occasional delicate scaly structures occurring at the base of carpels inside the bract whorl may represent vestigial carpel stipules of the kind described above. Although in such cases the carpels are not transformed into leaves, the vestigial (rudimentary) stipules may indicate a potential transformation. They are observed in the fossil *Eocercidianthus* as well (below).

Leaf-like bracts. Tiny stipulate leaves developing in the position of subtending bracts are observed in bud and are more frequent in *C. magnificum* from Kew than in the sampled trees from the other places. They are recognizable by a prominent leaf blade, which is relatively thick, involute, and shows a conspicuous apical gland or also a few smaller subapical glands. The stipules are membranous, varying in shape and distinctness from

small outgrowths at the base of the blade to the broadly flared lobes, dentate and considerably larger than the blade. Transitional morphologies between the leaf-like blades and standard pherophylls are bracts, in which the distinctness of the leaf blade and stipules is nearly lost in fusion or the blade is much reduced, the stipules forming most of the bract.

In a few cases, a gynoecium of four carpels is subtended by four leaf-like bracts (Plate XVII, figs. 1 – 4). The carpels are almost as long as the short-shoot leaf, tightly appressed to each other, with contorted stigmas. The leaf-like bracts are developed in both lateral and median positions (one facing the leaf is not shown on the photographs), although the lateral ones are somewhat larger. They are strongly involuted into a tube, the miniature copies of a likewise involuted short-shoot leaf, having prominent hemispherical apical glands (scars of such in Plate XVII, figs. 3, 4) and a few less distinct subapical ones, proportionally smaller than in the short-shoot leaf. Stipules of the short-shoot leaf protrude between the carpels and the lateral leaf-like bracts. The abaxial leaf-like bract is more delicate and with a less conspicuous apical gland.

In Plate XVIII, fig. 1, the gynoecium is partly enfolded by the leaf stipules and shows four carpels with stigmatic parts not yet extended. A lateral bract in front view has a narrow revolute central blade about 2/3 of carpel length, crowned with a prominent hemispherical gland. The stipules are the symmetrically developed triangular basal lobes onlapping a median bract. The opposite lateral and both median bracts are the standard pherophylls.

In Plate XVIII, figs. 3, 4 five carpels are at a somewhat more advanced developmental stage. A lateral bract on the left side has a relatively short blade with a reduced apical gland. The stipules are broadly fused with the blade, distally free, attenuate and flexed on ends.

In Fig. 27a, b, a gynoecium of six carpels, four of which are turned their placental sutures outside, has a well developed lateral leaf-like bract with stipules equal to the central blade. On the opposite side there are two adjacent leaf-like bracts with reduced stipules. In the posterior view, this gynoecium clearly shows the protruding lateral leaf-like bracts wrapping the peripheral carpels with their tiny stipules

In Fig. 27c, d, the blades still maintain their identity in the lateral leaf-like bracts, although the larger part of bracts is formed of the stipules. In a number of instances (Plate XIX, figs. 1 – 3), lateral pherophylls have lost their apical glands and other leaf-like characteristics, are overtopped by and partly fused with the stipules, but are still recognizable from the ordinary papery bracts.

Bracts at anthesis. At anthesis, the floral stalk is distally expanded into a slightly convex receptacle with prominent shoulders (cushions), at which the bracts are attached. The fully developed bracts are lingulate or flabellate, membranous, with irregular distal processes. It can be noticed that lateral shoulders are not quite symmetrical and do not make a straight line across the receptacle, one being at least slightly raised above the other.

The lateral bracts are fully, if but somewhat unequally developed, decurrent and basally fused to the stalk, free and flaring above, adhering the carpel wall or slightly spreading. The median bracts are more variable, some equal to the lateral, the other



Fig. 27. *Cercidiphyllum magnificum* Nakai, Kew, pistillate structure in bud: a, b, abaxial and adaxial views of a 5-carpellate gynoecium with leaf-like lateral bracts; c, d, lateral leaf-like bracts of a narrow blade and broad stipules (b, standard bract, L, short-shoot leaf, l, leaf-like bract, S, short-shoot leaf stipule, s, leaf-like bract stipule).

much reduced. They arise at the slightly different levels, somewhat, or even distinctly, above the lateral bracts, but in contact with them or even coalescent at base, forming an irregular whorl (Plate XX, figs. 1, 2, 5).

Yet in about half of gynoecia examined the median bracts of a pair are markedly different, one much smaller than the other or one flared and the other linear to hair-like (Plate XX, figs. 3, 4; Plate XXI, figs. 1 – 6). When replaced by linear processes they may be long and flexible or minute, barely raised over the basal cushion.

Plate XX, figs. 1 – 4 show a repeatedly observed situation, when one of the median pherophylls is a laminar bract, while in the opposite bract the free portion is reduced or substituted by an elongate, hair-like appendage arising from the cushion. Such hair-like structures are not vascularized. In 5 – 6-carpellate gynoecia, the inner phyllomes are either not developed or appear as hair-like processes (Fig. 23). If lateral bracts are connate at base, the reduced median bracts occur behind the border of their contiguous cushions (Plate XXI, fig. 4). Otherwise they are included in the border (Plate XXII, fig. 4).

The leaf-like bracts are not so conspicuous at anthesis as in early development, the leaf blade – stipule differentiation being lost or occasionally vaguely discernible as a linear appendage with an apical gland and two minute teeth (stipules) at base (Plate XXI, fig. 3).

Supernumerary bracts. A single gynoecium of *C. magnificum* in our material is aberrant in having two supernumerary empty bracts inserted between the carpels (Plate XXII, figs. 1 – 3). It has four carpels, all subtended by well-developed laminar bracts. The median bracts are insignificantly smaller than the lateral, one contiguous with the lateral bracts at base, forming a somewhat asymmetrical whorl, the other basally constricted. The two empty bracts are distinctly separated from the external whorl being inserted at a higher level and situated on both sides of a median carpel, which is endowed with its own subtending bract on the outside (Plate XXII, fig. 3). The intrafloral bracts are of about the same shape and dimensions as the external bracts.

PLACENTA AND OVULES

The juvenile carpels are horse-shoe-shaped in transverse section (Fig. 28), the adaxial lobe strongly protruding and invaginated, the margins supervoluted and fused at the back-to-back contact of the coils at some distance from the edge. The placental ridge is formed over the fusion zone as a production of the fusion meristem. The abaxial wall increases and swells over the cleft, and the ovary grows as a tubular structure. The ovules are distichously arranged, one row slightly above the other, with a fusion meristem bridging the gap and later developing into a solid ridge intruding the locule. The ovules appear on the marginal lobes that form the outer integuments later in development. They have a homogeneous cell structure from which a globular nucellar body subtended by the collar-like inner integument is differentiated.

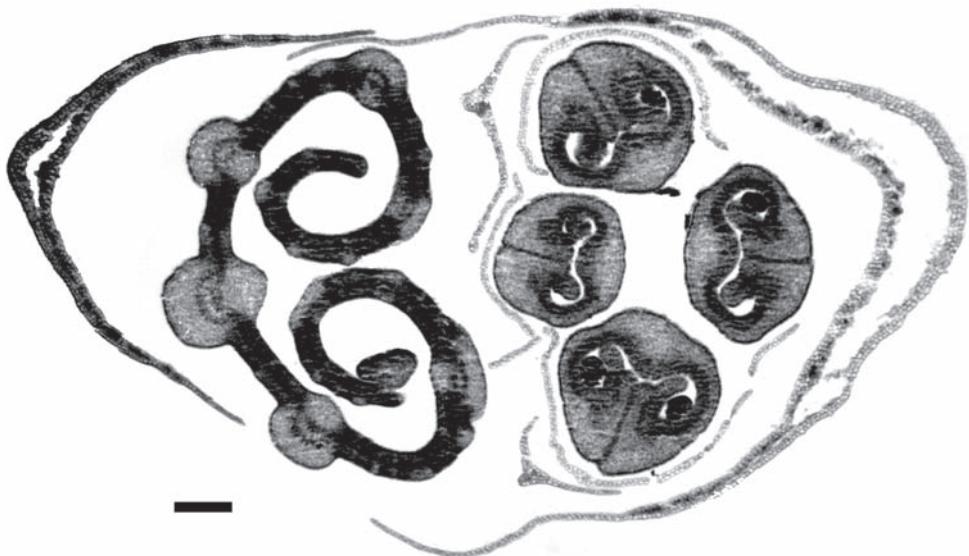


Fig. 28. *Cercidiphyllum magnificum* Nakai, Kew, pistillate structure in bud: transverse section showing the vernate prophyll and similar features in the carpels with primordial ovules. Scale bar = 200 µm.

In the carpels extracted from the floral buds, the locule is sterile over a short distance basally as well as apically (Plate XXIII, figs. 2, 3; Plate XXIV, fig. 1). The transversely striate endodermal lining of narrow tabloid cells is evident at this stage. The placenta appears as a pectinate structure with marginal lobes developing into ovule primordia. The midrib and lateral extensions are invaded by vascular strands (Plate XXIII, fig. 1; Plate XXIV, fig. 3). The developing ovules are distichous, the two opposite rows nearly converging over a shallow groove on the inside face of placenta. They are about 15 per row, but some placentas may have 16 ovules in one row against 13 in the other. The ovules are distally decreasing, but a few basal ones may also be reduced.

The meristematic lobes are elongate-ovate or slightly obovate, apically rounded, forwardly inclined, decurrent, straight or somewhat curved near the apex where differentiation of the nucellus and inner integument commences with concentric cell alignments at both poles. In transcurrent light, a one-layered epidermis with dense cross walls is clearly differentiated from the darker inner mass of longitudinally filed cells. The foci of concentric cells mark the apical nucellar site and the incipient inner integument near the base (Plate XXIV, figs. 2, 3).

At anthesis, the locule is narrow elongate, tapering to the apex, truncate at base, lined with a delicate transparent endodermal layer. The basal 1/5 of the locule and the apex are sterile, the rest is filled with a thick intrusive placental ridge bearing two rows of ovules (Plate XXV, figs. 2 – 4).

The placental ridge can be seen by opening the carpel over the abaxial suture (Plate XXV, fig. 1). It is externally protruding as a stout rib with an indistinct median channel. The adaxial aspect is plane with a median groove between the two concrescent vascular bundles. An occasional ovule may arise laterally on the ridge, but normally the ovules are spread in two adaxial files along the median groove. They are dense, 10 – 14 per file, alternate and occasionally crisscrossed, ascending at acute angle, decurrent and apically upcurved. Before the integuments are differentiated, the ovules appear as stalked glands tightly appressed and overlapping over the median groove, giving the placenta a transversely plicate leaf-like aspect (Plate XXV, fig. 5).

At a somewhat more advanced stage, individual ovules are separated by narrow sinuses, showing a hemispherical nucellus in line with chalaza or slightly upturned. Both integuments are distinctly marked, the inner one appearing as a low collar, which is slightly raised on the posterior end (Plate XXVI, figs. 2 – 4). The outer integument is a relatively massive goblet-like asymmetrically bilobed structure, with the anterior lobe depressed and rounded, the posterior protruding, upcurved and pointed, occasionally flared as a miniature leaf lobe (Plate XXVI, figs. 1, 3).

The ovules are vascularized by slender forking veins that depart from a placental bundle, enter on the posterior side of the ovule and curve toward the base of the nucellus or else run to the sinus sending arms to integumental lobes of both adjacent ovules (Plate XXVI, fig. 5; Plate XXVII, fig. 3). The vein pattern is quite similar to that supplying the marginal glands of juvenile leaves (Plate IX, figs. 3, 4).

FRUIT AND SEED

On reproductive short shoots, the fruits are radially diverging into a narrow vortex, or, as a result of basal torsion, are flabellately spread in one plane, their sutures all turned to one side (Table XV, fig. 2). They are hard follicles crowned with stout, reflexed stylopodia, the stigmas sometimes persisting. Basally, the fruits are shortly inconspicuously stipitate, almost sessile, slightly expanded and callous, with their subtending bract cushions protruding as low rigid collars, smoothly rounded or occasionally lobbed, reddish brown or yellow, brighter than the fruits, which are dull dark brown with glistening bluish gray waxy patches. The stylopodia are ridged like the fruit stalk and the back of the follicle is strewn with minute lenticels (Plate XV, fig. 4). These stem-like characteristics are probably conferred on the fruits with lignification of the wall. The flanks are covered with finely ramified striation. The opening suture is strongly convex and grooved, often with an undulate placental ridge persistent between the margins.

Seeds develop from orthotropous ovules that are precocious at fertilization and keep growing until dispersal, taking up with expansion of the locule. In fruit, seeds are lumped in two masses stuck to the wall of the locule.

Seeds of *Cercidiphyllum* are usually described as anatropous with a one-sided chalazal wing, which is not normally the case. The most typical situation (Plate XXVIII, fig. 1) represents an elongate samara with a bilateral wing. The chalazal lobe is pointed, the micropylar irregularly truncate. The basal margin is convex, smoothly arched, involving hilum, a callous elliptical scar (a hole in transparent seed) situated near the middle or somewhat displaced toward the micropylar end. The dorsal margin is nearly straight, with a shallow concavity above the seed body, thickened along the chalazal lobe, irregularly undulate along the micropylar lobe. The seed body is elliptical, nearly straight or only slightly curved, more convex on the lower (originally ventral) side, with a circular chalazal cap and a shortly protruding micropyle. It is turned obliquely to the long axis of the encircling wing, gently inclined or nearly parallel to the hilar scar, the micropyle pointing to the front lobe and slightly reflexed. The body is traversed with sclerenchymous raphe fibres that extend to the end of the front lobe.

The raphal strand departs from the hilum and runs in a broad arch over the chalazal lobe making a hair-pin turn. A weaker arm diverges from the loop and extends short distance toward the chalazal end of the lobe.

A variant of this morphotype (Plate XXVIII, fig. 2) shows a crescent-shaped wing with both lobes well developed, but the micropylar lobe somewhat shorter and bluntly pointed. The seed body is more steeply inclined toward the elongate hilum scar, but is separated from it by a broader stripe of wing, while on the opposite side the wing is uninterrupted, but quite narrow over the chalaza. Sclerenchymous ridges stretch longitudinally across the seed body, but curve forward over the micropylar lobe. The raphal strand sends a short arm to chalazal lobe as in the previous case.

A seed in (Plate XXVIII, fig. 3) differs in having a long pointed chalazal lobe and a broadly truncate micropylar lobe, whereas the seed body is shifted closer to the hilum, which results in the steeper upcurved sclerenchymous ridges. Plate XXVIII, fig. 4 represents a similar situation, but the wing is spindle-shaped, with dorsal and ventral stripes of nearly the same width. The loop of the vascular strand is acutely pointed, with the short arm nearly median over the chalazal lobe.

An anomalous seed in Plate XXVIII, fig. 7 has nearly symmetrical bilobed wing, shallow convex and shortly interrupted over the chalaza, but broadly convex ventrally, with hilum shifted toward the front lobe. Another anomaly, a seed with one-sided rather shapeless chalazal wing (Plate XXVIII, figs. 5, 6) corresponds to the conventional description of *Cercidiphyllum* seeds as samaras of anatropous polarity and a chalazal wing. The seed body is steeply inclined toward the hilar side, the micropyle reaching to the ventral margin, but far off the hilum. The reverse arm of the vascular loop extends in straight line along the dorsal margin. The micropylar lobe is a narrow fringe over the front side of the seed body. In this rare variant, the wing is obviously underdeveloped. A further wing expansion between hilum and micropyle and over the micropylar end would result in the typical seed morphology, in which the seed body would approach the midline of samara, turning micropyle away from the hilum as in Plate XXVIII, fig. 2.

SUMMARY OF MORPHOLOGICAL FINDINGS

Briefly summarized here are new findings and those contradicting the commonly held opinions on vegetative and reproductive morphology of *Cercidiphyllum*:

- The long shoot – short shoot system ramifies by new long shoots replacing the short-shoot reproductive structures;
- New long shoots produce elliptical foliage leaves. Otherwise all foliage of the branching shoot system is formed of the short-shoot reniform leaves;
- In the reproductive shoot development, the floral stalk and leaf petiole are stem-like eustelic structures produced by unequal dichotomy of the short-shoot axis;
- Of three imbricate – convolute short-shoot cataphylls, the upper one is calyptate, enfolding the floral stalk with a solitary stipulate leaf;
- The renovation bud is sunken in a pit at the base of the short-shoot leaf and is protected by stipule;
- Both androecia and gynoecia are subtended by membranous bracts that in early development are occasionally replaced by miniature stipulate leaves identical to those produced by the leafy long shoots replacing reproductive structures;
- Marginal glands are a prominent feature of all vernate leaves, including the leaf-like bracts. They are formed of columnar palisade cells on a basement of a small-celled epitem, supplied by a short offshoot of intramarginal vein. The glands are shed or reduced in mature leaves that develop a system of leaf blade hydathodes supplied by blind veinlets;
- The stomata are of two size categories, the larger ones associated with hydathodes irregularly amphicyclic, occasionally with laterocytic subsidiary cells;
- The staminate structures of *C. japonicum* are more distinctly zygomorphic than those of *C. magnificum* and differ in fewer stamens and more numerous bracts (four and two, respectively); the associated leaves have larger leaf stipules relative to the leaf blade;
- The stamens develop in centripetal sequence, the peripheral ones separated before differentiation of the central (apical) group. The androecial bracts are not associated with particular groups of stamens except in the case of teratological developments;
- Hair-like processes occasionally arise from inside the bract whorl. Supernumerary bracts and hair-like processes may develop in association with defective stamens and pruned filaments;
- The pollen grains are triporate, with microverrucate – scabrate ornamentation. Pores are covered with a puffed out granulate membrane. The tectum is sparsely microporate, formed of the heads of irregularly spaced bacula. The foot-layer is almost as thick and as dense as the tectum, but endexine is relatively poorly developed;

- The pistillate structures are stalked fascicles of 2 – 6 carpels, spiral-decussate, all attached at the slightly different levels, typically each subtended by a bract, but some lacking bracts or occasional bracts empty;
- In the 4-bracteate gynoecia, the most common situation is one bract of the median pair reduced to a linear process above the basal cushion. In 5–6-carpellate gynoecia, distal carpels are bractless or associated with linear appendages. A tendency of distal bract reduction does not extend to the carpels;
- The carpels consist of a tubular ovary and a shallowly plicate stigmatic extension that is precociously developed in the primordial carpel already. The ovary appears as a vernate leaf with supervoluted margins, coiled toward their abaxial side, the abaxial wall strongly thickened and protruding over the median cleft;
- The placenta develops over the fusion zone of supervoluted carpel margins, appearing as a pectinate lamina with a median ridge and distichous lobes differentiated into free nucellus and collar-like integuments. It is intrusive into the narrow locule lined with a delicate endoderm.
- The ovules are distichous on the inner side of placental ridge, orthotropous in early development, bitegmic. The inner integument is slightly and the outer strongly asymmetrical with protruding posterior lobe. The ovules acquire hemitropous polarity later in development. The ripe seeds are samaras with a bilobed orbicular wing. Raphe loops over the posterior lobe sending a short arm to the wing extremity.
- In addition to the reproductive structure – leafy shoot conversion, there are incidents of naturally occurring subtending bract – leaf and carpel – leaf conversions, evolutionary significance of which will be discussed after description of fossil allies.

6. FOSSIL ALLIES

Reniform serrate leaves are widespread fossils since the Late Cretaceous. They are commonly compared with and sometimes assigned to *Cercidiphyllum*, although other generic names, such as *Populus*, *Cocculus*, *Paliurus*, *Zizyphus* etc. had been also applied (reviewed in Krassilov, 1976). Because of widespread convergence of foliar features, fossil plant classifications presently operate with leaf genera. Morphotaxa are established for other plant organs as well. When different organs of critical taxonomic importance are confidently assigned to one and the same plant, an assemblage taxon of natural affinities can be introduced.

Trochodendroides is one of the most commonly used names for reniform leaves with acrodromous venation, comparable to *Cercidiphyllum*. In the abundant Late Cretaceous and Paleogene plant localities of northern Eurasia and North America, such leaves are repeatedly associated with follicular fruits and racemose or paniculate infructescences assigned to morphogenera *Nyssidium*, *Joffreya*, and *Trochodendrocarpus*. Generic name *Trochodendrospermum* is used for dispersed seeds occasionally found *in situ*. It is fairly probable that these fossils are parts of a plant representing a widespread natural genus or a group of allied genera of Cretaceous and Tertiary angiosperms. Their species content is difficult to define because of extreme polymorphism of both vegetative and reproductive structures. The maximum abundance of these forms is recorded at about the Cretaceous–Tertiary boundary and through the Paleocene.

Brown (1939) has assigned the assemblage genus of *Trochodendroides* type leaves and *Nyssidium* type infructescences to extant genus *Cercidiphyllum*, and subsequent studies seemed to confirm their alliance to the Cercidiphyllaceae, with consequences for interpretation of floral structures in *Cercidiphyllum* (Swamy & Bailey, 1949; Crane, 1984; Van Heel, 1987). Frequent references to this kind fossil material have produced an impression that *Cercidiphyllum* is exceptional among “living fossils” in having extensive fossil record (Endress, 1993; Takhtajan, 2009).

However, despite a general similarity in fruit morphologies, the racemose and paniculate inflorescences (infructescences) of *Trochodendrocarpus* – *Joffreya* group (trochodendrocarpoids) exhibit no significant similarities to carpellate fascicles of *Cercidiphyllum*. In the fossil group, the follicles are spirally arranged with a tendency for pair-vise conjugation and proximal fusion, as in the Hamamelidaceae, never observed in *Cercidiphyllum*, where

the primary arrangement is decussate, transformed into spiral-decussate. The opening sutures of trochodendrocarpoid carpels are facing each other rather than facing subtending bracts, the presence of which is problematic in the fossil forms.

The recently recognized staminate organs of trochodendrocarpoids are strobilliform with spiral bracts, each subtending a flower of numerous stamens (Golovneva, 2006; Krassilov & Kodrul, 2008), finding analogies among the Hamamelidaceae, whereas in *Cercidiphyllum* staminate structures arise opposite the solitary short-shoot leaf and are subtended by a lateral pair (or sometimes also a median pair) of small bracts. In *Alasia*, the stamens at anthesis have short filaments (long filaments in *Cercidiphyllum*). The anthers are dorsifixed (basifixied in *Cercidiphyllum*), introrse (latrorse in *Cercidiphyllum*) and the connectives are only slightly if at all produced. The pollen is tricolporate with long colpi nearly reaching to the poles. Ornamentation of mesocolpia, although of the same general type as in *Cercidiphyllum*, is more closely comparable to the scabrate–canaliculate type characteristic of the Fagaceae (Krassilov & Kodrul, 2008).

Therefore, both pistillate and staminate structures of trochodendrocarpoids are fairly different from those of *Cercidiphyllum* and unlikely as morphological precursors of the latter. They may represent a separate line of angiosperm radiation, of phylogenetic affinities with the Hamamelidaceae, rather than Cercidiphyllaceae (Krassilov, 1976; Krassilov & Fotyanova, 1995).

Moreover, the recently found Turonian inflorescences (Krassilov et al. 2005) are much more *Cercidiphyllum*-like than the geologically younger *Trochodendrocarpus*–*Joffrea* group. The associated leaves *Eocercidiphyllites* are readily recognizable by prominent marginal glands as in the juvenile leaves of extant *Cercidiphyllum*, but lacking or inconspicuous in *Trochodendroides*.

EOCERCIDIPHYLLITES PLANT

Cercidiphyllum-like forms were found in the Gerofit Canyon on the western slope of Arava Valley, a southern extension of the Dead Sea Rift. The plant-bearing deposits are confined to the upper part of the Ora Formation that comprises thick shale sequences alternating with limestones, dolomites and marls. The Middle Turonian (about 90 million years) geological age of the plant-bearing sequence is based on ammonite records below and above the Upper Shale Member (Bartov et al., 1972; Freund & Raab, 1969; Lewy, 1989; Krassilov et al., 2005).

About 50 species are recognized in the Gerofit assemblage belonging to 15 angiosperm orders: the Ranunculales, Nymphaeales, Nelumbonales, Trochodendrales, Hamamelidales, Juglandales, Rosales, Myrtales, and Sapindales of dicotyledons and the Najadales, Pontederiales, Arales, Cyclanthales, Arecales, and Typhales of monocotyledons (Krassilov et al., 2005).

Sedimentological, taphonomic and plant morphological evidence, including the numerical representation of fossil plant morphotypes, their preservation and distribution

over sedimentary facies, revealed a catenic sequence of mangrove, freshwater aquatic, wetland and inland plant communities (Fig. 29). The wetland plant communities are of a tropical – subtropical aspect, whereas the inland community, represented by allochthonous material, is dominated by temperate broadleaves. Most conspicuous among them is a *Cercidiphyllum*-like plant represented by the leaf, fruit, and seed morphotaxa *Eocercidiphyllites*, *Eocercidianthus*, and *Eocercidispermum*, respectively. These fossils are associated with rare platanoid leaves *Platanervia*, samaroid schizocarps *Dicarperonia* Krassilov comparable with extant *Dipteronia* (Sapindaceae), and xeromorphic *Myrtophyllum*, as well as occasional flowers and seeds of hamamelid and rosid affinities. Notably, the extant species of *Cercidiphyllum* and *Dipteronia* have overlapping ranges in the mountainous areas of central China (Fu, 1992).

Diverse insect damages were found on *Eocercidiphyllites*, including galls of a monophagous species indicating a specific host plant – parasite association (Krassilov & Rasnitsyn, 2008).

Leaves. The morphospecies *Eocercidiphyllites glandulosus* Krassilov includes long-petiolate serrate reniform, elliptical and deltoid leaves with acrodromous to semicraspedodromous venation and conspicuous marginal glands (Plate XXIX, figs. 1 – 7). The most frequent reniform and rounded-elliptical leaf blade variants correspond, respectively, to the short-shoot and long-shoot forms in extant *Cercidiphyllum*, but the less common deltoid morphotype, broadly cuneate and asymmetrical at the base, with the relatively weak basal veins (Plate XXIX, fig. 7) is not normally represented in *Cercidiphyllum*.

The leaf margins are serrate, with the teeth first appearing near the petiole insertion as low serrations gradually increasing to the typical shape and size, which is broadly conical, asymmetrically biconvex, ending in a prominent mamilliform gland with an apical nipple-like beak. Occasional teeth have an additional non-glandular serration on

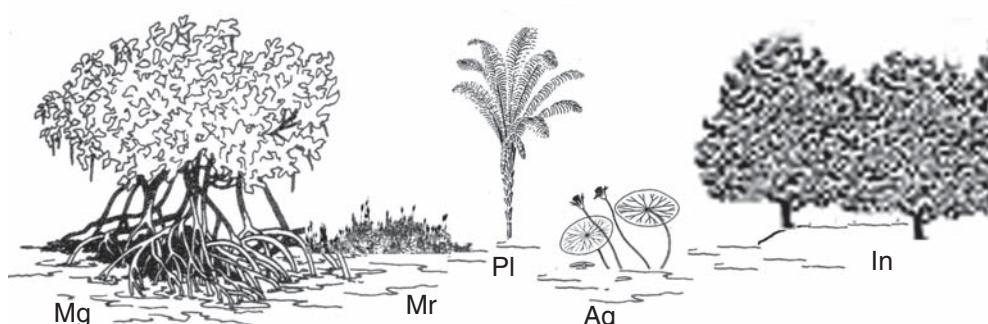


Fig. 29. Reconstructed catenic sequence of vegetation zones in the Turonian of Gerofit, southern Israel (from Krassilov et al., 2005): Mg, mangrove zone, Mr, marshes, P, back-marsh palm zone, Aq, freshwater vegetation, In, inland broadleaved forest with *Eocercidiphyllites* plant.

their dorsal side (Plate XXIX, fig. 3). The leaf venation is acrodromous, with the laterals branching to the outside, their stronger basal branches running into the teeth. The distal branches are as strong as the tertiaries, running into sinuses between the teeth. The tertiary veins are scalariform, occasionally branched, forming a rather regular intercostal series of slightly angular arches scalloping before the margin and sending out short offshoots that converge to the gland (Plate XXIX, fig. 2). The quaternary veins are only slightly weaker than the tertiary, irregularly branching, scalariform, sometimes percurrent. The 5-order venation is locally distinct, forming a fine polygonal network. Notable for comparison with *Cercidiphyllum* are leaf morphotypes with the petiolar vascular strand asymmetrically split before entering the blade (Plate XXIX, fig. 5).

Some smaller, supposedly underdeveloped leaves in our collection differ in their semicraspedodromous venation and in steeper, denser, often unequal marginal serration. The differences are like between mature and juvenile leaves of extant *Cercidiphyllum*, in which the lateral veins are as a rule less conspicuously acrodromous than in mature leaves (Plate XXIX, fig. 8).

Large mamilliform glands are the most distinctive feature of both juvenile and mature leaves. The species epithet “*glandulosus*” refers to this feature.

Reproductive structures. A reproductive structure *Eocercidianthus bracteatus* Krassilov found in association with *Eocercidiphyllites* leaves is a fascicle of four follicles, subtended by two short bracts on a stout stalk distally expanded into a dome-like receptacle (Plate XXX, figs. 1, 2). Black coaly scars of vascular bundles on the receptacle indicate that follicles, although apparently whorled, were attached at the slightly different levels over a shallow coil of a spiral – decussate phyllotaxis. The lateral pair is represented by an elongate follicle on the left side, one on the right side being torn-off several millimeters above the base and partly exposed on the rock surface distally. One follicle of the median pair is fully preserved, in the other a piece between the basal stalk and expanded part is missing, but easily traceable. The follicles are attached by the long tapering base, elongate-elliptical in the expanded part, abaxially (on the side facing subtending bract) convex, adaxially straight, bluntly pointed, with the apex protruding as a short beak. They are laterally flattened, with both abaxial and adaxial sutures impressed as distinct ridges. The surface is densely transversely striate. The subtending bracts are flabellate or lingulate, 2 mm long, acute, obliquely spreading and slightly reflexed, apparently thick, leaving a concave impression. Another specimen (not figured) shows two disarranged fascicles of widely spreading follicles that are somewhat larger than in the previous example.

Orientation of the follicles is difficult to discern from the material at hand, but the better preserved of the whorl is turned its convex margin outside, facing subtending bract. Accordingly it is accepted for detached follicles that their straight margin is adaxial, the convex one abaxial. There are about 10 detached follicles, some of which are split over their straight adaxial margin (Plate XXIX, fig. 4). They are about 22 mm long, 6 mm maximum breadth shortly before the apex, indistinctly stipitate, showing a

scalariform series of distinctly marked transverse veins that are parallel to each other and regularly spaced, occasionally anastomosing midway, but more frequently near the margins, forming two series of small areoles.

In an obliquely compressed follicle (Plate XXIX, fig. 5), the adaxial suture is bordered by two primary veins that are nearly 1 mm apart in the upper third converging toward the beak. Here also the secondary veins form a scalariform pattern with rare anastomoses. Impressions of minute scales are faintly marked at the base, but this feature is better preserved in the largest follicle in our collection, 24 x 7 mm, with two small laterally spreading appendages at base and an elliptical protrusion between them (Plate XXIX, figs. 3, 6). The appendages are about 1 mm long, slightly falcate, with minute basal lobes. They were originally described (Krassilov et al., 2005) as persistent perianth lobes, but after finding carpels converted into a tubular vernate leaf with bilobed stipules (Fig. 26) and similar structures occasionally present at the base of normal carpels in extant *Cercidiphyllum*, a possibility occurs of the persistent basal scales in *Eocercidiphyllites* being carpillary stipules.

Seeds. Impressions of imbricate seeds are preserved inside open follicles. They are shed in coalescent masses or separately as flat samaras about 5.5 x 3 mm. The seed body is ovate, with the long axis orientated at about right angle to the funicle (hemitropous), the micropyle and chalaza at opposite ends, but not exactly in line with each other, the chalazal end rounded and slightly bent down, the micropylar end shortly beaked.

The wing is orbicular, completely encircling the seed body, asymmetrical. The posterior (chalazal) end is broadly rounded, the anterior (micropylar) end is attenuate, bluntly pointed or narrowly rounded. The ventral margin is straight or shallowly concave and the dorsal margin is convex to arcuate. Hilum is expressed as a minute notch from which the funicular bundle departs. It runs toward and curves around the chalaza, then extending as a ridge over the seed body and the posterior wing lobe to a minute notch at the end of it.

Variations of seed shapes include elliptical samaras rounded on both ends, with the seed body orientated somewhat obliquely to the long axis (Plate XXXI, figs. 1 – 4), as well as those tapering to one or both ends. Asymmetry of the wing is variably expressed in unequal development of anterior and posterior lobes, one typically short crescent-shaped, the other longer and tapering to the end. The seed body is irregularly pitted. The wing is concentrically striate and apparently membranous, leaving a faintly marked impression coated with a delicate carbonaceous film.

COMPARISON WITH EXTANT *CERCIDIPHYLLUM* AND FOSSIL ALLIES

The leaves of *Eocercidiphyllites glandulosus* are dimorphic, with both the reniform and elliptical variants corresponding, respectively, to the short-shoot and long-shoot leaves of extant *Cercidiphyllum*. However, leaf polymorphism appears more extensive in the fossil

species, surpassing both *japonicum* and *magnificum* and with some variants (a deltoid form) rarely if at all finding analogy in the extant species.

Prominent marginal glands are characteristic of juvenile extant leaves, decreasing with maturity, whereas in the fossil leaves they are fairly prominent in all leaf morphotypes as their most constant distinguishing character. Whatever the function of the glands may be, in *Cercidiphyllum* it was lost or altered at maturity, whereas in *Eocercidiphyllites* it remained vital through the life of leaves. Morphologically this phenomenon falls under the category of recapitulation, a persistence of an adult ancestral features as a juvenile feature in descendent forms.

Some other distinctions are also related to recapitulation. Thus, in extant *Cercidiphyllum*, juvenile short-shoot leaves differ from the full grown foliage leaves in palmate venation with a pair of nearly straight copiously branched basal laterals that form a semicraspedodromous pattern along the margin. Intrabasal veins are feebly developed or lacking in such leaves. Later in development, the intrabasal veins increase and nearly catch up with the basal pair acquiring an acrodromous turn. Marginal prominences of juvenile leaves are unequal serrate or even irregular double serrate. In the mature leaves, the teeth are broader, divided by shallow sinuses and altogether more regular. In *Eocercidiphyllites*, the occasionally preserved juvenile leaves are strikingly similar to those of extant *Cercidiphyllum* in their palmato-pinnate venation with a strongly developed basal pair, as well as in the irregular serrate and sometimes doubly serrate marginal prominences. But in the fossil form, these presently juvenile features are retained in the full-grown leaves.

In *Eocercidianthus*, the general aspect of pistillate structures is like in extant *Cercidiphyllum*, indicating that characteristic features of the family have appeared early in the history of flowering plants and were conserved in the lineage. However, in the extant species, stipules at the base of follicles are an exceedingly rare feature related to a secondary carpel – leaf conversion, whereas in the fossil form they must have been much more common to be preserved in a sample of about 10 follicles. Together with the leaf-like venation, the carpillary stipules contribute to the leafiness of follicular carpels, probably an original feature in the cercidiphyllids.

The Cretaceous follicles are larger than in the extant and Tertiary representatives, but contain smaller seeds that were stuck in open fruits and were shed in lumps. This indicates a less efficient seed dispersal mechanism than in extant *Cercidiphyllum* with its flowing papery seeds. Fruit dehiscence appears to have been adaxial in the fossil form thus lacking a peculiar and for many researchers intriguing feature of extant *Cercidiphyllum*. However, abaxial dehiscence occurs in some magnoliids and ranunculids as well. Its appearance in *Cercidiphyllum* lineage is perhaps functionally related to increase in seed size and efficiency of seed dispersal as a feature of anemochorous syndrome.

The seeds are essentially like in *Cercidiphyllum*. The raphe trace indicates anatropous polarity assuming a hemitropous configuration with expansion of the wing in much the same way as we inferred for extant *Cercidiphyllum*. The wing is orbicular, but smaller than in *Cercidiphyllum* and with micropylar lobe relatively stronger developed. In *Cercidiphyllum*

lum, the micropylar lobe appears first, as probably was the case in the fossil form, but is then overgrown by the chalazal lobe. In *Eocercidispernum*, the funicular bundle does not describe a hair-pin loop characteristic of *Cercidiphyllum*, which is obviously related to a much shorter chalazal lobe. Straight course of vascular bundle is an anomalous pedomorphic feature in extant *Cercidiphyllum*.

OTHER EXTINCT CERCIDIPHYLLIDS

As discussed above, the widespread *Trochodendrocarpus*–*Joffreya* group (trochodendrocarpoids) with paniculate or racemose inflorescences of inconsistently paired and partly connate carpels are closer to hamamelids than cercidiphyllids. The Turonian *Eocercidiphyllites* is as different from *Trochodendrocarpus*–*Joffreya* group as is the extant representative of the lineage. It belongs to a Gondwanaland group of Cretaceous angiosperms, geographically separated from the Laurasian trochodendrocarpoids.

Cercidiphyllocarpus from the Late Cretaceous of Sudan (Vaudois-Miéja & Lejal-Nicol, 1987) is scarcely related to the Cercidiphyllaceae. Figured specimens of this morphotype appear to represent a ribbed syncarpous fruit.

Nishida (2006) has described from the Upper Cretaceous (Coniacian – Santonian) of Hokkaido an axis with about 35 spirally arranged dorsally dehiscent follicles containing numerous tightly packed winged seeds. He considers this fossil to be a solitary perianthless flower of cercidiphyllid affinities. This interesting fossil is less similar to extant *Cercidiphyllum* than *Eocercidianthus*, perhaps representing an intermediate form between the cercidiphyllid and ranunculid groups of early angiosperms.

CRETACEOUS RANUNCULIDS

The mid-Cretaceous angiosperms of supposed ranunculacean affinities (“ranunculids”), such as *Ternaricarpites floribundus* or *Hyrcantha decussata* are herbaceous plants very different from *Cercidiphyllum* in vegetative morphology, but sharing with this relict genus the irregular spiral – decussate phyllotaxis, follicular carpel morphotype, sometimes with an abaxial dehiscence suture, and other features of a potential phylogenetic significance. A hypothetic derivation of Cercidiphyllaceae from herbaceous forms makes comparison with ranunculids pertinent to the following discussion.

Paleobotanical findings (reviewed in Krassilov & Volynetz, 2008) suggest that herbaceous growth habit appeared early in the evolutionary history of ranunculids and was perhaps primary for the group. It is well known that herbaceous plants are under-represented in the fossil record. This may explain rarity of fossil ranunculids. However, in the mid-Cretaceous they were more common than afterwards and were represented by a number of morphotaxa suggesting a considerable diversity and morphological

disparity. Examples are *Caspiocarpus paniculiger* Krassilov et Vachrameev (1979) from the Middle Albian of Kazakhstan, a herbaceous plant with a slender stem bearing a pair of palmately lobate leaves and a terminal tripartite paniculate infructescence of small condensed racemose paracladia, each bearing up to ten 1–3-ovulate follicles (Fig. 30a). This plant was compared to ranunculids in the widest sense on account of its general habit, leaf morphology, dorsi-ventricidal dehiscence of follicles and the structure of ovules with two one cell thick integuments as in the modern Ranunculaceae and Circaeasteraceae.

Hyrcantha karatscheensis (Vachrameev) Krassilov from the same horizon is represented by slender branched axes bearing binate leaves and terminal fruits of 3–5 urn-shaped ventricidal follicles crowned with a broad sessile stigma (Fig. 30d) as in the Paeoniaceae, a controversial family morphologically linked to both the Ranunculales and Dilleniales (Cronquist, 1981).

H. decussata (Leng et Friis) Dilcher, Sun, Ji et Li from the Early Cretaceous Yixian Formation of northeastern China differs mainly in the decussate arrangement of carpels (Dilcher et al., 2007). This feature is pertinent to a possibility of ranunculid derivation of the Cercidiphyllaceae.

Callicrypta chlamydea Krassilov & Golovneva from the Lower Cenomanian of Siberia (Krassilov & Golovneva, 2001) is an actinomorphic flower less than 2 mm wide (Fig. 30b), functionally pistillate, although found with sticking pollen grains probably produced by a staminode. The perianth is 3-seriate of a relatively massive calyx and a corolla of dimorphous inner and outer petals. The gynoecium is apocarpous of small ascidiform carpels. Our analysis pointed to the Menispermaceae and Arborellaceae as the nearest extant groups, at the same time revealing a significant similarity between the two (*Amborella* has been traditionally assigned to the Monimiaceae, but presently is more commonly placed in the vicinity of Nymphaeaceae: Mathews & Donoghue, 1999; Endress, 2001).

The tricolpate reticulate pollen grains associated with *Callicrypta* are of the type found *in situ* in *Freyantha sibirica* Krassilov et Golovneva from the stratigraphically coeval horizon in West Siberia (Krassilov & Golovneva, 2003), a racemose staminate inflorescence, terminal on the axis with minute prophylls. The staminate flowers consist of fasciculate stamens subtended by calyptrate bracts (Fig. 30c). The alleged affinities with the Menispermaceae and Sargentodoxaceae make *Freyantha* assignable to the ranunculid plexus. The recently described carpellate infructescence *Cathiaria* Golovneva et Oskolski, probably of the same plant as *Freyantha*, is a panicle of short racemose paracladia bearing several dorsicidal follicles (Golovneva & Oskolski, 2007), comparable to *Caspiocarpus* (above), but with a laminar structure (inflorescence bract or prophyll?) adnate to the paracladia in early development.

Achaenocarpites capitellatus Krassilov & Volynetz is perhaps the most confident mid-Cretaceous ranunculid being assigned to this group on the basis of both vegetative and reproductive morphology (Fig. 31). Its leaves, basically ternate, correspond to the type shared by all ranunculids, the diversity of their adult leaf morphologies depending on the extent of marginal growth (Kürbs, 1973). The pistillate structure is a head of achenes surrounded by a bracteate perianth. This plant is found in the tuffaceous

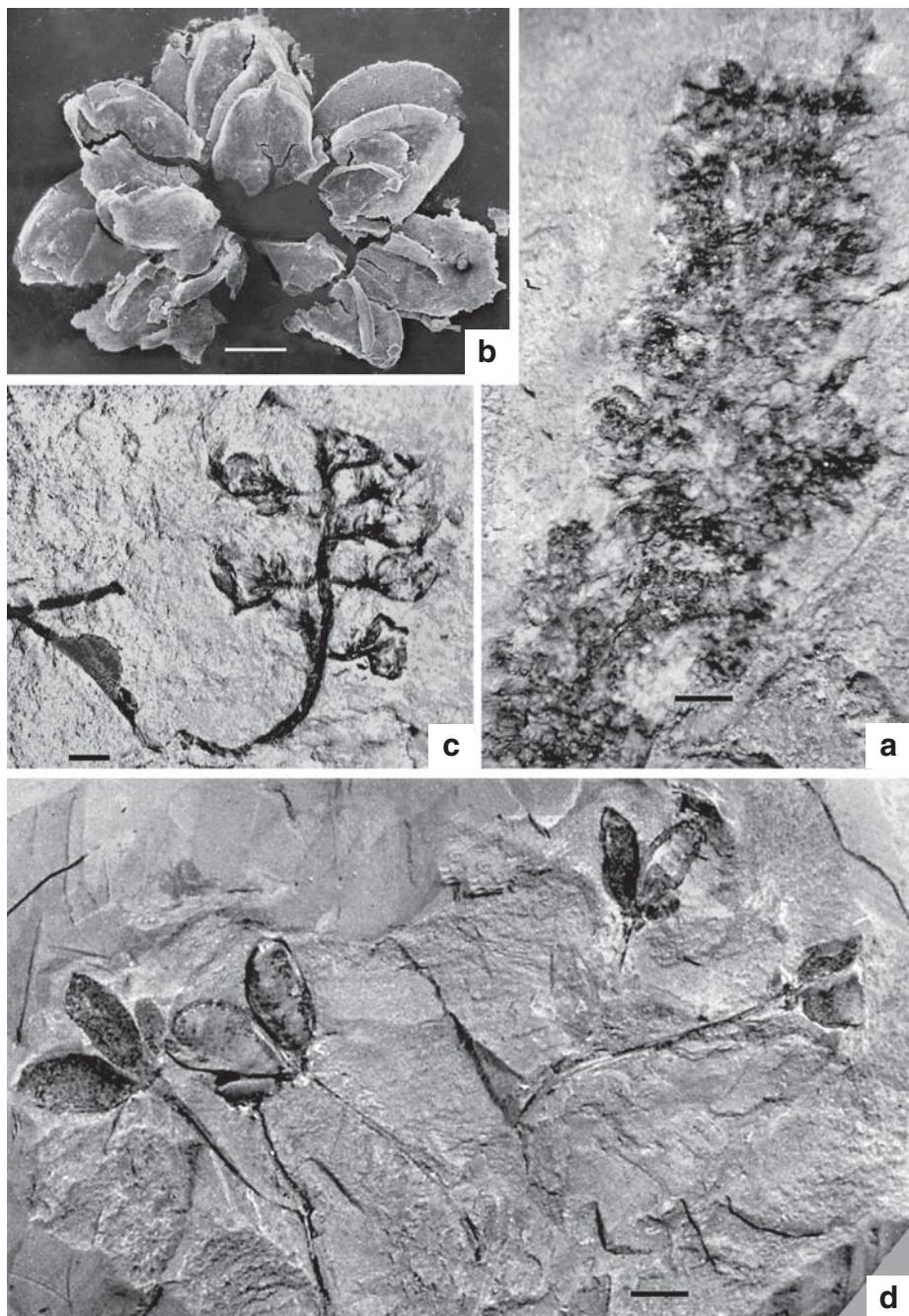


Fig. 30. Early ranunculid angiosperms: a, *CaspioCARpus paniculiger* Krassilov et Vachrameev (Krassilov, 1984); b, *Callicrypta chlamydea* Krassilov & Golovneva (Krassilov & Golovneva, 2004); c, *Freyantha sibirica* Krassilov & Golovneva (Krassilov & Golovneva, 2001); d, *HyrCANtha karatscheensis* (Vachrameev) Krassilov (Krassilov et al., 1983). Scale bars 0.25 mm (a) and 0.5 mm (b – d).

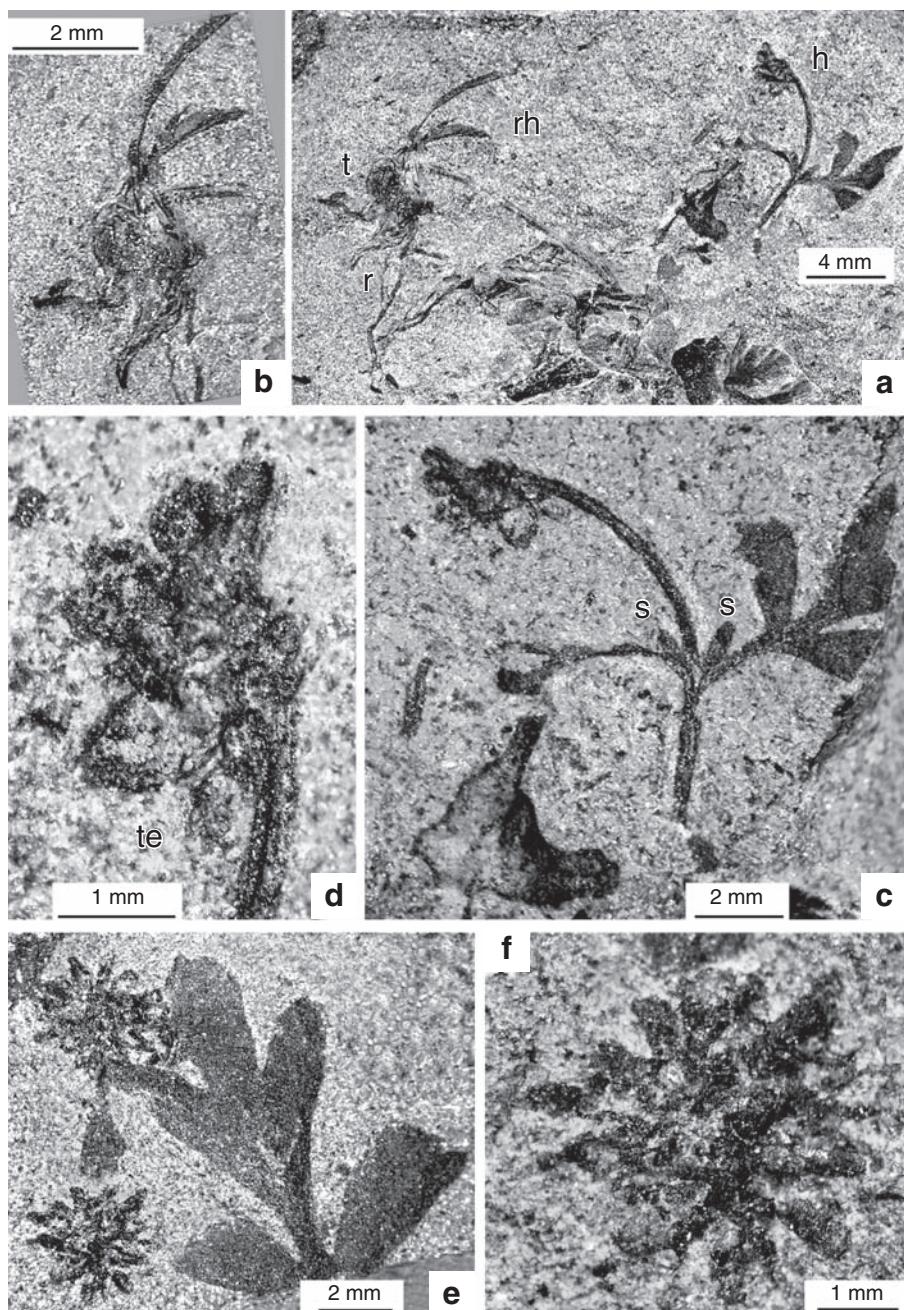


Fig. 31. Early ranunculids angiosperm *Achaenocarpites capitellatus* Krassilov & Volynetz: a, whole plant with branching rhizome (rh), tubers (t), adventitious roots (r), leafy stem with a terminal floral structure (h); b, tubers enlarged; c, stem with a pair of leaves (S, leaf stipules) and a terminal head; d, flower with two persistent tepals (te) and gynoecium developing into a head of achenes, e, leaf in slab association with two heads of achenes, f, head enlarged (after Krassilov & Volynetz, 2008).

Lower Cretaceous (Albian) deposits of Primorye, Far East in association with another rhizomatous form, *Ternaricarpites floribundus* Krassilov et Volynetz, supposedly forming a pioneer community on ash fallouts.

These recent findings seem to support the classical “ranalean” theory of angiosperm phylogeny, with the large heterogeneous families Ranunculaceae, Menispermaceae, and Berberidaceae, presently forming the bulk of the ranunculids, and a number of not unanimously recognized monotypic families, such as the Kingdoniaceae, Circaeasteraceae, Lardizabalaceae, Sargentodoxaceae, Paeoniaceae, Glaucidiaceae, Amborellaceae, and those to be erected for fossil forms, linking this group to the orders of remote ranunculid affinities, including the Cercidiphyllales. Among them, *Ternaricarpites* Krassilov et Volynetz from the Albian of the Ussuriysk Bay, Far East is the more significant on account of its sympodial branching, prominent floral prophyll and dorsicidal carpels.

TERNARICARPITES, A POSSIBLE RANUNCULID PRECURSOR OF EARLY CERCIDIYPHYLLIDS

Ternaricarpites floribundus Krassilov et Volynetz from the Albian Ussuriysk Bay locality near Vladivostok is described (Krassilov & Volynetz, 2008) as having a slender stem, basally rhizomatous and sympodially branched. The basal leaves are pinnatisect with open venation. The presence of caudine leaves remains unconfirmed. Flowers are terminal on lateral branches, occasionally axillar at branching nodes, with a slightly zygomorphous perianth of 5 unequal bracteate tepals, connate at base. Venation of tepals is similar to that of leaf lobes. Fruit is a ternate follicetum of dorsicidal follicles with seeds in rows along the abaxial suture.

One specimen shows about 20 fruiting axes with slender branches arising either sympodially, to one side or, at some distal nodes, dichopodially, to both sides of the penultimate axis (Plate XXXII, fig. 1). Ultimate branchlets bear terminal fascicles of ternate follicles that are also produced at the branching nodes.

Another instructive specimen is a branching axis, rhizomatous at base, bearing a terminal flower subtended by a linear prophyll and with a 5-lobed somewhat zygomorphous perianth, the lobes of which are basally connate for about 1/3 of their length (Plate XXXII, figs. 2, 3). The lobes show a distinct midrib giving off dense oblique, slightly arching lateral veins. A similar type of venation was observed in the leaf lobes. A ternate fruit in the left part of the picture may belong to the same branching system, but actual connection cannot be traced. Plate XXXII, figs. 4, 5 show similar follicles, 6 – 8 mm long, shortly stipitate, pointed or cleft at the tip, with an abaxial keel of two parallel ridges representing the dehiscence suture, which is occasionally gaping, exposing seed impressions aligned with the ridges.

The dimorphism of basal and caudine leaves, characteristic of the Ranunculaceae, is not proved, but seems probable in *Ternaricarpites*, the basal leaves of which are of

the same general type, but differ in details of segmentation and venation from the associated detached leaves. Both terminal and axillary position of flowers (fruits) on the branching shoots find its analogy in the floral organography of the extant ranunculid tribe Isopyreae (Tucker & Hedges, 2005). A monochlamydous perianth of five unequal tepals, with the larger one in a median abaxial position may result from organogenesis typical of this tribe (systematics overviewed in Tamura 1993). Perianths of five tepals (sepals) occur in *Caltha* L. and some other Helleboreae and are zygomorphous in the Delphineae. The numbers of follicles vary in these groups, but ternate fruits commonly occur in *Trollius* L., *Delphinium* L., *Aquilegia* L., *Kingdonia* Balf. et Smith, and some other helleborid and isopyrid genera.

Characters of *Ternaricarpites floribundus* atypical of the present day ranunculids are the sympodial branching of fertile axes, both terminal and axillary floral fascicles, and the abaxial dehiscence of the follicles. However, the morphological diversity of present day ranunculids includes these characters (their modifications) as well. In the Ranunculaceae, solitary flowers are typically terminal, but leaf-opposite in *Ranunculus* subgen. *Batrachium* (DC.) Peterm. The axillar inflorescences are sometimes single-flowered. The dehiscence may involve both ventral and dorsal sutures. Therefore, such features do not preclude assignment of *Ternaricarpites* to ranunculids, at the same time suggesting affinities with other, probably allied families, in particular, the *Cercidiphyllaceae*. The old idea of woody ranunculids thus gains support from the fossil record.

Taphonomically, the Ussuriysk Bay locality represents a re-deposited ash-fall material with imbedded plant debris and coal grains. Preservation of whole plants, as well as the joint occurrences of rhizomes, branching stems, detached leaves, achenocarpic heads and dispersed achenes indicate deposition at or near the growth site, with no or insignificant transportation and sorting. Fragmentation of plant material is mostly post-depositional, by slumping and sliding of water-logged tuffaceous sediment.

In slab assemblages, the two species of rhizomatous angiosperms, *Achaenocarpites capitellatus* and *Ternaricarpites floribundus*, are constantly associated with *Anemia* ("*Asplenium*") *dicksoniana* (Heer) Krassilov, a small-leaved representative (or a close ally) of an extant schizaeaceous fern genus, in which creeping forms of open periodically dry to boggy habitats are rather common. Both ferns and angiosperms had pinnatisect leaves of a similar general aspect, with slender rachises and decurrent leaflets (pinnules) or lobes. This fern – angiosperm assemblage is interpreted as representing a pioneer community of a few co-adapted early colonizer species growing on fresh fallouts of a volcanic landscape.

7. DISCUSSION OF *CERCIDIPHYLLUM* MORPHOLOGY

In this study of extant *Cercidiphyllum* and fossil allies, new features are found in all domains of both vegetative and reproductive morphology, including the branching modes, phyllotaxis, foliage leaf homology, epidermal structure, reproductive shoot architecture, prophyll, carpel morphotype, placentation, ovule/seed development and pollen grains. This information is here discussed on account of the lingering controversies concerning the shoot system and floral structures of the genus. New and preferred interpretations are considered in regard of taxonomic status of the genus and its evolutionary significance. Evolutionary inferences are based on new developmental and paleobotanical evidence.

At the morphological level, it was long ago recognized that *Cercidiphyllum* is an archaic relict angiosperm bringing to us flavor of the Cretaceous Period. At the same time, its reproductive morphology was interpreted, in the spirit of the dominant evolutionary paradigm, as drastically reduced from a common angiosperm prototype, the diclinous flowers being represented by solitary pistil and, less convincingly, by solitary stamen or indefinite group of stamens, gathered in pseudanthial inflorescences. Evidence for such interpretation was sought in such morphological peculiarities as the abaxial dehiscence of carpels, as well as in the fossil record.

Unconventional opinions were expressed by such eminent morphologists as Melville (1963), Croizat (1964), Meeuse (1966, 1972, 1975), Hutchinson (1973), and Leroy (1980). Dilcher (1979, p. 324) concluded from paleobotanical evidence that “the so-called “reduced” flowers of such orders as the Trochodendrales, Cercidiphyllales, Eupteleales, Hamamelidales and Piperales may be considered initially simple rather than reduced from a monoclinous (bisexual) ancestor. Independent lineages of some anemophilous flowers developed early and perhaps separately from entomophilous flowers from a common diclinous (unisexual) ancestral stock”.

That descent opinions were overshadowed by the dominant paradigm and remained unknown to a larger part of botanical community does not prove their deficiency in factual evidence or logic. It only proves that the more people work in science the more dogmatic the science becomes. My impression is that many “evo-devo” researchers working at front line of plant biology never heard of any alternatives to the text-book

morphological paradigms. In this chapter I would bring some unconventional points of view to the attention of such researchers in the first place.

SHOOT SYSTEM

In many angiosperms, the vegetative and reproductive shoots are far diverged, the mode of branching in one not necessarily being the paradigm for the other. In *Cercidiphyllum*, a sympodial branching of reproductive shoot, first recognized by Harms (1916) was not thought to be extended to the vegetative body. Yet this study suggests that the leafy and reproductive shoot systems of *Cercidiphyllum* are developmentally interlinked. Moreover, in this plant the shoot system is most peculiar in both leafy shoots and reproductive structures arising from the uniformly built short shoots.

Both male and female reproductive structures develop from the dormant buds of the short shoot renovation covered with three successive cataphylls that are produced in a tight spiral, the upper one forming a calyptra, in which the floral stalk and its solitary leaf are enclosed before anthesis. The major function of the short shoots is, therefore, reproductive. However, the long shoot branching system also arises, in sympodial manner, from the short-shoot renovation bud or else by conversion of floral axis into a leafy shoot with distichous elliptical leaves. Such vicarious leafy shoots are strikingly similar to the pistillate structures they replace in the precocious elongation of the basal peduncle-like internode and in the flower-like clustering of several primordial leaf pairs before emergence. The shoot then grows by elongation of successive internodes, and the leaves become widely separated along the axis. Short shoot buds are then regenerated in the leaf axils. Yet such long shoots are sometimes terminated with a reproductive stalk (Plate II, fig. 3).

Thus a critical feature of *Cercidiphyllum* morphology is production of leafy branches in the potentially reproductive short shoots. If we add to this the fact that in the branching long shoot – short shoot system all foliage leaves are the short-shoot leaves developing from prophylls of the floral stalk, then it becomes clear that in *Cercidiphyllum* the vegetative body is mainly produced in the developmental line of fertile organs.

LEAVES AND PROPHYLLS

Four kinds of phyllomes are produced, including the short-shoot cataphylls, prophylls of reproductive shoots, floral bracts, and the long-shoot foliage leaves. The cataphylls are not differentiated into leaf blade and petiole, lack stipule and are characterized by disorganized subparallel venation resembling phyllodic monocot leaves with alternate strong and slender veins connected by the short cross-veins (Fig. 32). A sometimes discernible vestigial blade at the end of the midrib supports their interpretation as phyllodic structures.

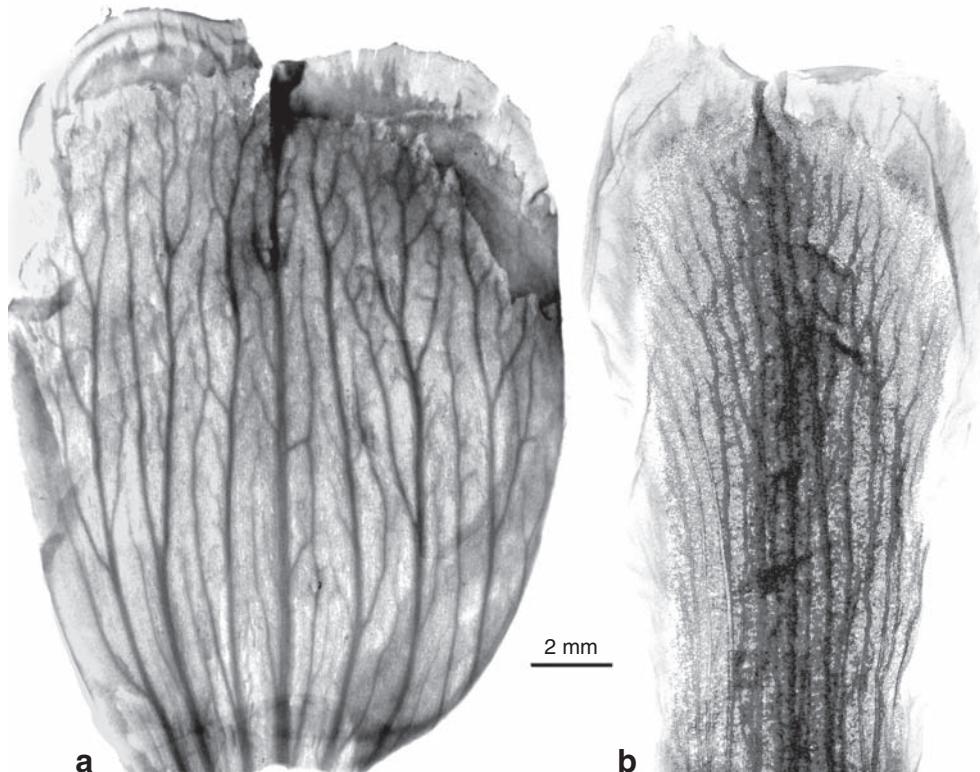


Fig. 32. *Cercidiphyllum magnificum* Nakai, BIN: short-shoot cataphyll III venation.

The solitary leaf of reproductive short shoot is sometimes interpreted as the fourth cataphyll. Yet morphologically it is not a cataphyll. Moreover, it is separated from cataphylls in time and space, being produced after the period of dormancy and off the spiral cataphyll series.

The leaf petiole and floral stalk are nearly equal arms of a dichotomous division (Plate IV, figs. 1 – 3) that can be compared to bifurcation of the inflorescence meristem in *Petunia* that, according to Souer et al. (1998), yields two meristems of approximately equal size. One terminates into a floral meristem and the other maintains its inflorescence identity. The specification of the floral meristem after bifurcation involves the *ABERRANT LEAF AND FLOWER (ALF)* gene, which is expressed in both the floral and vegetative meristems. A mutant *alf* phenotype is excessively leafy and does not produce normal floral organs. Souer et al. (1998) suggest that expression of *alf* in leaves points towards an old function of *ALF* in the foliar development that in *Petunia* has been lost in the course of evolution. A homologous gene might have caused transformation of a partial inflorescence into leaf after bifurcation of the reproductive shoot axis in *Cercidiphyllum* lineage thus giving rise to the floral stalk – leaf association in the present day species.

Perhaps relevant to the possibility of floral branch – prophyll transformation is a mutation of *LEAFY*, a developmental gene responsible for initiation of floral meristems in *Arabidopsis*, in which the partial inflorescences or basal flowers alone are converted into leaves with axillary shoot meristems (Schultz & Haughn, 1991; Weigel et al., 1992).

Notwithstanding the conceivable inflorescence branch – leaf transformation, the short-shoot leaf is the first phylome of a series in which subtending bracts and their replacing tiny leaves are produced. Its association with the reproductive structure extends to their mutual enclosure in the distal cataphyll. In the case of reproductive structure transformed into leafy shoot, the short-shoot leaf maintains the same position in regard of the long shoot leaves. It is of the same morphological type as the subsequent phylomes of the series, including the vernation mode, glands and stipules, but is slightly different in shape and the vascular supply. Therefore, by its developmental characteristics and morphology the short-shoot leaf qualifies for the morphological status of prophyll. This means that in *Cercidiphyllum* prophylls of the floral axis develop into the major type of stipulate long-petiolate reniform foliage leaves, the petioles of which harbor the short shoot renovation bud.

The long-shoot leaves develop on the vicarious leafy shoots replacing reproductive shoots and are characterized by the relatively short petioles, persistent stipules, elliptical leaf blades and semi-crasspedodromous venation. The tiny leaves of the floral receptacles are identical to the vernate leaves of the vicarious leafy shoots. Vernate leaves of all types are involuted toward their adaxial side. Except in the cataphylls, the vernation mode of which is intermediate between imbricate and convoluted (Fig. 2), the leaf margins are supervoluted (doubly coiled). In cataphylls, the margins may overlap forming a calyptra screwed at the apex.

GLANDS AND STOMATA

The juvenile leaves and leaf-like bracts have large protrusive apical glands and smaller marginal glands, the multicellular structures supplied by intramarginal veins. Glands are reduced and partly shed in full-grown leaves of extant *Cercidiphyllum*, but persist in the Cretaceous *Eocercidiphyllites* (above). If the function of marginal glands is primarily hydathodal, their reduction can be related to development of the extensive system of leaf surface hydathodes supplied by the blind veinlets. Such system is not ascertained for *Eocercidiphyllites*.

Stomatal pattern in *Cercidiphyllum* is strongly affected by hydathodes and their supplying blind veinlets (Figs. 33 – 35). Ordinary stomata are seen in a concentric arrangement around a hydathode or spreading in radial files away from it. Recent developmental studies show that stomata are produced by a dedicated cell lineage, in which cell division and differentiation are regulated by a network of developmental genes and patterned through intercellular signaling (reviewed in Bergmann & Sack, 2007; Hara et al., 2007; Kanaoka et al., 2008; Casson & Gray, 2008; Pillitteri & Torii, 2007; Pillitteri et al., 2008). Activation of developmental genes requires MAP kinase cascades and the receptor-like

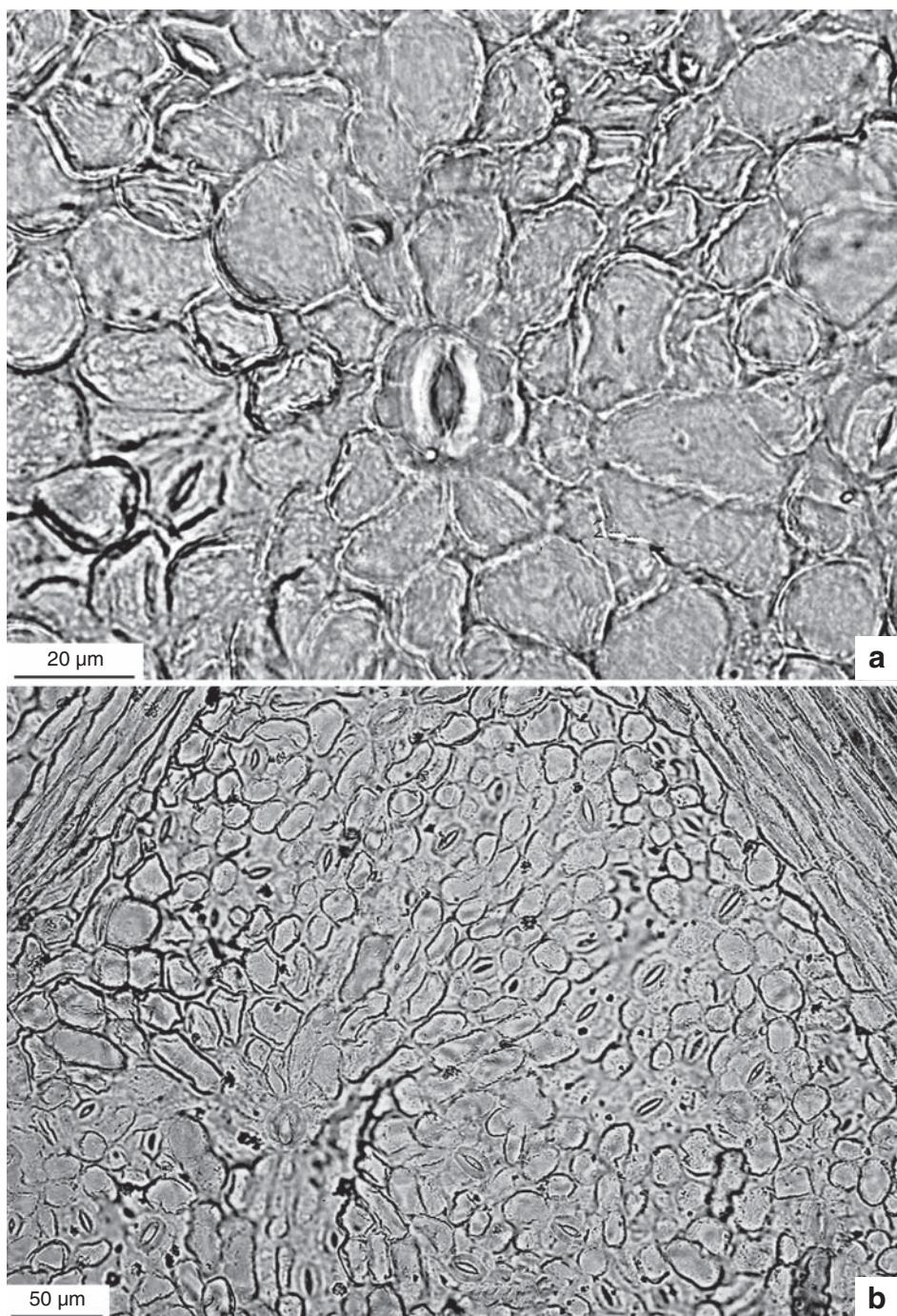


Fig. 33. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, stomata: a, hydathodal stoma with four small laterocytic subsidiary cells; b, hydathode (arrow) at the center of the radially spreading stomatal files.

cytoplasmic kinases of *ERECTA* (*ER*) family, which participate not only in stomatal regulation, but also in the control of floral development (Shpak et al., 2004). The effects of excessive cell proliferation due to *ER* must be evident in both stomatal and floral developments, thus potentiating their correlation.

At the same time, stomatal gene expression is mediated by plant hormones transported through the venation network. In particular, distribution of stomata is affected by the epidermal auxin-focusing mechanism for positioning of the major veins (Scarpella et al., 2006), and the related process of hydathode formation (Candela et al., 1999; Aloni, 2001; Aloni et al., 2003, 2005). These processes are manifested through the stomatal patterning in the vicinity of the auxin transport channels (vein sheaths) and the epidermal auxin maxima (leaf tips, hydathodes).

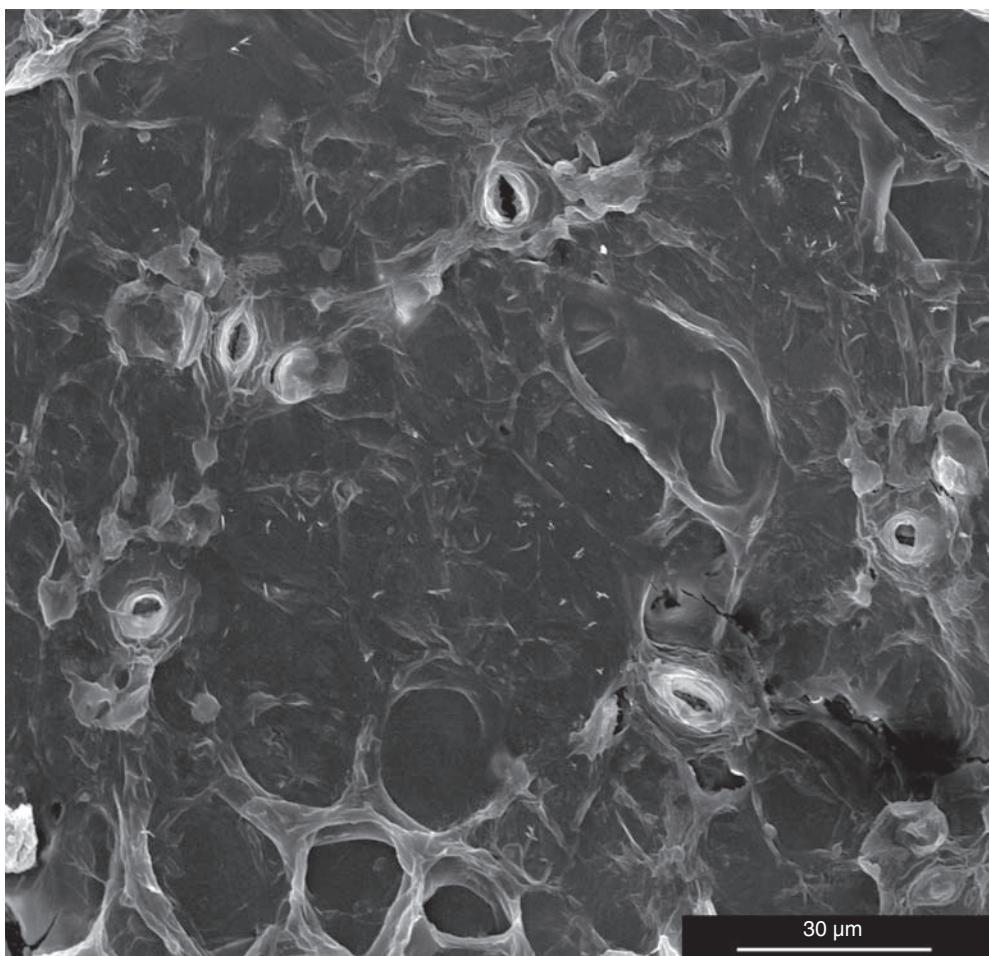


Fig. 34. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU: hydathode with concentrically arranged ordinary stomata, SEM.

In *Cercidiphyllum*, ordinary stomata are of a widespread anomocytic type, but the giant stomata associated with the blind vein sheaths and hydathodes are characterized by proliferation of subsidiary cells, with a tendency for amphicytic configuration. Additional paracytic subsidiary cells (Fig. 33a) are evidence of a mild *four lips (4l)* type regulatory disorder (Bergman & Gray, 2007; Casson & Gray, 2008) of multiple causation, probably involving the auxin sensitive transcription factors.

The excessively developed apical glands of juvenile *Cercidiphyllum* leaves marks the leaf tip auxin maximum, whereas the concentric and radial arrangement of ordinary stomata around the leaf surface hydathodes is spectacular evidence for stomatal pattern regulation by the hydathode auxin maxima (Aloni et al., 2003, 2005).

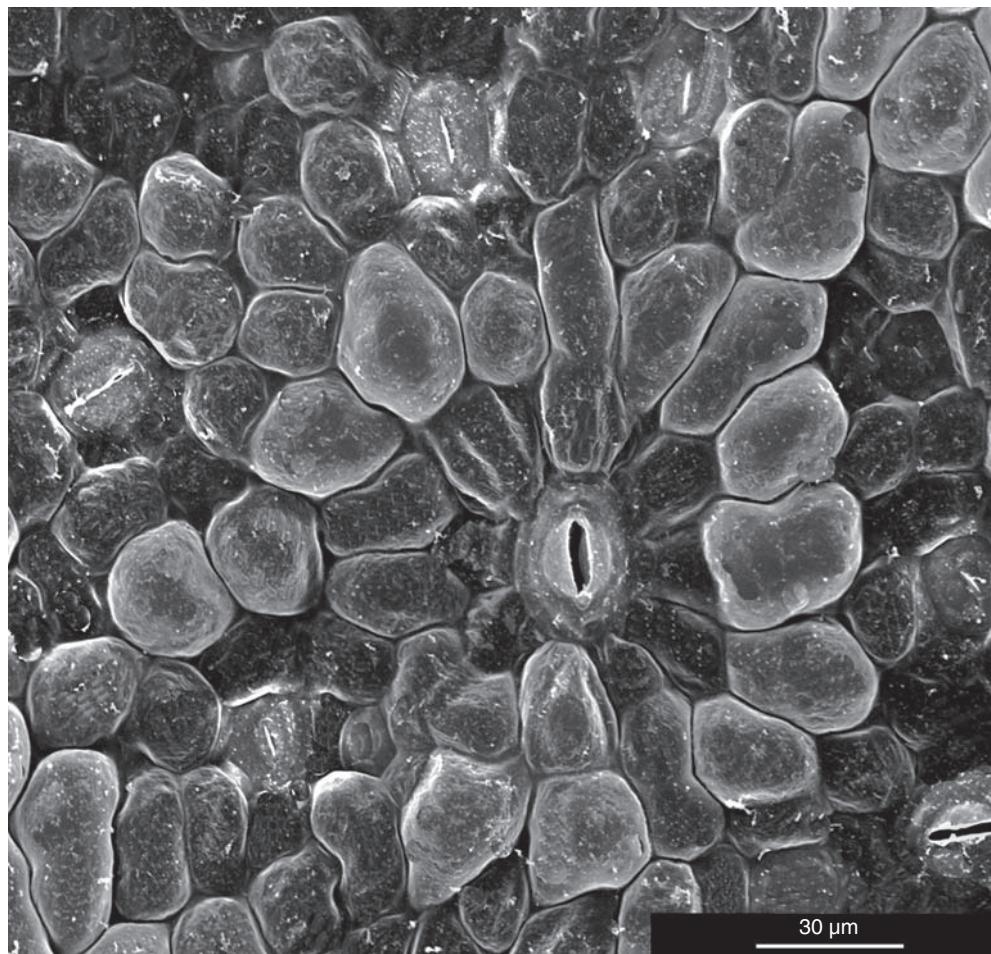


Fig. 35. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU: stoma-like hydathode opening and the concentrically arranged ordinary stomata, SEM.

TYPОLOGY OF FLORAL STRUCTURES

Because interpretation of floral structures is crucial in regard of systematic position and evolution of *Cercidiphyllum* and allies, a few general notes on floral morphology seem pertinent here. The origin of flowering plants is still a controversial problem, but all agree that flowering plants must have originated from some plants that had no flowers. It just could not have been otherwise, because flowering plants are those having flowers whereas having flower is a unique characteristic of flowering plants.

Once upon a time it was taken for granted that even ferns produce cryptic flowers of a kind. The necessity of definition came with understanding that not all, but only flowering plants possess flowers. An attempt to avoid circular reasoning by defining flower as a structure consisting of carpels and/or stamens boils up to more circularity because carpels and stamens are nothing else but ovulate and pollinate organs of flowering plants. Such definitions raise a semantic barrier between flowering plants and their putative predecessors, which no evolutionary approach had surmounted so far.

Morphological study may reveal unrealized growth points or vestigial structures, such as blind buds or intercarpellary bracts, suggesting the origin of flower from a more diversified structure, in which some parts were lost.

Classical morphology is typological in the sense that deviations from an ideal state are invariably ascribed to reduction. Interpretation of floral structures in *Cercidiphyllum* as extremely congested inflorescences is an example of typological reasoning. Inflorescence is made of flowers if but reduced to a solitary carpel. Still it will be good to know where the boundary between flower and non-flower lies, or how far the sweet smell (and morphology) must change for us to call a rose by any other name.

In *Cercidiphyllum*, phyllomes are present on the floral receptacle, although a tendency to their elimination can be inferred from the reduction gradient from the fully developed basal (lateral) to the hair-like distal (median and inner) bracts of the pistillate floral structures. The process is nearly accomplished in the staminate floral structures that are true flowers by conventional criteria. Yet the flexible development of subtending bracts, the imprecisely spiral – decussate phyllotaxy, the inconstant numbers of fertile units, which in the androecia is indefinite and in the gynoecia wander from two to six, are intriguing in a terminal member of a lineage given no less than 90 million years to accomplish all morphological transactions on the way to conventional flowering plant.

DEVELOPMENTAL EVIDENCE OF FLOWER – INFLORESCENCE TRANSFORMATIONS

Classical morphology of floral structures provides us with only two notions, inflorescence and flower. Inflorescence is a gathering of flowers. Any fertile part of inflorescence is

flower. Inflorescences congested into flower-like structures are pseudanthia. Incidentally, floral structures of *Cercidiphyllum* have been once regarded as flowers then re-interpreted as congested inflorescences, or pseudanthia, the original flowers being drastically reduced, supposedly to a single carpel (stamen?), a convenient unit for whatever restructuring. A possible prototype of inflorescence is a shoot of infinite growth with lateral branches bearing flowers. Inflorescence can be reduced to flower, but transformation of flower into inflorescence is counter morphological intuition. These notions has to be revised in the light of recent developmental research.

In flowering plants, the initiation of floral meristems is determined by *LEAFY* (*LFY*) and orthologs, encoding a transcription factor, controlling expression of many downstream genes that specify floral meristem identities and organogenesis (Lohmann & Weigel, 2002; Bomblies et al., 2003; Blazquez et al., 2006; Hamés et al., 2008). Mutations in *LFY*, the orthologous *FLORICAULA* (*FLO*) in *Antirrhinum majus*, and the *ABERRANT LEAF AND FLOWER* (*ALF*) gene in *Petunia* decrease expression of homeotic floral genes acting at different structural levels of the ABC developmental model (Weigel & Meyerowitz, 1994). This results in complete or partial interconversions of meristem identities.

According to Souer et al. (1998), modification of the expression pattern of *LFY* can change an infinite inflorescence structure into a finite floral structure (Weigel & Nilsson, 1995). The constitutive expression of *LFY* in *Arabidopsis* leads to precocious formation of terminal flowers, while in aspen the flowering is accelerated from 8 – 20 years to five months. In the *terminal flower1* (*tfl1*) mutant of *Arabidopsis* and a homologous mutant in *Antirrhinum*, the ectopic expression of *lfy* and *flo* in the apex leads to the formation of a terminal flower (Bradley et al., 1996, 1997).

In a number of examined species, mutants defective in *LFY* or *FLO* show severe defects in flower development (summarized in Souer et al., 1998; Blázquez et al., 2006), such as replacement of flowers by leaves with axillary meristems producing secondary shoots, but progressively acquiring floral identity with activation of the homeotic *ABC* genes. The ABC model includes the homeotic genes *APETALA1* (*AP*) 1 – 3, *AGAMOUS* (*AG*), and *PISTILLATA1* (*PI*) expressed in consecutive floral whorls: AP1 and AP2 in the first and second whorls, AP1, AP2, AP3 and PI – in the second, AP3, PI and AG – in the third, and AG – in the fourth (Theissen & Saedler, 2001; Theissen & Melzer, 2007). The *AGAMOUS-LIKE* (*AGL*) 2, 4, and 9 genes expressed in the inner whorls have been renamed *SEPALLATA* (*SEP*), because the triple mutant *sep 1/2/3* converts all floral organs into sepals (Pelaz et al., 2000).

The role of the *TERMINAL FLOWER1* (*TFL1*) gene is opposite to that of *LFY* or *AP1* in maintaining proliferation of the inflorescence meristem (Shannon & Meeks-Wagner 1991). A mutant *tfl1* causes replacement of inflorescences by flowers and conversion of cauline leaves into subtending bracts. Notably, *TFL1* is expressed in the center of the apical meristem. In *tfl1* mutants, ectopic expressions of *LFY* and *AP1* invade the inflorescence apices that are converted into flowers.

Pelaz et al. (2000) investigated the expression of *SEPALLATA* (*SEP*) MADS-box genes in floral development. They found that triple mutation *sep1/2/3* confers sepal-like characters upon the floral organs of the perianth and stamen whorls (B and C organs of the ABC model), expressing the sepal epidermal cells and stomata. The forth whorl, normally represented by two fused carpels, is converted into an additional flower that reiterates the basic pattern of the floral whorls. Thus, the triple mutant flower acquires infinite growth and produces apparently endless reiteration of flowers. It is up to morphologists to reveal what types of inflorescences are likely to evolve by reiteration of floral structures that come to follow this kind morphogenetic mode.

Anyway, interconvertibility of flower and inflorescence must be taken into account in interpreting intermediate situations, for which the traditional reduction model of morphological transformation is no longer acceptable as a sole possible explanation. In particular, *Cercidiphyllum* represents a situation, in which a flower-like structure of intermediate flower – inflorescence characteristics might have never been a gathering of true flowers. Instead, it may represent an ancestral condition of flower in making.

PREFLOWER

It becomes obvious that diversity of floral structures in angiosperms is not limited to flowers, inflorescences, and pseudanthia. Rudall et al. (2009) even spoke of *nonflower* in the case of inverted sequence of staminate and carpellate organs. Developmental studies reveal intermediate situations between flower and inflorescence, which erode the distinction between finite and infinite structures.

The recognition of flower to be a reproductive short shoot was a breakthrough to morphological definition, but gymnospermous strobili are also reproductive shoots. Then what is the difference? I defined flower as a short shoot terminated with fertile organs and no sterile organs inside the fertile area (Krassilov, 1988, 1997). This definition assumes that fertile floral organs alone are produced in the center of the apical meristem (except underdeveloped fertile structures, such as staminodes or carpellodes). In distinction, *Ginkgo* and fossil allies have their biovulate stalks on short shoots with basal bracts, but interspersed with leaves. Similarly, the bennettitalean flowers are short shoots producing perianth-like bracts and stalked ovules interspersed with peltate scales. Although whorled in a flower-like manner, they are not true flowers.

The above definition does not exclude a possibility of gymnospermous flower as well as a transitional situation – *preflower* – in angiosperms with an apically protruding receptacle (the Cyclanthaceae) or intrafloral phyllomes.

The epitome preflower is the floral structure in *Eoantha*, an extinct genus of Early Cretaceous anthogonetophytes (Krassilov, 1986), consisting of a perianth whorl of many linear bracts, a gynoecial whorl of four ovulate cupules and a terminal bract whorl on top of the protruding gynophore (Fig. 36a, b). Transformation of preflower into flower by

the manifest fertility of floral apex is evident at the anthogonetophyte level already, with the ABC rule seemingly observed in *Preflosella nathania* Krassilov of the same geological age (Fig. 36c), having the perianth and androecial whorls topped with a biovulate cupule (Krassilov & Bugdaeva, 1999).

Although preflower is conceived of as a condition preceding true flower, it can actually result from developmental transformation of a typical floral morphology. Developmental studies suggest that preflower structure can be primary as well as secondary, conferred by regulatory disorders and assimilated in the course of evolutionary development. A choice between these alternatives requires analysis of historical information as well as of the current tendencies in the floral morphogenesis, such as:

- (1) Transformation of spiral arrangement into decussate and verticillate arrangement, with irregular spiral – decussate and spiral – verticillate arrangement of fertile organs and subtending bracts as intermediate states;
- (2) Transformation of spiral-decussate arrangement into centripetal developmental sequence over fertile zones, which requires expansion of floral stalk into floral

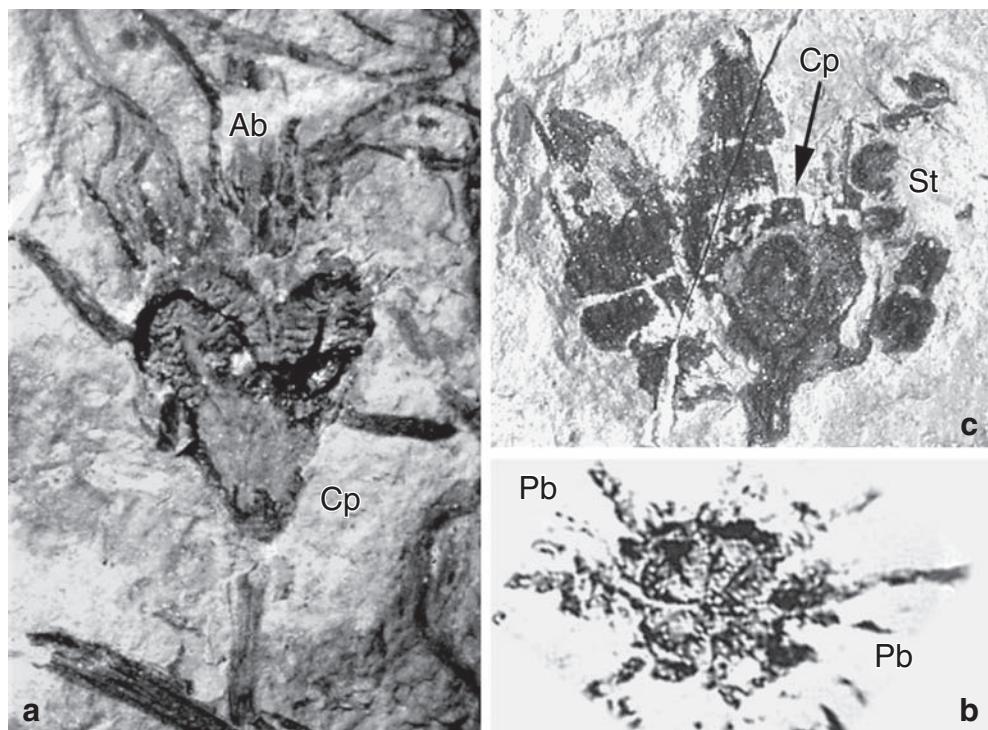


Fig. 36. Preflowers in the Early Cretaceous anthogonetophytes; a, *Eoantha zherikhinii* Krassilov, a four-lobed ovulate cupule (Cp) with an apical tuft of linear bracts (Ab); b, same in plane view, showing perianth bracts (Pb) (after Krassilov, 1982); c, *Preflosella nathania* Krassilov, the first monoclinous preflower with a perianth of broad bracts, an ovulate cupule (Cp) and sporangiophores (St) (after Krassilov & Bugdaeva, 1999).

- receptacle, in *Cercidiphyllum* incipient in the pistillate structures, but far advanced in the staminate structures, with the apical cluster well defined;
- (3) Weak developmental correlation between fertile organs and pherophylls, virtually lost in the staminate structures;
 - (4) Reduction of distal pherophylls in the pistillate structures;
 - (5) Elimination of pherophylls from the staminate zone;
 - (6) Foliation of the shoot system by the floral prophylls;
 - (7) Increase of leaf production by the floral structure – leafy shoot conversion;
 - (8) Foliation of reproductive structures by the bracteate pherophyll – leaf conversion and occasional production of ectopic pherophylls (empty bracts).

While the tendencies 1 – 5 indicate ongoing transformation of a preflower assemblage of fertile and sterile organs into incipient flowers, 6 – 7 may represent an opposite trend evoking a retrograde development of floral characters.

CARPEL TYPOLOGY

Carpels in *Cercidiphyllum* are rather typical follicles, a seemingly simple and putatively primitive carpel type. Its interpretation is however a matter of a lingering discussion. It was for long time held to be representative of a conduplicate megasporophyll, a widely accepted prototype of carpellate structures (Bailey & Swamy, 1949; Yan et al., 2007). This interpretation was supported by the SEM images of primordial carpels that supposedly became plicate at a very early developmental stage (Van Heel, 1987; Yan et al., 1987).

Here the carpel of *Cercidiphyllum* is described as consisting of an openly plicate stigmatic extension and a tubular ovary with an adaxially prominent midrib and super-convolute margins, therefore similar to the vernate prophylls and the leaf-like pherophylls except that the latter are inrolled toward their adaxial face. The converging margins, of which placenta is being formed, are orientated face to face with the likewise involuted leafy pherophylls. In transverse sections, both juvenile leaves and juvenile carpels appear horse-shoe shaped (Fig. 28). Cleared carpels show a fusion zone at the contact of the marginal coils at some distance from the edge. The placental ridge is formed over the fusion zone as a production of the fusion meristem. Free marginal leaf lobes form the outer integuments of primordial ovules the nucelli of which are differentiated as their axillary buds (Plate XVII, figs. 1 – 3; Fig. 28).

The carpels are, thus, revolute (wound toward their abaxial side) rather than conduplicate. Only the precociously developed stigmatic lobe that correspond to the glandulate leaf apex raised over the marginal coils qualifies as explicitly plicate. The sterile part formed of an excessively developed adaxial lobe overtopping the tubular growth is a feature of plicate carpel, the typology of which has been worked out by Troll (1932) and developed by Eber (1934), Baum (1952) and Rohweder (1967). It was originally introduced on account of ranunculid carpels with cylindrical ovary produced by congenital fusion of converging

margins forming the fertile cross-zone overtopped by an abaxial protrusion. Margin fusion is a variable feature in peltate carpels. It can be partly postgenital, incomplete, and scarcely forming an annular primordium that remains horse-shoe shaped in transverse section. Troll (1932) has designated such carpels as latently peltate or epeltate, but they do not differ from the typically peltate in the development of the sterile apical lobe and placentation (see also Leinfellner, 1958; Guédés, 1971; Weberling, 1989). The tubular growth of the ovary is partly due to the production of a thick placental ridge and swelling of the abaxial wall, in *Cercidiphyllum* with a possible contribution of carpel stipules that are normally indiscernible as distinct morphological structures (but appear as such in aberrant gynoecia).

Carpel in *Cercidiphyllum* thus can be seen as a variant of peltate type. However, its leaf prototype can be found not in the predominantly phyllodic ascidiform leaves of *Sarracenia*, sometimes used as a prototype of peltate carpels, but at the much closer quarters, in vernate foliage leaves and the leaf-like pherophylls of *Cercidiphyllum* plant itself.

A distinction from the typical plicate carpels, stressed by the proponents of the reduced inflorescence interpretation of pistillate morphology in *Cercidiphyllum* (Solereder, 1899; Harms, 1916) is the direction of coiling, towards the abaxial side (involute) in leaves, but toward the abaxial side (revolute) in carpels. In fossil *Eocercidianthus*, the follicles appear involuted like the leaves and even more leaf-like than in extant *Cercidiphyllum*, which implies that in the latter the opposite polarity of carpels is derived, resulting from inversion of coiling in the course evolution, perhaps facilitating seed dispersal by the outside dehiscence.

Guédés (1971, p. 225) has asserted that “the homology between floral and vegetative phyllomes is as obvious now as ever despite all ‘neo-morphologic delusions’, and this is still plainer when teratologic data are taken into consideration”. Under neomorphological illusions he included the cupular carpel concept by Long (1966) and the gonophyll concept by Melville (1969). Indeed, in the case of *Cercidiphyllum* at least, the homomorphism (but not necessarily the homology) of leaves and carpels is only too evident. It is accentuated by occasional development of delicate scales at the base of the carpels (in the fossil form also), corresponding to stipules, as well as by the gland – ovule homeomorphism.

OVULE – GLAND HOMEOMORPHISM

Juvenile carpels are similar to vernate leaves, the sterile apical portion corresponding to the glandular apex raised over the marginal coils. Cleared vernate leaves show marginal glands inside the sac formed by the doubly coiled margins and appearing very much like juvenile ovules distichous on the placental ridge. Transverse sections are horse-shoe shaped in both vernate leaves and carpels, with the glands topologically equivalent to the ovules except that marginal coils are free in leaves and the placental ridge is not formed (Fig. 28).

Both gland and ovule primordia appear as hemispherical lobes of homogeneous cells. In ovules, these lobes form the outer integuments later in development. In glands, they form the small-celled basal platform, or epithecum. The inner integument is differentiated as a collar-

like structure encircling the globular to dome-shaped nucellus formed of thin-walled cells with a nucellar beak as a low apical prominence. In glands, a girdle of thickened cells marks the base of a globular or dome-shaped body composed of thin-walled elongate cells, their butt-ends forming a smoothly rounded roof, sometimes with a prominent central papilla.

The ovules are vascularized by slender forking veins that depart from the placental bundles, enter on posterior side and curve up toward the base of the nucellus or else run to the sinuses sending arms to integumental lobes of both adjacent ovules (Plate XXVII, figs. 2, 3).

The vein pattern is quite similar to that supplying the marginal glands by short offshoots of the intramarginal veins, entering and extending short distance up the small-celled funnel-shaped basal platform (Plate IX, figs. 2, 3).

The gland – ovule similarity in shape, histological structure and topology accentuates the leaf – carpel homeomorphism, the evolutionary significance of which is discussed below.

SEED EVOLUTION

As mentioned above, the carpels in *Cercidiphyllum* are revolved their opening sutures to the outside, in distinction from the fossil form *Eocercidianthus*, in which they are involuted like the vernate leaves. An adaptive meaning of inversion might have been a facilitation of seed dispersal by wind. Indeed, shed carpels of *Eocercidianthus* contain unshed seeds, an unusual situation for *Cercidiphyllum* with its easy flowing seeds delivered to the outside through the abaxial suture. The ripe seeds are samaras in both the extant and fossil forms, but certain evolutionary changes are evident and seem congruous with evolution of carpels.

It is shown (above) that in *Cercidiphyllum* the wing of samara is not one-sided, as is often stated in the literature, but typically bilateral or nearly orbicular. One-sided wing is a rare anomaly recapitulating *Eocercidispermum* morphology. Relative to *Eocercidispermum*, seeds of *Cercidiphyllum* have evolved towards a larger size, greater wing length to seed body length ratio, nearly symmetrical bilateral wing shape, and the broadly looped raphal bundle. Such newly observed features of *Cercidiphyllum* seed morphology as a sclerified raphal ridge extending beyond the seed body over the micropylar wing lobe, as well as a forking of vascular bundle in the chalazal lobe are obviously correlated with expansion of the wing (Plate XXVIII, figs. 1 – 7).

The developmental sequence of ovule to seed polarity is from orthotropous at the time of open integuments and protruding nucellus to anatropous, with a chalazal wing and the posterior integumentary lobe only slightly expanded, to hemitropous, with the seed body turned at nearly right angle to funiculus or slightly curved (subcampylotropous). Notably, the hemitropous polarity is not transitional between orthotropous and anatropous, as the case may be in other angiosperms (Maheshwari, 1950), but secondary, owing to expansion of the wing between hilum and micropyle at a later developmental stage. The track of the raphal bundle has changed with configuration of the wing, first

straight between hilum and chalaza, as in the fossil form, then involved in the growth of the chalazal wing lobe, describing a loop with a branching tendency at the turning point and later stretched forward with expansion of the micropylar wing lobe. The raphal loop is obviously related to the sequential development of wing lobes, which may explain its parallel development in plant species that may or may not be phylogenetically allied.

STAMINATE TWO-STAGE FLOWER

Interpretation of staminate floral structure is the most controversial issue in *Cercidiphyllum* morphology. It is unduly affected by interpretation of the pistillate structures as condensed inflorescences. However, in the latter case such interpretation is based on the presence of bracts in the carpillary zone and the abaxial position of the opening suture, both arguments inapplicable to staminate structures. In many angiosperms, as well as gymnosperms (*Ginkgo*) staminate and pistillate structures represent different grades of morphological evolution, one inapplicable as a model for interpretation of the other.

While in the classical interpretations, pistillate flowers were envisaged as solitary carpels, a reduction of staminate flowers to a solitary stamen was not considered an option for *Cercidiphyllum*. Since homology implies topological equivalence, for the carpels and stamens being interpreted as homologous they should be similarly positioned in relation to subtending bracts. But the androecia are not endowed with so many bracts. Therefore, staminate “flowers” in *Cercidiphyllum* are usually described as clusters of stamens that are “indistinct” or “difficult to delimit” (Takhtajan, 2009, p. 105). Since two bracts is a norm in *C. japonicum*, the androecia, distinctly zygomorphous, would have only two flowers that are indeed difficult to delimit.

In fact, the bracts do not maintain a definite position in relation to stamens except in the case of underdeveloped or damaged (pruned) stamens that sometimes associate with supernumerary bracts and appear as distinct structures (Plate XIII, figs. 1, 2; Fig. 15). Such abnormalities do suggest a developmental correlation between stamens and bracts, but not of the nature of flowers and their perophylls.

The androecium of *Cercidiphyllum* is developmentally differentiated into irregularly concentric peripheral zones and a central group of a distorted spiral arrangement, in which separation of individual stamens is appreciably retarded. At the stage when peripheral stamens are well differentiated around the meristematic mass of still uncertain identity in the centre, or apex (Plate IV, fig. 4; Fig. 38a), the staminate structure is essentially a preflower. Then, after a developmental discontinuity, the activity of androecial meristem identity genes is fostered or released in the central zone and formation of the flower is completed.

The two discontinuous developmental stages are no longer discernible at anthesis. Both intact and sectioned androecia from floral buds do not show definite stamen clusters that could be interpreted as flowers, although stamens are somewhat irregularly distributed. Stamens stick to each other, and later in development the filaments inter-

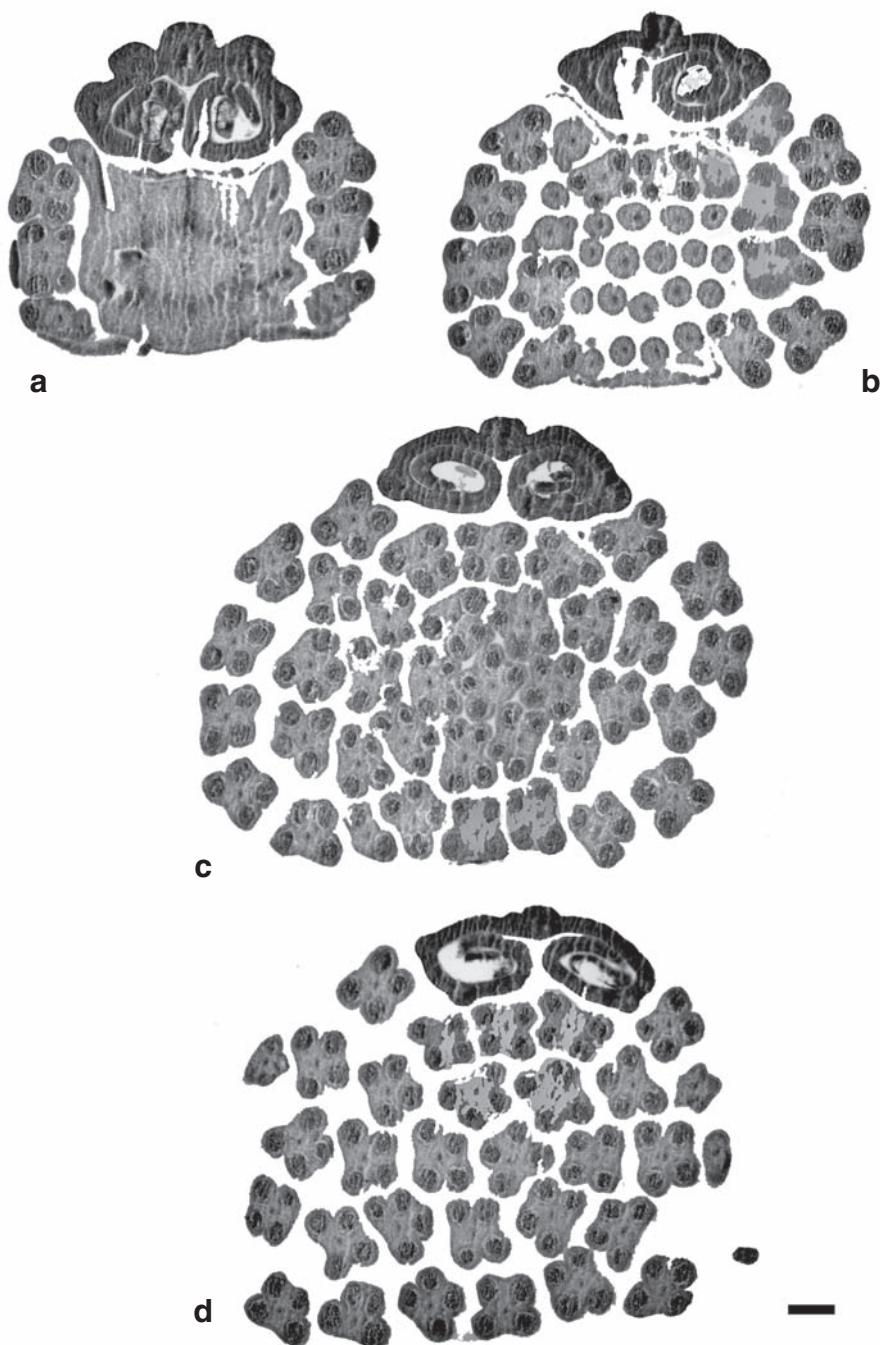


Fig. 37. *Cercidiphyllum magnificum* Nakai, Kew, transverse sections of staminate buds: stamen differentiation. Scale bar = 200 μm .

weave. Slight irregularities in distribution of stamens over the androecial receptacle can be found in *Cercidiphyllum* as in all androecia with many stamens. The central zone is completely occupied by stamens leaving no room to any axial structures (Fig. 37c, d). Yet Remizova (in Remizova et al., 2009) has found a bisporangiate stamen in the apical position among the central group of tetrasporangiate stamens, indicating an occasional deficiency of a stamen identity gene expression at the apex.

Pollen grains have been usually described as tricolpate, but the apertures are circular or nearly so, sometimes lalongate (stretched parallel to equator), with the encircling raised borders and exinal folds radiating from them. The coarsely granular pore membrane is puffed out rather than infolded. Triporate type is considered advanced over the tricolpate, but in *Cercidiphyllum* it is well expressed in unripe pollen grains, with a tendency of the pores being stretched at maturity. The pollen wall ultrastructure reveals such supposedly primitive features as nearly homogeneous tectum, irregular columellate infratectum, massive foot layer and a uniformly thick endexine.

CONVERSION, CONVERGENCE AND ECTOPIC DEVELOPMENTS

An intriguing feature of *Cercidiphyllum* are naturally occurring abnormal developments similar to experimentally induced mutations in *Arabidopsis* and other model plants of developmental studies. They fall into three categories designated as conversion, convergence and ectopic developments. In conversions, a plant organ is replaced by an organ of a different morphologically and functionally category. Convergence is a partial conversion, in which common characters are developmentally conferred on organs of different morphological/functional categories without change of function. Ectopic development is abnormal occurrence of an otherwise unaltered plant organ. These organographic anomalies are interrelated. At the level of genetic regulation they may differ as strong and weak expressions of a mutant gene.

Both *C. japonicum* and *C. magnificum* show the reproductive structures – leafy shoot and the subtending bract – leaf (leaf-like bract) conversions. A rare case of a carpel – leaf conversion was observed in *C. magnificum*. This species also exhibits ectopic bract development – the supernumerary empty bracts of pistillate structures, whereas an ectopic floral stalk was observed on top of a long shoot with elliptic leaves in *C. japonicum*. The inflorescence characters in the floral structures of the genus, as well as the carpel – leaf and the primordial ovules – leaf glands homeomorphisms are here interpreted as evolutionary assimilated developmental convergence.

Reproductive structure – leafy shoot conversion. Both pistillate and staminate structures can be involved in the floral axis – leafy shoot conversions that occur in occasional

short-shoot pairs or in one short shoot of a pair, its counterpart producing a normal floral structure. However, in some trees conversions may involve most short shoots of a branching system. The changes in conversion frequencies may be functional, regulating leaf mass production in response to environmental stimuli, although their environmental correlates are yet to be revealed.

A signal for the switch of a potentially fertile axis to sterile development must be of a local origin, often involving only one bud of a pair and perhaps related to occasional concentration of signaling matter, the nature of which can only be deduced from comparative developmental studies. The fact that sterilization involves few short shoots in one regional setting (e.g., *C. japonicum* from the MSU and MBG, Moscow) or many short shoots in another setting (Kew) may indicate an unknown environmental regulation component. Ongaro & Leyser (2008, p. 67) have concluded from experimental studies that “flexibility in axillary meristem activity makes possible substantial variation in shoot system architecture, allowing the plant to adapt its architecture to the prevailing

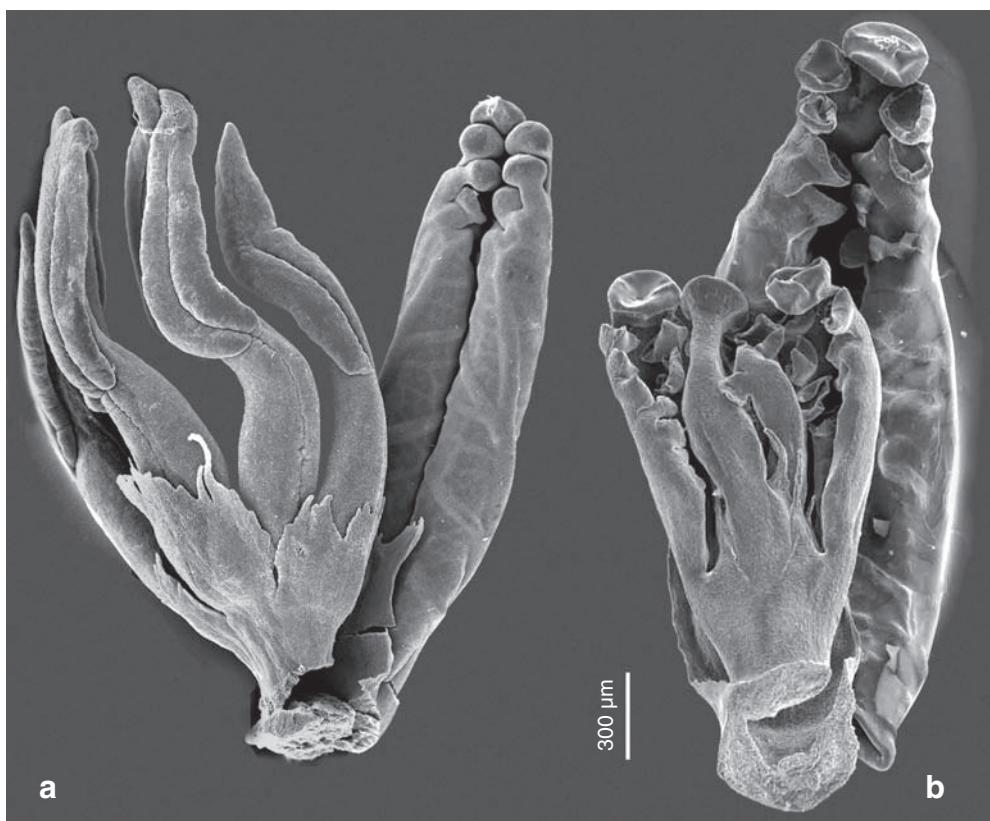


Fig. 38. *Cercidiphyllum japonicum* Sieb. et Zuc., Kew, gynoecium – leafy shoot conversion in the pistillate bud, SEM.

environmental conditions. Hence it is not surprising that axillary bud activity is regulated by a wide range of environmental inputs”.

The pistillate structure – leafy shoot conversions do not affect either the short shoot architecture or the morphology of its three cataphylls and a solitary prophyll of the floral axis that develop in a reniform foliage leaf, while the vicarious shoots produce elliptic foliage leaves. The leaves appear in three decussate pairs, as the carpels (Fig. 38), but their disposition is changed to distichous with elongation of internodes. An occasional ectopic development of a floral stalk on top of a vicarious leafy shoot reveals a potential for resuming floral development after the intervening period of leaf production.

Bract – leaf conversion. Sterilization of fertile shoots is not developmentally related to the replacement of the regular scaly pherophylls (subtending bracts of floral receptacle) by miniature leaves, which happens in about 1/5 of floral structures in *C. magnificum* and less frequently in *C. japonicum*. This aberration is inconsistent in sometimes involving all pherophylls or more often the lateral pair only or a single pherophyll of a set, but in all such cases one or more pherophylls show intermediate features between regular bracts and leaves.

The bract – leaf conversions seem developmentally regulated, the scaly bract shape being restored through a reduction series of transitional forms, from miniature leaves with well differentiated leaf blade and stipules to inflated stipules overgrowing the blade that gradually loses its morphological identity (Plate XIX, figs. 1 – 3; Figs. 39a – f, 40a – d). Alternatively, the stipules can be reduced, whereas the leaf blade is transformed into a linear bract.

Notably, the leaf-like bracts are identical to juvenile leaves of vicarious long shoots that replace fertile axes, both looking as miniature copies of vernate foliage leaves that are involuted their adaxial surface inside. In both, the stipules are distinct, although variably developed, laminar or hair-like. The disproportionately large marginal glands appear at the primordial stage already and are excessively developed at and near the apex. They disappear in reverse order when the vicarious tiny leaves are transformed into scaly bracts.

Probably relevant to the bract – leaf conversions of the type observed in *Cercidiphyllum* are the *terminal flower 1 (tf1)* mutants in *Arabidopsis*, in which individual flowers are supported by caulin leaves (Shannon & Meeks-Wagner, 1991).

Carpel – leaf conversion. In a 4-carpellate gynoecium with three normally developed and one leaf-like subtending bracts, one carpel is found to be replaced by a tubular structure with a massive apical gland, resembling a vernate foliage leaf (Fig. 26). It has two small bilobed stipules that are comparable to the delicate scales sometimes developed at the base of carpels in both extant *Cercidiphyllum* and fossil *Eocercidianthus*, here interpreted as carpel stipules. This rare conversion type may witness a developmental association of carpels and foliage leaves bearing on the problem of their homeomorphism.

The carpel – leaf homeomorphism is traditionally interpreted, in the spirit of Goethe’s (1790) ‘Metamorphose der Pflanzen’, as evidence of carpel derivation from



Fig. 39. *Cercidiphyllum magnificum* Nakai, Kew, bract – leaf conversion in pistillate buds with 5 – 6 carpels: a, with scaly bracts; b – d, with lateral leaf-like bracts bearing apical glands (arrows); e, f, with reduced leaf-like bracts lacking apical glands (s, stipules of the leaf-like bracts), SEM. Scales = 500 μ m.

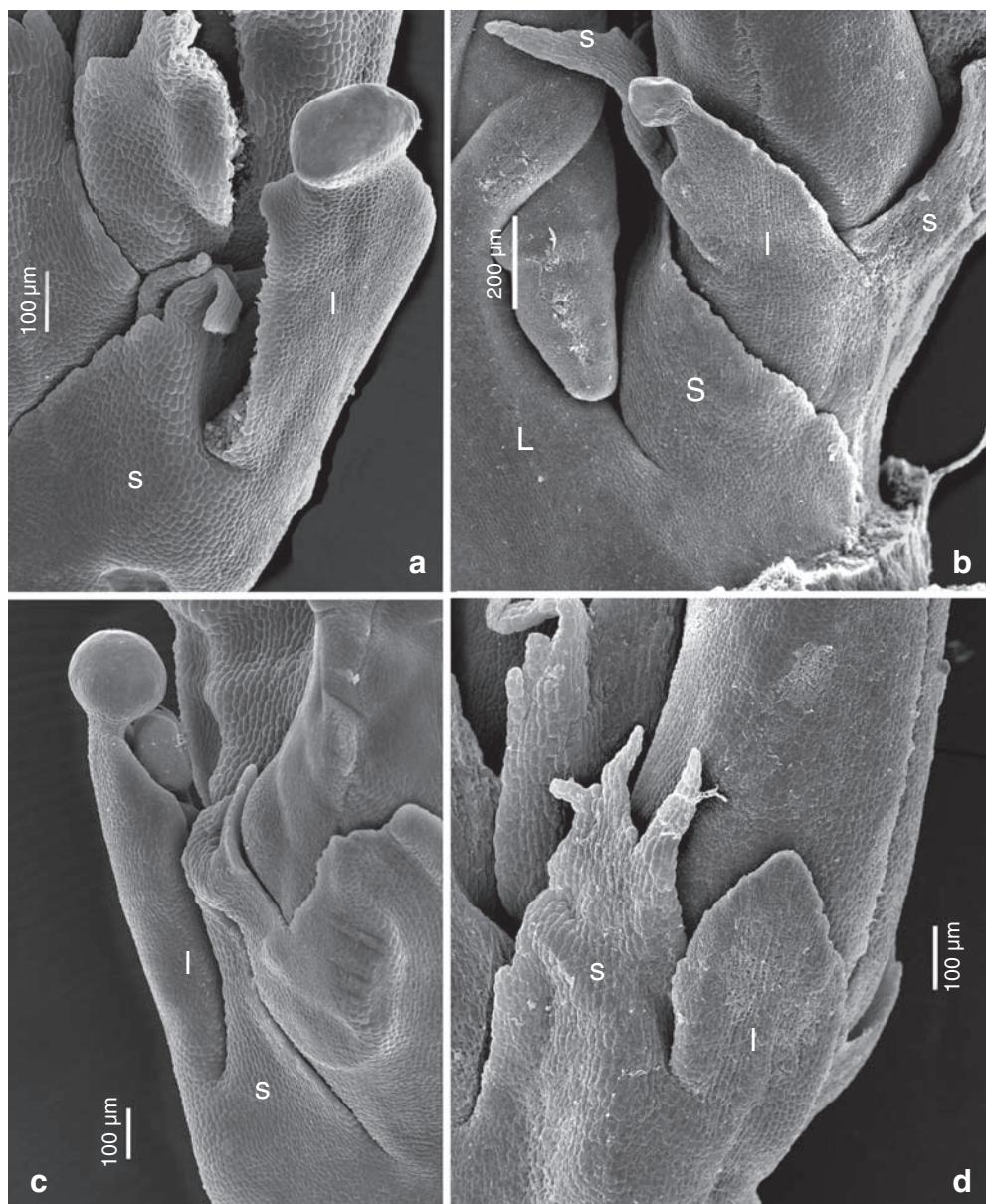


Fig. 40. *Cercidiphyllum magnificum* Nakai, Kew.: bract – leaf conversion in pistillate buds with 5 – 6 carpels: a, with a solitary median-abaxial leafy bract; b, with a spread lateral leaf-like bract; c, with involuted lateral leaf-like bract; d, with a somewhat reduced leaf blade and a prominent stipule (L, short-shoot leaf blade. S, short-shoot leaf stipule, I, leaf-like bract blade, s, leaf-like bract stipule, b, scaly bract), SEM.

fertile leaf (sporophyll). In *Cercidiphyllum*, not only the carpels are like vernate leaves, but also the ovules develop like the marginal leaf glands. The naturally occurring carpel – leaf conversions, although rare, seem to support the idea of the leaf – carpel homology.

However, in the absence of a plausible prototype in the immediate angiosperm predecessors, the homeomorphism might as well be acquired by convergence. Normally, organs of different functional commitments tend to diverge morphologically. In the case of follicles and leaves, no such tendency is observed, which suggests a developmental mechanism that sustains and possibly increases the morphological similarity of leaves and carpels facilitating their convergence.

The conversion – convergence phenomena in *Cercidiphyllum* find their analogies in mutant floral phenotypes of other angiosperms (mainly *Arabidopsis*, a model plant for developmental studies) caused by regulatory disorders. The developmental data on regulatory gene expressions in both floral and vegetative organ meristems, as well as on the loss of function in homeotic floral genes are immediately related to this problem. The *LEAFY* and orthologs, controlling activity of a number of homeotic ABC genes, are expressed in leaf primordia during the vegetative phase of growth increasing with approach to the floral transition. In *Arabidopsis*, *lfy* mutants may cause conversion of the first flowers on the floral shoot into leaves with their associated axillary meristems (Schultz & Haughn, 1991; Weigel et al., 1992), which may correspond to the supposed floral branch – prophyll conversion in *Cercidiphyllum* (above). Such and similar abnormal developments can be reversed to norm by activation of floral homeotic genes independent of LFY (Bowman, 1997).

The *TERMINAL FLOWER 1 (TFL1)* gene, the developmental role of which is opposite to that of *LFY* in determination of the flower/inflorescence meristem identities, is expressed both in vegetative and inflorescence meristems and controls both the length of the vegetative phase (flowering time) and the determination of the inflorescence shoot (Bradley et al., 1997). One of the remarkable effects of *tfl1* mutant is the development of cauline leaves supporting individual flowers (Shannon & Meeks-Wagner, 1991).

It is known from developmental studies that triple mutants lacking the ABC activity convert floral organs into leaves. On the other hand, ectopic expressions of ABC genes may induce a weak convergent tendency in cauline leaves, but fail to convert vegetative leaves into floral organs (Bowman et al, 1991a,b; Mizukami & Ma, 1992; Krizek & Meyerovits, 1996). Pelaz et al. (2001) have studied this problem by modifying expression of *SEPALLATA (SEP)*, an additional and largely redundant class of floral organ identity genes, the loss of which convert the B and C level floral organs into sepals. They found that in *Arabidopsis* a constitutive expression of A and B genes may cause a slight convergence of cauline leaves toward petals leaving the basal rosette leaves unaltered. However, by combining the AP1, AP3, and P1 transgens with those of SEP, it was possible to enhance the cauline leaf – petal convergence and even to achieve a nearly complete transformation of the rosette leaves into petals. The effect seemed to reflect the *SEP* expression levels (Pelaz et al., 2001). These experiments show that a number of developmental genes involved

in determination of the floral meristem identity can produce a mutant floral organ - leaf conversion or convergence, the morphological effects of which are correlated with the gene expression levels. When epigenetically transmitted, such changes in the expression levels might have played a crucial role in morphological evolution.

TAXONOMIC IMPLICATIONS

The present day taxonomic decisions are no longer based on a personal expertise in the field, but are "strongly recommended" by a well organized team of researchers (APG II), most of which are experts in a different fields. Legitimacy of such recommendations is questionable, to put it mildly. Anyway, they imply replacement of conceptualism by conventionalism, the purpose of which is to secure membership in the team in the first place. Molecular phylogeny is based on a number of assumptions, such as gradual evolution, molecular clock, adequacy of genomic and morphological events, as well as correspondence of morphological disparity to divergence time, none of which is rooted in factual evidence. It is acceptable as an analytical supplement to organismic phylogeny, but not as its substitute. "New" solutions provided by the molecular phylogeny turn out to coincide with anachronistic morphological solutions, such as the assignment of *Cercidiphyllum* to Saxifragales, once popular among plant morphologies, but abandoned 150 years ago (Baillon, 1871).

On the other hand, this study shows that new morphological facts can be found despite a long history of research. What we found in *Cercidiphyllum* may seem unique for the genus, but one cannot be sure before a broader survey is made.

Morphological features used in plant phylogeny and taxonomy are produced by morphogenetic processes of immense complexity and for the most part poorly understood. Among them, branching is one of developmentally most intricate, tuned by the fine balance of promotive and inhibitive factors (Ongaro & Leyser, 2008). Since branching mode lies at the base of other morphogenetic processes, it logically has to be given priority in phylogenetic reconstructions and classification.

Branching in *Cercidiphyllum* is rather unconventional and presently appears to be unique or seldom shared. The renovation bud develops in a pit at the base of leaf petiole, a feature shared with few lower dicotyledons, in particular, *Platanus* (Keeler, 1900). Enclosed buds represent an intermediate situation between exogenous branching of shoots and endogenous branching of roots, potentially of a high, but not yet realized, taxonomic value (despite striking difference in bud production, *Castaneophyllum* and *Platanus* s.s. are thought to be congeneric: Kubitzki, 1993).

The short shoot structure, with a solitary prophyll developing into a foliage leaf is shared with *Tetracentron* (Endress, 1993), otherwise unusual for extant angiosperms, but perhaps derivable from a condition known in *Clematis*, the Ranunculaceae, in which the fertile axis develops a solitary or a few prophylls before the terminal flower is produced

(Tamura, 1963, 1993). A unique situation in *Cercidiphyllum* is foliation of old branching systems by the short-shoot prophylls alone.

The long shoot – short shoot production is cyclic in *Cercidiphyllum*. Not only the short shoots arise from the leaf axils of long shoots, but also the long shoots are produced by the reproductive short-shoots. The replacement of fertile axis by leafy shoots is unique for *Cercidiphyllum*, but again finds a probable prototype in the Ranunculaceae with inflorescences produced by the axillary shoots after a period of vegetative growth (Tamura, 1993). In occasional long shoots of *C. japonicum* a floral receptacle was regenerated in a terminal position after producing several leaf pairs (Plate II, Fig. 3).

The long shoot phyllotaxy in *Cercidiphyllum* is spiral – distichous transformed into spiral – decussate or whorled in the short shoots. These kind transformations are well studied in *Ranunculus* and *Clematis*, with decussate arrangement arising as incomplete phylotactic series in the latter (Haccius, 1950; Tamura, 1980). Inconsistency of decussate pairing may suggest that in *Cercidiphyllum* this feature is secondary.

In both reniform and elliptical leaves, the primary venation is basically pedate, as in the entire-leaved Ranunculaceae and *Tetracentron*. The leaf glands seems unique, but this should be verified by more comprehensive comparative studies. The stomatal structure is anomocytic of ranunculid type, but in the hydathodal stomata encyclocytic, with an occasionally developing pair of small laterocytic subsidiaries, conceivably a derived condition.

The pistillate structures are usually considered to be reduced inflorescences on account of intercarpellate bracts, the interpretation extended to the staminate structures with no such bracts. Here the intermediate flower – inflorescence characteristics are associated with preflower rather than pseudanthium. No close analogies are found, but transitions form finite to infinite inflorescences in the Ranunculaceae (*Aconitum*) seem developmentally related.

The leaf-like subtending bracts may indicate derivation from prophylls, but they represent developmentally regulated conversions perhaps related to a general tendency of increasing leaf mass during evolutionary transition from herbaceous to arboreal habit.

The number of carpels varies among regional samples. Five can be more common number than four and six is not an exception. Moreover, three rather than four primordial carpels is a widespread condition of early development (Fig. 22). The gynoecium is more likely composed of two trios than two pairs, the decussate arrangement resulting from reduction of one member of a trio or both trios. It is therefore possible that in *Cercidiphyllum* the basic gynoecial structure is ternate rather than decussate, which may have a phylogenetic significance in view of the ubiquitous ternate arrangements in the Ranunculaceae.

Carpels in all lower angiosperms have been once interpreted as vernate – involuted or conduplicate – fertile leaves. The peltate concept is presently almost unanimously accepted for uniovulate carpels in the Ranunculaceae and is extended to multiovulate follicles as well, although Troll himself has designated some of them as epeltate (reviewed in Guédés, 1971; Weberling, 1989). In *Cercidiphyllum*, the adaxial lobe is precociously developed, followed by the tubular growth of the ovary. The carpels are strikingly similar

to vernate leaves of the same plant, seemingly a primitive condition, but actually perhaps derived (see above). The adaxial vs. abaxial dehiscence is a flexible condition in the Ranunculaceae, some of which having an intrusive placenta.

Early reduction of the inner integument in *Cercidiphyllum* ovules is a developmental feature found also in ranunculids with multiovulate carpels and bitegmic ovules. The ovule polarity evolves from orthotropous to anatropous to hemitropous (as in Ranunculeae), owing to a late expansion of the wing between the hilum and micropyle. A hair-pin loop of vascular bundle over the chalazal lobe is likewise related to expansion of the lobe, a process that can be responsible for a similar raphe configuration in the Trochodendraceae (Endress, 1993).

The centripetal stamen initiation and stamen morphology with a basifixed anther and protruding connective are widespread among lower dicotyledons, but lateral dehiscence is less common, occurring in *Euptelea* (Eupteleaceae), also comparable on account of pollen morphology, although the apertures are transitional from porate to shortly colporate in the latter genus. Large pores with raised radially plicate borders are more typically represented in the Ranunculaceae. In *Cercidiphyllum*, this apparently advanced apertural type associates with a rather primitive irregularly baculate infrastructure, massive foot layer and slender uniformly developed endexine.

To conclude, *Cercidiphyllum* shows a combination of primitive and derived character states as can be expected of a survivor of a basal angiosperm lineage. Not enough is known to discriminate between uniquely derived characters and homeomorphies, but reproductive characters, such as the carpel type or seed morphology, heavily bearing on taxonomic decisions, seem more likely to be homeomorphies than the branching pattern, foliation, prophylls and glands.

The leafy shoot production in reproductive line is matched by the Ranunculaceae (although occurring as a rare development in other families). The reproductive shoot morphology indicates affinities to the Eupteleaceae and Trochodendraceae, the latter similar in the floral prophylls developing into foliage leaves.

Intrafloral phyllomes might have been common in initial flowers (preflowers) and were retained in some extant hamamelid genera. The carpel structure as here interpreted finds its equivalents in the ranunculid cluster mostly. The seed shows a hair-pin loop of raphe bundle as in the Trochodendraceae (where it can also be ascribed to chalazal expansion), but differs in the secondarily hemitropous configuration and in bifurcation of the vascular strand. The triporate apertural type occurs in derived ranunculids, while the laterocytic stomata is typical of trochodendroids.

We agree with Swamy and Bailey (1949, p. 205) in that “nothing is to be gained in transferring such genera as *Tetracentron*, *Trochodendron*, *Euptelea*, and *Cercidiphyllum* into close relationship with Hamamelidaceae or Saxifragaceae...”. Morphological comparisons lead us to comply with Takhtajan (1969, 2009), Smith (1971), and Rao (1986) in placing this genus, together with the closely allied fossil forms, in a separate order Cercidiphyllales, supposedly one of several small satellite orders of the Ranunculales.

8. RELEVANCE TO GENERAL PROBLEMS OF PLANT EVOLUTION AND DEVELOPMENT

Morphological evolution is an alteration of developmental patterns. Before the advent of the so-called synthetic theory of evolution (which is in fact a model of population polymorphism puffed out of all proportions at the expense of more significant theoretical components), the relationships between development and evolution constituted the core of evolutionary theory developed by such personalities as Serres, Agassiz, Muller, Darwin, Cope, Eimer, Garstang, Bolk, Scindewolf, Goldschmidt, and others (reviewed in Krassilov, 1977a). Its most comprehensive analysis and formalization can be found in Severtsov (1939). Major evolutionary changes were represented as *deviations* from developmental pattern typical of a taxon, including *coenogenesis* (regulated deviation of early developmental stages) and *phylembryogenesis* (non-regulated deviations giving rise to new phylogenetic developments). *Pedomorphism*, or non-regulated deviation in early development, *fetalization*, or “surfacing” of juvenile character states in adult forms, *neoteny*, or precocious reproductive development were widely discussed as sources of fundamental evolutionary (macroevolutionary) novelty extensively supported by paleontological and recent material. Such abbreviations of the typical developmental sequences gave way to new directions of evolutionary advancement maintained by prolongation of development, or *anaboly*.

‘Synthetic’ theorists, ever alert to the host of Lamarck, mounted a formidable opposition to the phylembryogenetic mechanisms of macroevolution that were proclaimed typological, old-fashioned, and, above all, irrelevant. In effect, this concept was ousted from evolutionary biology to be re-discovered, after half a century of silencing and destruction, by the present day “evo-devo” studies.

MORPHOGENESIS AND ORGANOGRAPHIC RULES

In plants, developmental studies are focused on regulation of organ-specific meristems. Organography of a plant species is determined by regularities of meristem production in regard of the positional information conferred on the dedicated cell lineages. Organoraphic patterns convey developmental regulations that are obligatory for all mor-

phological domains or specific for each of them. Thus, *Cercidiphyllum* appears to observe a unified organographic rule over the hierarchy of branching points. The short-shoot renovation point is produced at an unequal division of floral axis giving rise to the floral stalk and prophyll of a stem-like petiole anatomy. Renovation bud is sunken in a pit at the base of petiole and is subtended by the stipules. The primary growth points develop into renovation buds producing, after a period of dormancy, the short-shoot increments or contributing to the long shoot production. Renovation meristem is systematically regenerated as satellite growth points when required by topological information. Yet satellite growth points may develop into blind buds with no organ produced.

The basic unit of organographic pattern is an asymmetrical pair of foliar – floral structures that is reproduced, with miniaturization, down the hierarchical branching system. A hierarchy of leafy structures is produced in the process, all involuted toward their adaxial surface, facing the fertile organ of the pair. When a carpel is replaced by leaf, a blind bud develops in the axil of it. When the carpel stipules are present, they also associate with a blind bud.

We are used to think of unrealized structures as of phylogenetically reduced, which is not necessarily the case. Developmental rules like one described above require production of meristematic points in all the topologically equivalent positions, which does not mean that all such growth points had ever realized their morphogenetic potentials. Blind growth points need not be invariably interpreted as a testimony of a structure lost to reduction in the course of evolution. Although progenitorial floral structures might have had more hierarchical levels than are normally represented in the present day *Cercidiphyllum*, there is no ground for assuming a lost axis at each satellite growth point or adding imaginary carpels on account of assumed axes. No unequivocal evidence of transformed racemes has ever been presented for *Cercidiphyllum*, and the manifest conservatism of branching style since the mid-Cretaceous (*Eocercidianthus*) practically excludes such alien architectures in the lineage.

In *Cercidiphyllum*, the leaf – fertile structure pairing is invariably observed in the basal carpels and their pherophylls, but is violated in the subsequent pairs by reduction and loss of pherophylls (Fig. 24). The number of bracts does not correspond to the number of carpels because of bract reduction in the distal bract – carpel units as well as on account of empty bracts in the basal whorl or even interspersed with carpels, as in Plate XXII, figs. 1 – 3. Bract reduction is somewhat erratic, mostly involving the median pair, but in a considerable number of cases not two, but only one of the median pair is reduced. Free parts of subtending bracts can be completely lost to reduction, but decurrent parts (cushions) persist in the whorl.

The developmental correlation of carpels and pherophylls is disturbed in the pistillate structures and is practically lost in the staminate structures on the way of pherophyll transformation into the perianth-like bract whorls. Stamens develop in a centripetal sequence and are indistinctly clustered in no definite topological relations to the androecial bracts, except in teratological cases. The lateral and median bract pairs are unequally

developed or the latter are missing giving the androecia a conspicuous zygomorphy. Such structures require a far going deviation from the basic developmental rule giving rise to a more flower-like pattern over the preflower – true flower gradient.

In transformation of fertile receptacles into leafy shoots, the asymmetric floral stalk – prophyll division is replaced by the nearly symmetric production of the slightly unequal decussate leaf pairs. The homomorphism of organographic pattern in the fertile and their vicarious leafy structures is evident to the point when decussate leaf pairs are clustered on top of a peduncle-like basal internode. The juvenile leaf fascicles look much like the carpel fascicle before elongation of subsequent internodes that transforms them into distichous shoots.

These may be incidents of phylembryogenesis, but regulated coenogenesis also occurs. The scaly subtending bracts can be replaced by small leaves that are identical to foliage leaves in vernal mode and are differentiated into a glandular leaf blade and stipules. However, in later development the leaf-like pherophylls are transformed into scaly bracts that slightly if at all differ from typical bracts in occasionally showing the residual stipules or glands. The intermediate morphologies indicate that bracts of a typical cuneate or flabellate shape are formed of fused stipules that overgrow the blade, while linear bracts may consist of the blade alone or with the vestigial stipules at base.

Both the leaf-like bracts and conversion of fertile axis into a leafy shoot in *Cercidiphyllum* can be inflicted in the same way as in the *lfy* mutants in the model plants of developmental experiments (above). At the same time, recognition of morphological phenomena corresponding to mutations of developmental genes in such a relict plant as *Cercidiphyllum* may reveal their evolutionary significance.

The experimentally induced conversions of inflorescences into flowers and replacements of floral organs by leaves are caused by mutant expressions of the meristem identity genes and are at least partly reversible. Thus, in *Arabidopsis*, conversions of flowers into leaves caused by *lfy* mutants and the orthologous gene mutants in the other model plants (Schultz & Haughn, 1991; Weigel et al., 1992) can be regulated – reversed to norm – by activation of floral homeotic genes independent of LFY (Bowman, 1997).

Alternatively, a mutant gene expression releases the effect of regulatory genes, as in the *LFY* – *TFL1* interaction. In the *tfl1* mutant, the vegetatively biased floral meristems can be reverted to the norm by the ectopic expressions of *LFY*. Regulated deviations are of no consequence for phylogeny unless the pedomorphic characters are maintained through such processes as fetalization or neoteny, by which they acquire a major role in angiosperm phylogeny.

ANGIOSPERM ORIGIN AND PHYLOGENY

Recent progress in developmental studies has evoked a revision of evolutionary ideas based on comparative morphology and paleobotany. Since flower is considered to

be the major definitive structure of flowering plants, all evidence on regulation of floral development is potentially relevant to the problem of origins and evolution of the phylum.

LEAFY (LFY), a transcription factor that controls expression of homeotic genes that specify floral meristems is represented by a single copy in distinctions of the supposedly paralogous gene *NEEDLY (NLY)* in gymnosperms, two copies of which is required for differentiation of pollinate and ovulate organs. The LFY null mutant in *Arabidopsis* makes no stamens but still produce carpels, suggesting that *LFY* is required for male specification, but carpels can be specified by the LFY independent genes (Frohlich & Chase, 2007).

The universal role of *LFY* in angiosperms gave rise to an evolutionary model, in which the single copy *LFY* initially specified all-male reproductive structures. Female parts then appeared by ectopic transformations (Frohlich, 2003; Frohlich & Chase, 2007). A switch from *NLY* regulation to *LFY* regulation is considered to be a critical phylogenetic event underlying basic morphological restructuring and further evolution of angiosperm clades (Albert et al., 2002; Frohlich, 2003; Frohlich & Chase, 2007; Theissen & Melzer, 2007; Hamés et al., 2008).

Theissen and Melzer (2007) have applied the ABC and its derived ABCDE regulation models for explaining the origins and diversity of floral structures (in both models, the floral organ identities are determined by a combination of regulatory factors specific for each consecutive whorl of a conventional flower). They concluded that a typical ABC system might have originated from a more bizarre system by “sharpening” of ABC gene expression domains and the organ borders. At this, the shifting boundaries of ABC gene expressions may have contributed, independently in different angiosperm lineages, to diversification of flowers.

Pelaz et al. (2000, 2003) experimented with *SEPALLATA* mutants converting all floral organs into sepals and in various combinations with the A and B genes converting leaves into petals. They consider floral organs – leaf conversions as evidence in favor of Goethe’s (1790) theory of leaf as a basic structure from which all plant organs had derived.

The relevance of these and similar inferences from molecular developmental studies to morphological evolution can only be ascertained by joint efforts of molecular biologists, plant morphologists and paleobotanists. At this, morphological revision of even the most thoroughly studied plant species is as eminent as their molecular level “evo-devo” research. Molecular data have been so far obtained for a few model species and are not available for fossil plants. Extrapolations from these data assume similarity of naturally occurring morphological phenomena to those experimentally produced in the model plants.

Yet integration of data requires a deeper level reconciliation of methodological approaches. As in the case of molecular phylogeny (e.g., the assignment of Cercidiphyllaceae to Saxifragales, see above), conclusions form molecular developmental studies may suffer from uncritical adoption of dilapidated morphological theories. On the

other hand, developmental studies may alter traditional approaches to interpretation of morphological data.

As noted above, classical morphology adopts perfect development as a starting point, from which the less perfect states are derived by deviation and reduction, which provides a framework for evolutionary analysis. Yet it makes the origins enigmatic by systematically confusing incipient with vestigial. New developmental studies need not follow this track by automatically interpreting organ conversions and ectopic developments as residual ancestral conditions unless reliable historical precedents exist.

TENDENCES OF FLORAL EVOLUTION

Conversions, known to classical morphologists as metamorphoses, have inspired evolutionary thinking, if but in a speculative way. Goethe (1790) sought to explain plant metamorphoses by adopting leaf as a basic structure. Yet he was not particular about what came first. His Mephistopheles says:

Der Wein is saftig, Holz die Reben,
Der hölzerne Tisch kann Wein auch geben

In the Neo-Platonic spirit of the time, he believed in the essential oneness and interconvertibility of all things. Decandolle (1824) had developed Goethe's philosophical ideas into a morphological theory that became dogmatic and scarcely yielded even after the discovery of early land plants that produced sporangia and even cupulate seeds without producing leaves. Leaves appeared rather late in the history of plant kingdom, which implies their derivation from other organs.

Turning back to Guédés' (1971, p. 225) assertion that "the homology between floral and vegetative phyllomes is as obvious now as ever despite all 'neo-morphologic delusions'...", it must be reminded that all possible carpel prototypes in gymnosperms are not leaves. In the present day gymnosperms, the ovules can be enclosed in seed-scales with a stigma-like ligule (*Araucaria*) or in bracteate cupules (Ghetales). Paleozoic pteridosperms have produced cupulate ovules, whereas in glossopoterids the ovulate receptacles were enclosed by calyptrate leaf-like bracts, a prototype of the gonophyll model (Melville, 1963, 1969). At the late Mesozoic time of angiosperm origins, there were uniovulate and multiovulate cupules with apical appendages, as in *Baisia* (Baisiales) and *Eoantha* (Eoanthales) (reviewed in Krassilov, 2009). The cupules of *Caytonia* were described as a circinate leaf, but were reinterpreted by Krassilov (1977b) to be an urn-shaped cupule with a transverse opening subtended by a protruding abaxial lobe or "lip". In advanced species of *Leptostrobus* (Czekanowskials), the bipartite cupules had papillate stigmatic crests (Krassilov, 1997). Each of these enclosure types could have been transformed into peltate carpels without mediation of ascidiform leaves, a highly specialized leaf type occurring in advanced angiosperms.

The carpels of *Cercidiphyllum* might have served as evidence of derivation from leaves because of their conspicuous leafiness, but the fact that they resemble leaves of the same, rather than some progenitorial, plant provokes a suspicion that we in fact are dealing with a partial conversion or convergence of foliar and floral organs, a phylogenetically recent phenomenon, associated with (a) prophyll – foliage leaf conversion, (b) floral bract – leaf conversion and (c) reproductive structure – leafy shoot conversion. For all these cases, vegetative bias of floral primordia is the most plausible hypothesis.

A teratological example of ectopic ovule development on *Ginkgo* leaves is often reproduced as a prototype for angiosperm “megasporophyll”. Yet fossil ginkgophytes never showed foliar “megasporophylls”, which makes this example phylogenetically meaningless. It is in fact opposite to the floral – foliar conversions observed in *Cercidiphyllum*, illustrating the floral bias of a leaf primordium.

A general cause for such biases can be regulatory genes expressed, like *LFY*, in both floral and foliar meristems. Since morphological distinctions between reproductive and foliar structures are sharper in gymnosperms, it is logical to assume an increase of morphogenetic role of such ambivalent regulators over the gymnosperm – angiosperm transition.

An interpretation of floral structures in *Cercidiphyllum* as extremely congested inflorescences of extremely reduced flowers (advanced since Solereder, 1899 and persisting to Takhtajan, 2009) is in accord with the currently prevailing morphological paradigm, in which any atypical or imperfect floral structures is likely to be interpreted as congested or reduced. Yet flower must have evolved from a progenitorial form that was not a typical flower.

Insofar as angiosperms have descended from gymnosperms, there must have been transitional reproductive structures between strobili and flowers, such as *anthostrobili* or *pre-flowers* (Krassilov, 1997). Anthostrobili are cones with vericillate arrangement of basal sterile bracts (pericone) and bracteate seed/pollen organs, as in the bennettites and the recently recognized Mesozoic group of anthogonetophytes (Krassilov, 2009). Pre-flowers are analogous structures, but with sterile elements reduced or on the way of complete elimination from the apical zone, as seems to be the case in *Cercidiphyllum* and allied angiosperms.

An advanced group of cycadeoid bennettites (*Cycadeoidea* and allies) were cauliflorous with short unbranched stems covered with massive “flowers”. The anthogonetophytes were the low stature microphyllous plants with few phyllodic leaves and prolific reproduction. In both these groups, the anthostrobili were either dichinous (unisexual) or monoclinous (bisexual). A bennettitalean “flowers” typically had a perianth-like pericone differentiated into morphologically distinct outer and inner bracts. The androecial structures were leaf-like, typically pinnate, but the gynoecial structures were represented by stalked ovules mixed with peltate interseminal scales. The anthogonetophytes like *Eoantha* (Fig. 36) had a pericone of numerous linear bracts. The floral axis protruded above the whorl of bracteate ovules and was crowned with sterile bracts, similar to, but shorter than the pericone

bracts. An incipient ABC regulation system must have existed at this evolutionary level already, but scarcely permitting the floral meristem gene expressions to invade the apical zone (as it happens in the *tf1* inflorescence phenotype, see above).

From these comparisons, a progenitorial floral structure can be reconstructed as a preflower with vestigial sterile organs in the fertile zone. The pistillate reproductive structures in *Cercidiphyllum* correspond to this level of evolutionary advancement, with a tendency of further reduction and loss of intrafloral phyllomes. The tendency is further advanced in the staminate structures of the same plant, which are, technically, flowers, although retaining a discontinuous two-phase ontogenesis reminiscent of the preflower – flower transition (Fig. 38). Final consummation of the tendency is countered by the foliation tendency conveyed in the carpel – leaf, bract – leaf and fertile receptacle – leafy shoot conversions, showing that in the history of the lineage the vegetative bias of floral primordia might have at least periodically prevailed over the floral bias of foliar primordia.

During the transitional period, many plants of the anthostrobilus grade might have passed through the preflower – flower transformation, in which the balance of regulatory genes responsible for the fertile organ development and those maintaining vegetative growth was shifted toward fertilization of the apical zone and segregation of ABC genes have occurred. The diversity of floral structures may reflect an initial variation at the anthostrobilus – preflower level and/or secondary modifications in the LFY – ABC system, including secondary foliation of floral structures, as the case might have been in *Cercidiphyllum*.

Although liable to ectopic organ developments, the reproductive structures of this genus are strictly diclinous, never showing a slightest vestige of opposite sex. This, and the different levels of advancement in the pistillate and staminate structures, suggest that dicliny is primary in the lineage.

NEOTENIC TRANSFORMATION

Unlike in other gymnospermous and angiospermous trees with dimorphic long and short shoots, in *Cercidiphyllum* reproductive structures are converted into leafy shoots, and the short-shoot leaves (floral prophylls) foliate most of the branching system. This means that vegetative body of this plant is partly or mostly produced in the reproductive line, which suggests a neotenic ancestral form, in which vegetative body was much reduced relative to the reproductive sphere. Later in evolutionary history, the vegetative body was re-built in the lineage on the way to arboreal forms, with foliation of the floral receptacles and the carpel – leaf convergence as side effects of the process. Therefore, the lineage represents a phylembryogenic cycle starting with neotenic transformation (abbreviation of vegetative development) and proceeding in the prolongation (anaboly) mode.

Neoteny in plants is a special case of accelerate reproduction, in which vegetative growth prior to flowering is reduced to a scapose form or a short corm with a solitary

or few basal leaves resembling reproductive short shoots of descendent arboreal forms. In the latter case (presumably in *Cercidiphyllum*) reproductive short shoots may reiterate growth form of a neotenic ancestral plant.

Accelerate development is accompanied by shortening of internodes, verticillation and fusion of metamerous organs. Fusion is a byproduct of overlapped (telescoped) sequential developmental events, giving rise to hybrid fusion meristems of great morphogenic potentials. The phenomenon is of a very general significance in angiosperms, extending from leaves of phylloclade origin, with a new type of plate meristem arising from fusion meristem of original leaves or leaflets, to synflorescence, sympetaly, synandria, syncarpy, etc.

In *Cercidiphyllum*, apocarpy is maintained due to incomplete reduction of floral bracts that are only incipiently whorled. The leaf – bract transformation, in which the leaf blade and stipule identity is partly or completely lost in fusion is a step in perianth initiation, with both mono- and dichlamydeous perianths conceivably arising on the basis of the blade – stipule differentiation: the leaf blade lost to fusion results in a single whorl of bracteate tepals, or the inner and outer whorls of dimorphic tepals (sepals and petals) is formed of the leaf blade and stipules, respectively. The leaf blade – stipule origin can be inferred for the lemma – palea differentiation in grasses and their homologous structures in other monocots.

Flowers are assemblages of foliar and floral organs integrated by accelerate development, organ fusion, conversion and convergence over the separate, but interrelated homeodomains. As such, flowers require a more elaborate network of developmental regulators than gymnosperm cones. In the process of their evolutionary origin, a top controlling element, like *LFY*, must have been recruited among universal developmental genes forming short cuts to regulatory expressions of a greater number of homeotic genes than in any other group of higher plants.

More than one angiosperm lineage might have passed through neotenic transformations before the basic diversity of flowering plants has emerged. The process is evident at the anthogonetophyte level already represented by small herbaceous plants with phyllodic leaves and relatively massive preflower structures (Krassilov, 2009). Such neotenic morphology is a step back relative to the dominant Mesozoic gymnosperms, suggesting a simpler developmental regulation system. Replacement of the double-copy *NEEDLY*, a top determinant of gymnosperm reproductive development, by a single-copy *LEAFY* and orthologous genes as its substitutes in angiosperms can be assessed as a set-back in terms of developmental regulation, eroding boundaries of homeotic gene domains and facilitating organ conversion and characters convergence. *Cercidiphyllum* offers examples, such as foliar characters bestowed on the carpels (follicles) that are similar to vernate leaves of the same plant, with ovules developing in the position of marginal glands. Yet prospectively it was a set forth of a more flexible dosage-dependent boundary condition between leaves and floral organs (their respective meristem identities). A potential advantage of such regulation system lies in a broad involvement of leaves and their

morphological derivates in the reproductive/dispersal activities that led to a higher level of functional and structural integration.

From these general considerations we can try to deduce progenitorial forms of flowering plants and suggest how *Cercidiphyllum* relates. *Cercidiphyllum* is characterized by flexible development of floral characters that can be ascribed to ectopic expression of genes defining meristem identity and morphogenesis. At the same time, there is a system in its flexibility revealing character states (such as the leaf-like bracts and transitions to conventional bracts) that can be related to “retro-ectopic” gene expressions simulating a progenitorial morphology and considered to be atavistic at the level of morphological analysis.

Our idea of morphological primitiveness is mainly based on retro-ectopic gene expressions that betray an unaccomplished system of developmental regulation that persists in a precocious state through time. In *Cercidiphyllum*, the time appears to be about 90 million years. The basic morphology has appeared in the mid-Turonian already. The further development has mainly advanced the features (long stigmas, abaxial suture, and papery free-flowing samaras) related to anemophily and anemochory, but scarcely affected the mainstream regulation of meristem production.

Neotenic features in extant *Cercidiphyllum* are represented by the short-shoot leaves (floral prophylls) functioning as foliage leaves, as well as by ectopic foliation of floral receptacles, and most expressively in the precocious fertility of ovules that are still primordial at anthesis (Plates XXV – XXVII). They suggest an ancestral form, in which a drastic reduction of vegetative growth took place. Taking the short-shoot morphology as the basic for the lineage, representing neotenic progenitorial features, we can surmise an ancestral growth form with a discoid stem and three basal leaves, the third calyptrate, protecting floral bud, of which an unbranched fertile axis with a solitary prophyll and a terminal floral structure of a few ovulate and/or pollen organs have been produced.

With acquisition of perennial habit, new corm was produced by the floral bud that was regenerated axillary to the prophyll and imbedded in the petiole – a feature of endogenous branching characteristic of underground organs (Fig. 41). Further increase of plant body took place by producing secondary leafy shoots replacing the fertile axes, with a satellite prophyll and an axillary bud at each node. While increase in the plant body size was taken over by the secondary long shoots, the ancestral form was reiterated by the reproductive short-shoot morphology.

A developmental machinery with ambivalent regulatory gene expressions in foliar and floral primordia that are reciprocally biased might have invoked two opposite evolutionary tendency in *Cercidiphyllum* and phylogenetic allies: (1) centripetal reduction and elimination of sterile organs from the apical zone and (2) secondary foliation of floral structures. Our idea of advancement in the floral morphology reflects the net effect of these tendencies. When mainstream evolution has periodically switched from one tendency to another, as the case may be in *Cercidiphyllum* lineage, the phylogenetic interpretations are controversial.

For verification of this scheme we must turn to historical information conveyed by the fossil record.



Fig. 41. *Cercidiphyllum japonicum* Sieb. Et Zuc., MSU: a, dormant bud sunken in a pit at the base of petiole (S, stipules); b, dormant bud emerging at the leaf maturity, only stumps of stipules are left (S), SEM.

INFERENCE FROM PALEOBOTANICAL DATA

A widely held idea of early angiosperms entering the Mesozoic fern – gymnosperm communities as solitary newcomers and gradually outcompeting resident species does not comply with paleobotanical data. In fact, early angiosperms were never found amidst dominant Mesozoic forms of ferns or gymnosperms, which mean that they failed to penetrate undisturbed Mesozoic communities. Their superiority over Mesozoic gymnosperms was not evident over the main stable habitats of the latter. They appeared, together with herbaceous anthognethophytes of a similar habit, as members of the newly formed pioneer wetland communities (Krassilov & Bugdaeva, 1999, 2000), as well as colonizers of fresh fallouts in volcanic landscapes (Dilcher et al., 2007; Krassilov & Volynetz, 2008). Such communities became widespread at the time of environmental crisis caused by massive intracontinental and marginal volcanic activity (reviewed in Krassilov, 2003).

Early angiosperms for which the whole plant material is available were rhizomatous with tubers. Characteristic of this stage were the compound-ternate leaves as in *Hircantha* (Krassilov et al., 1983; Dilcher et al., 2007) or *Achaenocarpites* (Krassilov & Volynetz, 2008), and the basically 3-carpellate gynoecia (transformed into 6-carpellate, with 5 or 4-carpellate reduced variants). The relatively large blossoms were inflorescences of many small flowers, as in *Caspiocarpus* (Vakhrameev & Krassilov, 1979; Krassilov, 1984). Detached flowers found among small plant debris might come from disintegrate inflorescences. Calyptrate inflorescence bracts occur in *Freyantha* (Krassilov & Golovneva, 2001). Perfect flowers seem rare, becoming widespread at the next stage in the Cenomanian – Turonian (Krassilov, 2003), when the heterochlamydeous perianths also appeared (*Callicrypta*: Krassilov & Golovneva, 2003). Hypanthial flowers are mainly a later development as well (Krassilov et al., 2005). Apocarpy is the prevalent mode, with spiral carpels incompletely transformed into decussate or whorled. Carpels are follicles, as well as one-seeded nuts or achenes. Seeds are small and wingless landing near disseminating plants. Pollen grains are tricolpate semitectate in the dominant other groups of early angiosperms, some lineages of which, including *Cercidiphyllum*, evolving toward the porous tectate structure with a change of pollination syndrome (diverse dispersed pollen types have been ascribed to early angiosperms, but few were confirmed by *in situ* finds, a critical evidence in view of a widespread convergence of co-existing Early Cretaceous anthogonetophytes and angiosperms, see Tekleva & Krassilov, 2009).

These character assemblies indicate ranunculid affinities of *Caspiocarpus*, *Freyantha*, *Callicrypta*, *Achaenocarpites*, *Hyrcantha*, *Ternaricarpites* and allies, a sizable part of the Early Cretaceous angiosperm diversity based on the whole plant and whole flower fossil records. The Albian – Cenomanian ranunculids are a group of early angiosperms sharing some critical character states with the Ranunculaceae, Menispermaceae, Sargentodoxaceae and the other extant families of ranalean plexus, but scarcely assignable to any of these families, differentiation of which might have occurred much later in the history of angiosperms.

Among them, *Ternaricarpites floribundus* Krassilov & Volynetz is phylogenetically important as a possible link between the Early Cretaceous ranunculids and the later appearing cercidiphyllids. It is reconstructed as a rhizomatous, sympodially branched plant, scapose or with a few basal leaves. The flowers are terminal or sometimes axillar at branching nodes, opposite to a scaly prophyll. The bracteate perianth is a broad slightly zygomorphous whorl of 5 unequal bracts, connate at base, with a dense open venation as in the basal leaves. The fruit is a ternate follicetum of dorsididal follicles with numerous seeds filed along the abaxial suture. This plant, therefore, qualifies for a herbaceous precursor of what might potentially develop, with a manifold increase in size, into the peculiar cercidiphyllid branching pattern and reproductive structure.

Achaenocarpites, another rhizomatous plant from the same plant assemblage (Fig. 31) produced compound stipulate leaves and globular heads of small achenes, representing another line of ranunculid evolution supposedly linked to platanoids, a dominant mid-Cretaceous group with a solitary extant genus *Platanus*. Such widespread forms as

Sapindopsis, assigned to the Platanaceae on account of globular heads (Crane et al., 1993), seem related to *Achaenocarpites* and are here considered to be transitional between the mid-Cretaceous ranunculids and platanoids.

The tendencies recognized in the Early Cretaceous ranunculids were realized in the mid-Cenomanian – Turonian cercidiphyllids and platanoids that were essentially modern in both their vegetative and reproductive morphology. These phylogenetic events coincided with new developments in the community structure of the Cretaceous vegetation. Broadleaved forms appeared in the mid-Albian already, but at this stage (and through the Late Cretaceous in temperate regions) they were constantly associated with numerically prevailing conifers and perhaps confined to undergrowth of the needle-leaved forests. Fossil progenitors of *Cercidiphyllum* (*Eocercidiphyllites* – *Eocercidianthus*: Krassilov et al., 2005) belong to a relatively advanced stage of angiosperm evolution, when broadleaves became dominant in the arboreal plant communities, growing side by side with platanoids in the primeval angiosperm forests of southern Negev.

Thus, cercidiphyllids and platanoids are bound by common evolutionary history. They also share some developmental features rare in early angiosperms, such as renovation buds embedded in the leaf petioles. By this considerations, cercidiphyllids and platanoids might have been sister groups of ranunculid derivation. Trochodendrocarpoids, once considered to be immediate predecessors of *Cercidiphyllum*, differ in the pairwise syncarpy of their follicles gathered in racemes or panicles of a considerable morphological complexity, as well as in the cone-like staminate spikes of spiral bracts subtending axillary flowers. The pollen grains were tricolpate with long colpi (Krassilov & Kodrul, 2008). Their ancestry can be sought among the early hamamelids, constituting a minor component of the Early Cretaceous angiosperm communities and showing parallel developments to the ranunculid group. Yet much more has to be learned of early angiosperms before a historically valid phylogenetic scheme would emerge.

In the *Cercidiphyllum*-like plants from the mid-Turonian of the Dead Sea area (Krassilov et al., 2005), the pistillate structures (*Eocercidianthus*) were of the same level of complexity as in extant *Cercidiphyllum*, thus casting doubt on the reduction hypothesis. The mature foliage leaves (*Eocercidiphyllites*) had prominent marginal glands like in the juvenile leaves of extant *Cercidiphyllum*, in which the glands are shed or reduced at maturity. The follicles were even more leafy, with a well-developed system of scalariform transverse veins and sometimes with persistent carpel stipules (Plate XXX, fig. 6). The seeds were smaller, with rudimentary wing lobes.

The later history of the lineage is an example of evolutionary conservatism, with a few innovations, such as long stigmas, abaxial dehiscence, and papery free-flowing seeds being related to anemophily and anemochory, the effectiveness of which might have increased with plant size. However, the pistillate structures were fixed at the pre-flower stage owing to a flexible balance of the floral and foliar meristem production, enabling interconversions and convergence of fertile and sterile structures. Elimination of sterile structures from apical zone is further advanced in the staminate structures approaching the true flower condition.

9. CONCLUSION

Phylogeny, the origin of taxa, is a complex process that cannot be inferred from one set of data, but requires an interchange of evidence and ideas derived from evolutionary biology, comparative morphology, experimental morphogenesis and the fossil record. In this work, phylogeny of *Cercidiphyllum*, an archaic angiosperm, is reconstructed on the basis of developmental morphology and paleobotany, upon the guidelines provided by the phylemryogenetic theory of evolution

Cercidiphyllum, a relict genus of a lineage traced back to the mid-Cretaceous, is peculiar among the arboreal broadleaved angiosperms in the cyclic development of dimorphic branching system, including the reproductive short shoots arising in the axils of the long shoot leaves and the long shoots produced as the short shoot branches. The branching system is mainly foliated by the prophylls of reproductive shoots developing into foliage leaves. Thus, the bulk of vegetative body in this archaic angiosperm develops as ramifications of reproductive short-shoots. Its ancestral forms are thereby reconstructed as neotenic, switching to reproduction in early development.

The naturally occurring conversions of floral structures to leafy shoots resemble the experimentally obtained mutant expressions of regulatory genes controlling floral meristem identities in *Arabidopsis* and some other phylogenetically advanced angiosperms.

The floral structures, controversially interpreted as either incipient flowers or reduced inflorescences, seem to have been developmentally affected by the growth form morphogenesis, showing frequent floral bract to leaf conversion, rare carpel to leaf conversion and the carpel to leaf convergence.

The ambiguous floral morphology of *Cercidiphyllum* is here interpreted as a long-standing balance of conflicting tendencies of (1) elimination of sterile structures from the apical floral zone on the way from pre-flower to typical flower and (2) secondary foliation of the floral structures.

It is suggested that morphological peculiarities of *Cercidiphyllum* are evidence of a cyclic evolutionary history starting with gymnosperm forms of a well balanced vegetative and reproductive development. Through the gymnosperm – angiosperm transformation, the balance was disturbed by neoteny, a developmental regulation phenomenon accelerating reproduction relative to vegetative growth, with a more flexible regulation network coming to specify the floral and foliar meristem identities, the boundaries between which

were to a certain extent eroded, resulting in bizarre forms conveying a flexible regulation network. A dosage sensitive determination of meristem identity, as in the case of *LEAFY*, might have promoted developmental integration of foliar and floral structures, involving leaves in accessory reproductive functions.

The evolutionary potentials of neotenic forms lie in a higher level integration of floral and foliar structures, which is a precondition of new organs, flowers and carpels, rapidly appearing at the neotenic stage already. In the next round of morphological evolution, prolongation of vegetative growth and increase of plant body mass required floral – foliar conversions that affected the entire morphological structure, introducing vegetative bias to the floral meristems.

At the same time, the shortening of internodes and verticillation of lateral organs, associated with developmental acceleration, with subsequent functional differentiation of successive whorls might have led to parallel development of ABC type regulation system in the cycadeoid bennettites, anthogonetophytes and early angiosperms. In all these groups, phyllomes were either interspersed with floral organs or even proliferated in the central zone of receptacle, suggesting a less expressed apical dominance of the floral organ identity genes than in the modern flowering plants. In a few conservative forms, like *Cercidiphyllum*, the ancestral conditions were fixed at the essentially pre-flower level of floral development.

In the next round of morphological evolution, a size increase and rebuild of vegetative complexity in the arboreal line might have promoted the fertile structures – leafy shoot conversions, conferring leafy characters on reproductive organs. These processes might have enhanced morphological diversification of angiosperms. The ABC regulation system of homeotic gene expressions achieved high precision with functional differentiation of floral whorls, but was rendered flexible for the leaf mass to reproductive effort ratio being regulated by the floral – foliar interconversions. In regard of this model, the fossil record of weedy early ranunculids at the base of the cercidiphyllid lineage appears meaningful, although still incomplete.

The fossil record as we now know it is not intrinsically imperfect, as it is depicted in Darwin's "Origin of Species". It may be just not up to our expectations, which means that our expectations are grounded in imperfect theoretical premises. In particular, the gradualist expectations never come true because evolution is not gradual. Likewise, a one-directional course of evolution cannot be confirmed, because evolution is not one-directional.

On the one hand, any set of data is imperfect, and on the other hand the data are meaningless in the absence of theoretical guidelines for their analysis. This fully applies not only to paleontological, but also to experimental molecular data that offer a glimpse into the genetic regulation machinery, but do not cope with "so what" questions. Floral organs are experimentally shown to be conversable to leaves. Is it a confirmation of Goethe's foliar theory? Unlikely, since the foliar theory is disproved by the paleobotanical record of leafless early land plants. Does it still hold for angiosperms? Unlikely again,

because early angiosperms, and even the anthogonetophytes, were neotenic forms that developed not so many leaves. For example, *Ternaricarpites*, an Early Cretaceous angiosperm putatively ancestral to the cercidiphyllid lineage, does not seem to have produced cauline leaves at all. With increase in plant body size, foliation became a problem that might have been (partly) solved in the cercidiphyllids line by conversion of reproductive shoots into leafy shoots and floral organs into leaves. This model has to be tested by integrative morphological, developmental and paleobotanical studies.

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PLATES

Abbreviations:

BIN – Botanical Garden of Botanical Institute, Russian Academy of Sciences, St-Petersburg;
Kew – Royal Botanical Gardens, Kew;
MBG – Main Botanical Garden of Russian Academy of Sciences;
MSU – Botanical Garden of Moscow State University.

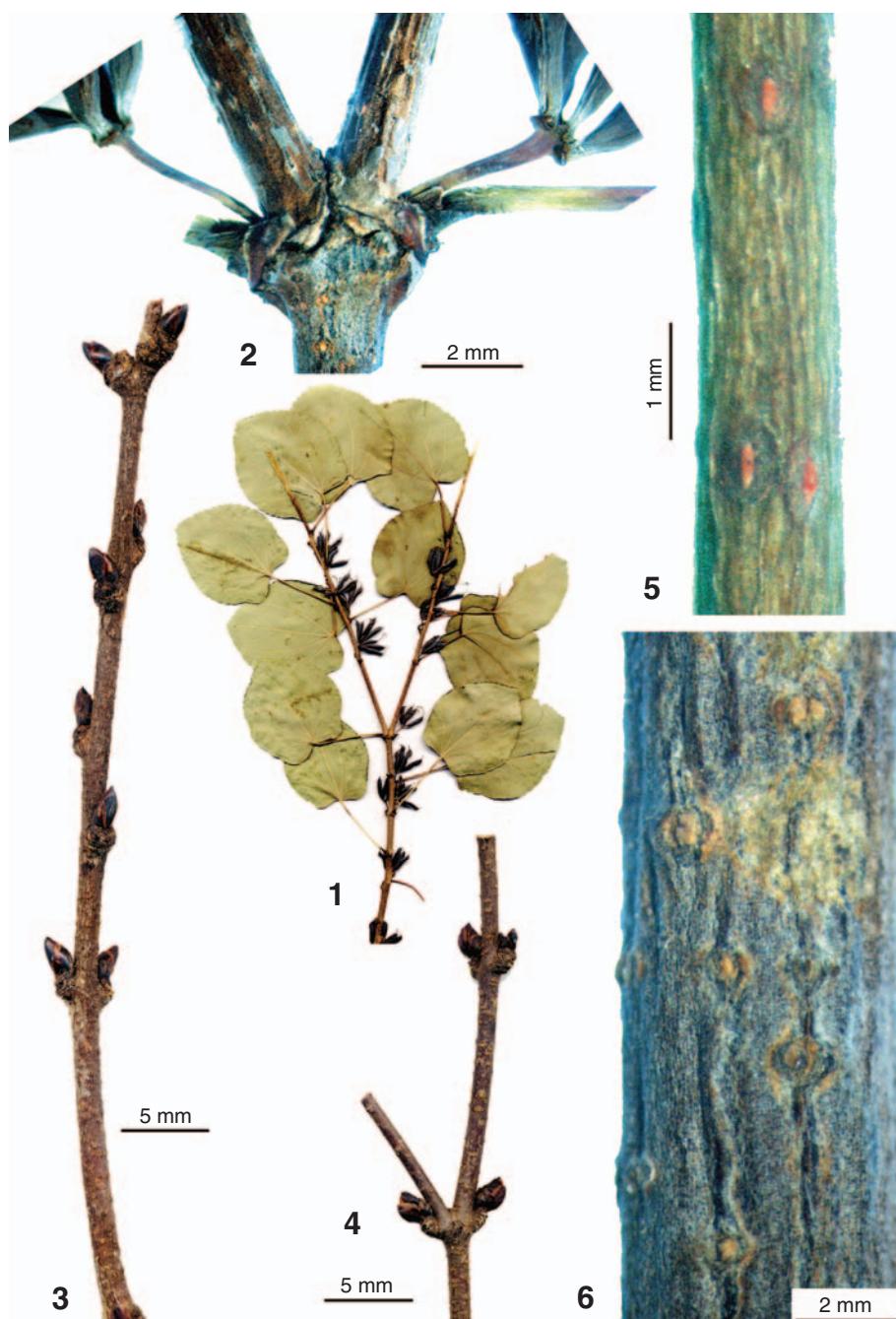


Plate I. *Cercidiphyllum japonicum* Zieb. et Zuc., MSU: 1, branching shoot system foliated with the reniform short-shoot leaves; 2, long shoots diverging from a pair of pistillate short shoots; 3,4, transitional alternate – geminate short shoot phyllotaxy; 5, 6, lenticels of young (5) and old (6) axes.

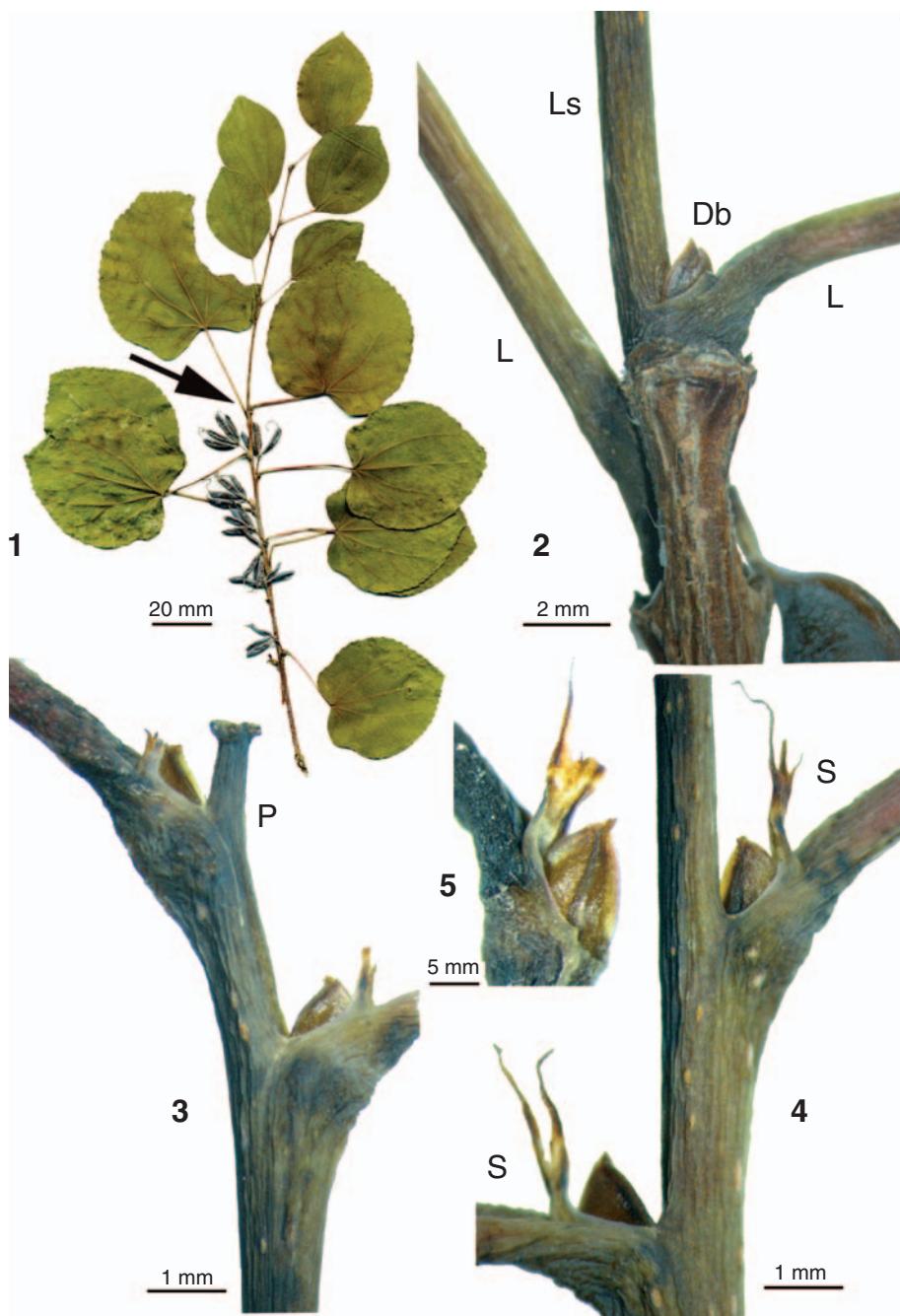


Plate II. *Cercidiphyllum japonicum* Zieb. et Zuc., MSU: 1, shoot system foliated with the reniform short-shoot leaves continued by a slender axis with distichous elliptical leaves (Ls); 2, node (at arrow in fig. 1) at which Ls arises in the position of a reproductive axis, with a dormant bud (Db) in the leaf axil; 3, floral stalk (P) terminal on a long shoot; 4, 5, persistent leaf stipules (S) of elliptical leaves.

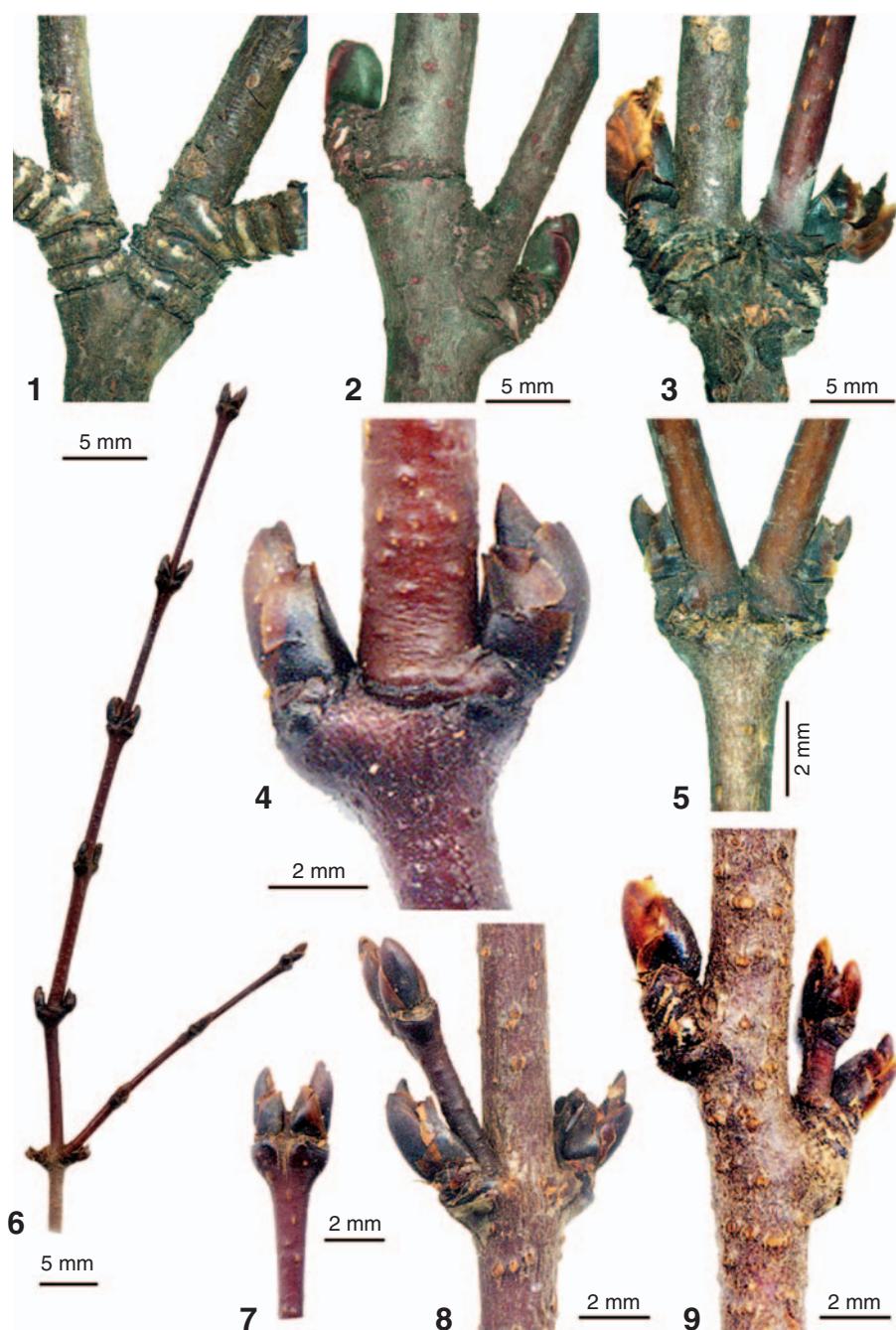


Plate III. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU: 1 – 9, examples of long branches arising from the basal or subsequent short-shoot increments (comments in the text).

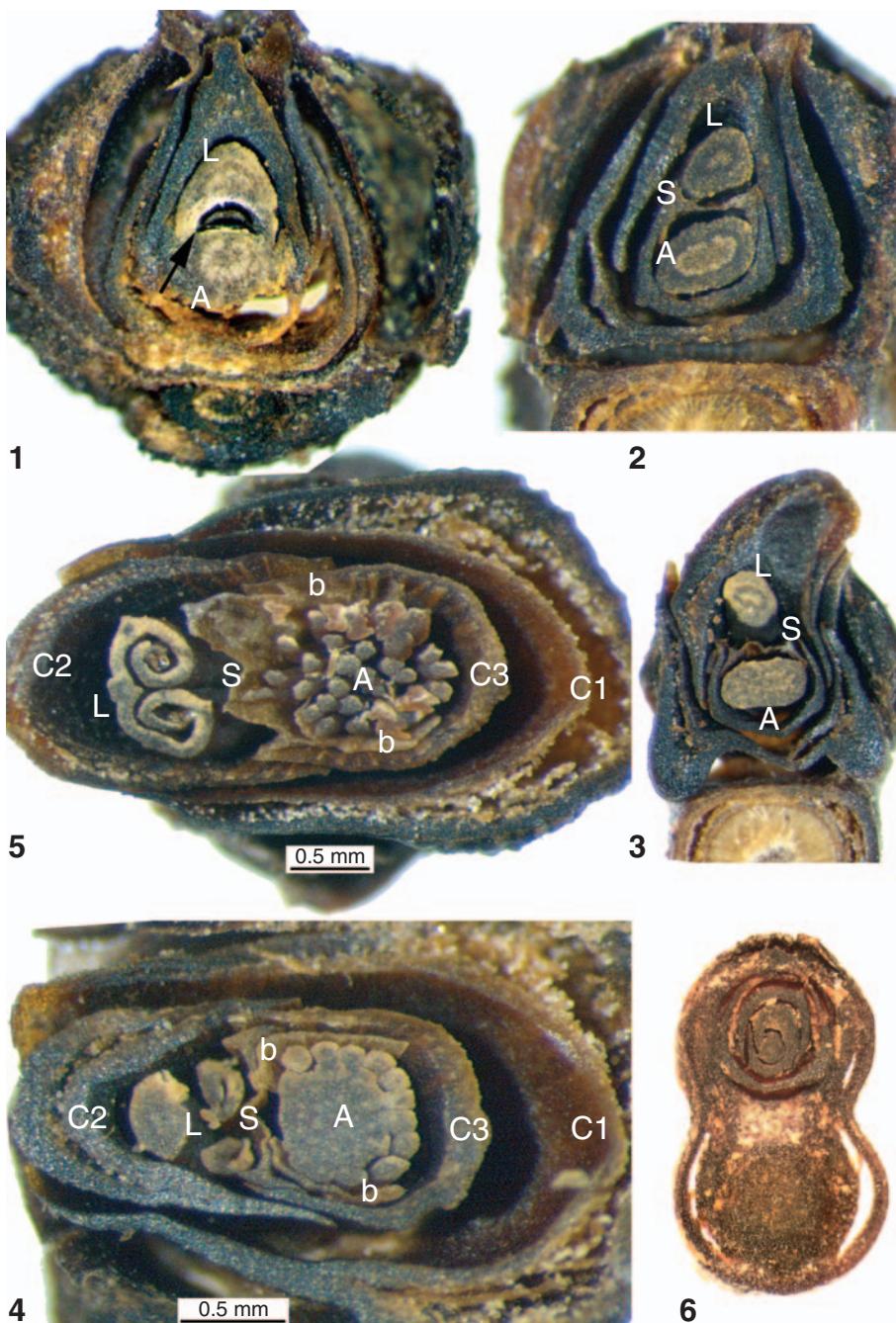


Plate IV. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, hand cut staminate buds: 1 – 5, successive levels of leaf – androecial stalk divergence; dormant bud is seen at arrow in Fig. 1; stipule is distinct from the level of Fig. 2 on; bracts and separation of peripheral stamens are evident in Fig. 4 (A – androecium, b – bract, C1 – 3, cataphylls, L – leaf, S – stipule); 6, paired short shoot buds cut perpendicular to the long shoot axis.



Plate V. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU: 1 – 3, leaf blade, stipule and androecium gradually released from the calyprate cataphyll III; 4, bud with cataphyll I cleft, exposing the involuted cataphyll III; 4, 5, shapes of leaf stipules.

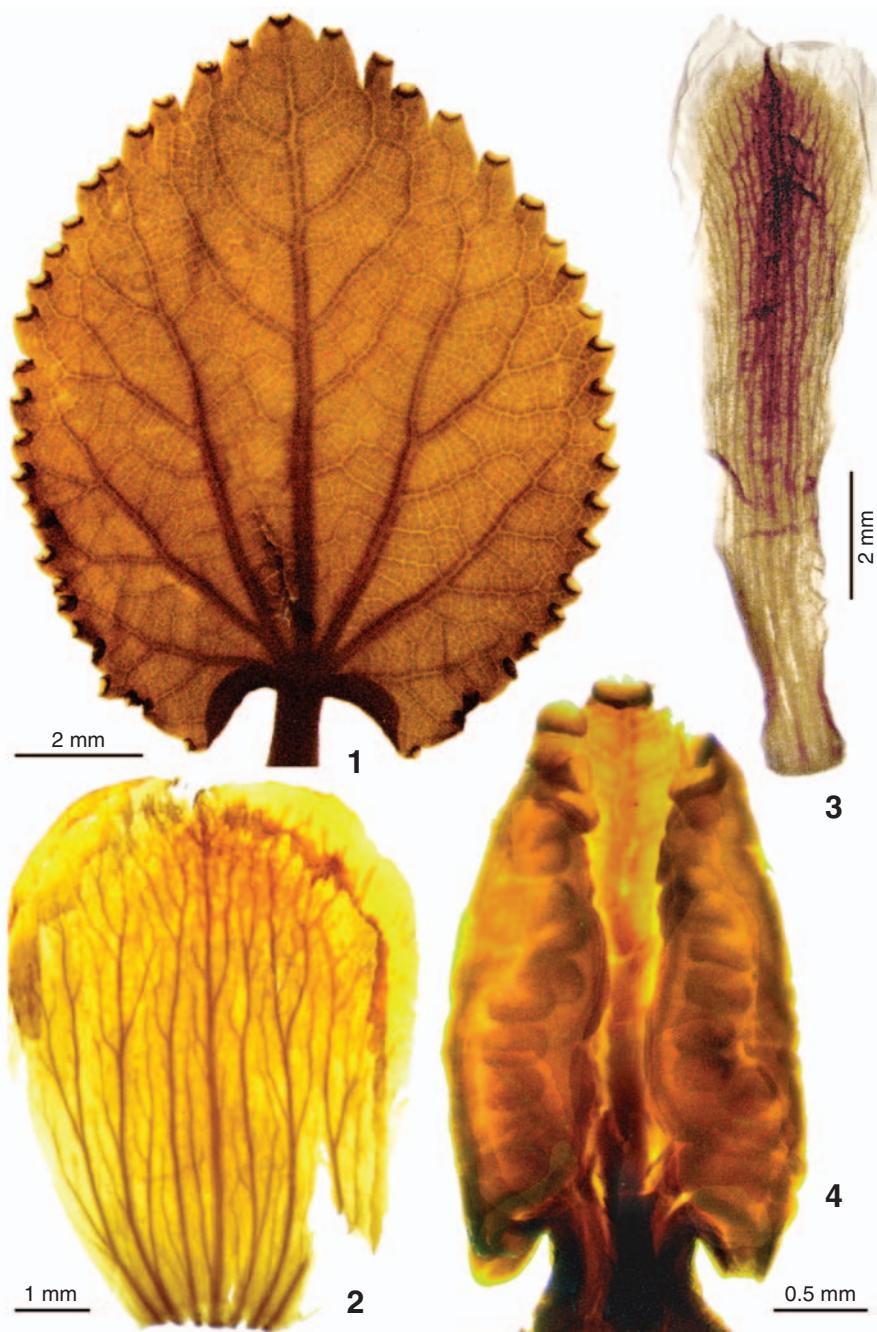


Plate VI. *Cercidiphyllum magnificum* Nakai, BIN: 1, mechanically spread vernate reniform leaf at anthesis, 2, spread cataphyll III in bud; 3, cataphyll III at anthesis; 4, partly spread vernate leaf in bud.

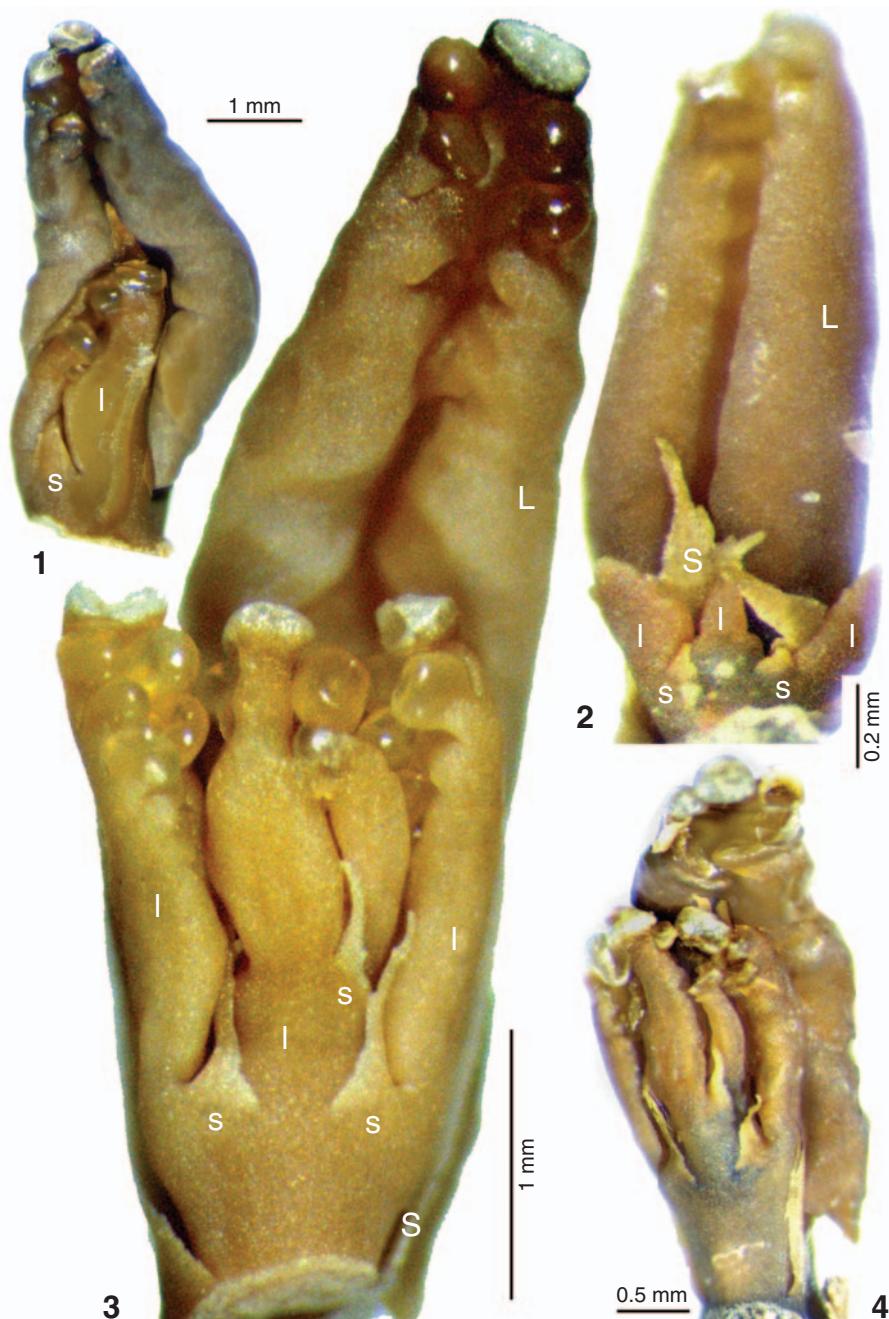


Plate VII. *Cercidiphyllum japonicum* Sieb. et Zuc., Kew: 1 – 4, various stages of leafy shoot development replacing reproductive structures in the short shoot bud, note apical glands and filiform stipules (L -short shoot leaf, I – new shoot leaf, S – short shoot leaf stipule; s – new shoot leaf stipule).



Plate VIII. *Cercidiphyllum japonicum* Sieb. et Zuc., Kew: leafy shoot development replacing reproductive structures in the short shoot bud: 1, 2, two leaf pairs are produced, 3, basal elongation starts at the three leaf pair stage; 4, basal internode rapidly elongates before emergence.

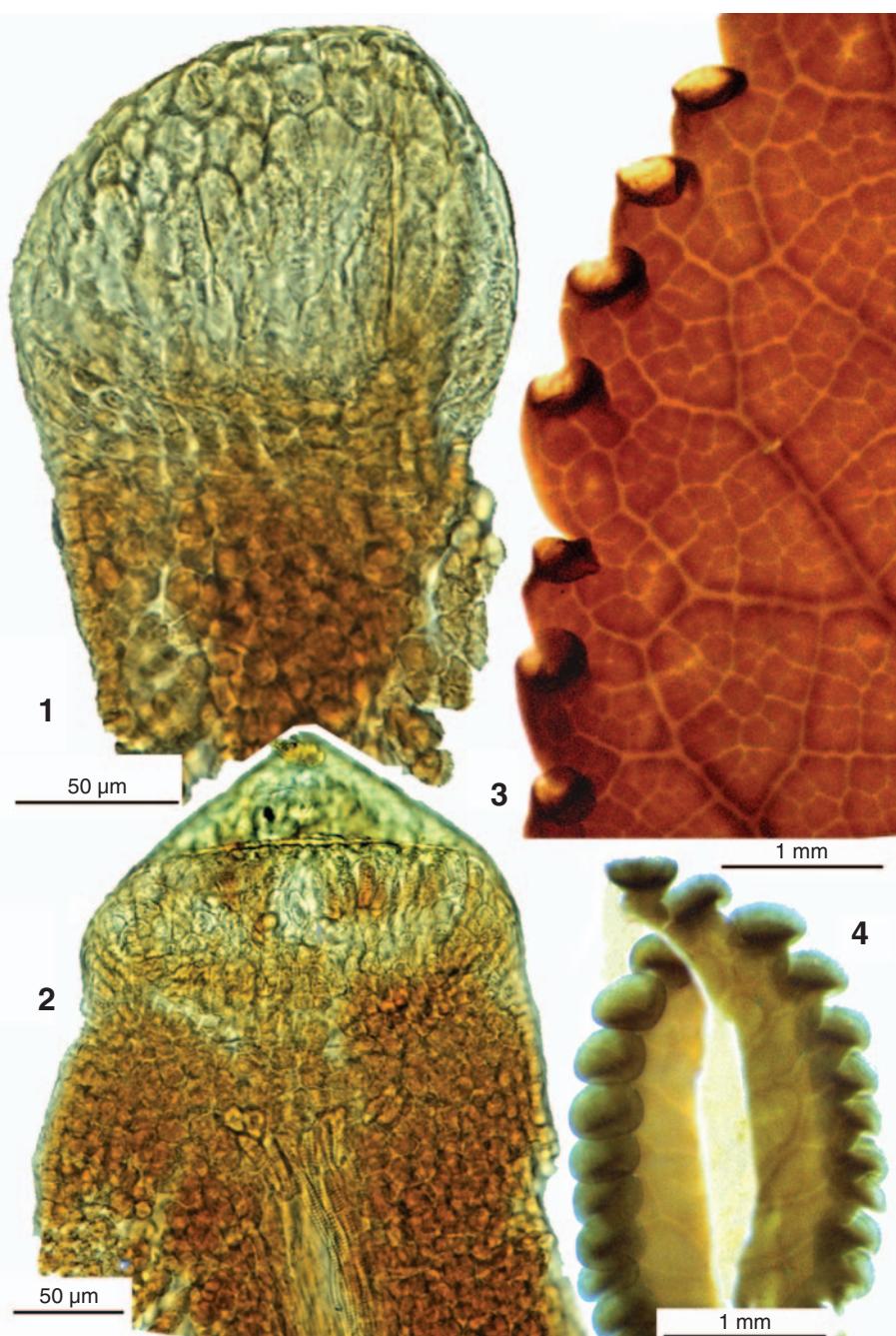


Plate IX. *Cercidiphyllum magnificum* Nakai, BIN, leaf glands: 1, 2, glands showing small-celled stalk and a head of columnar cells; 3, glands on vernate short-shoot leaf at anthesis; 4, glands on leaf in bud.

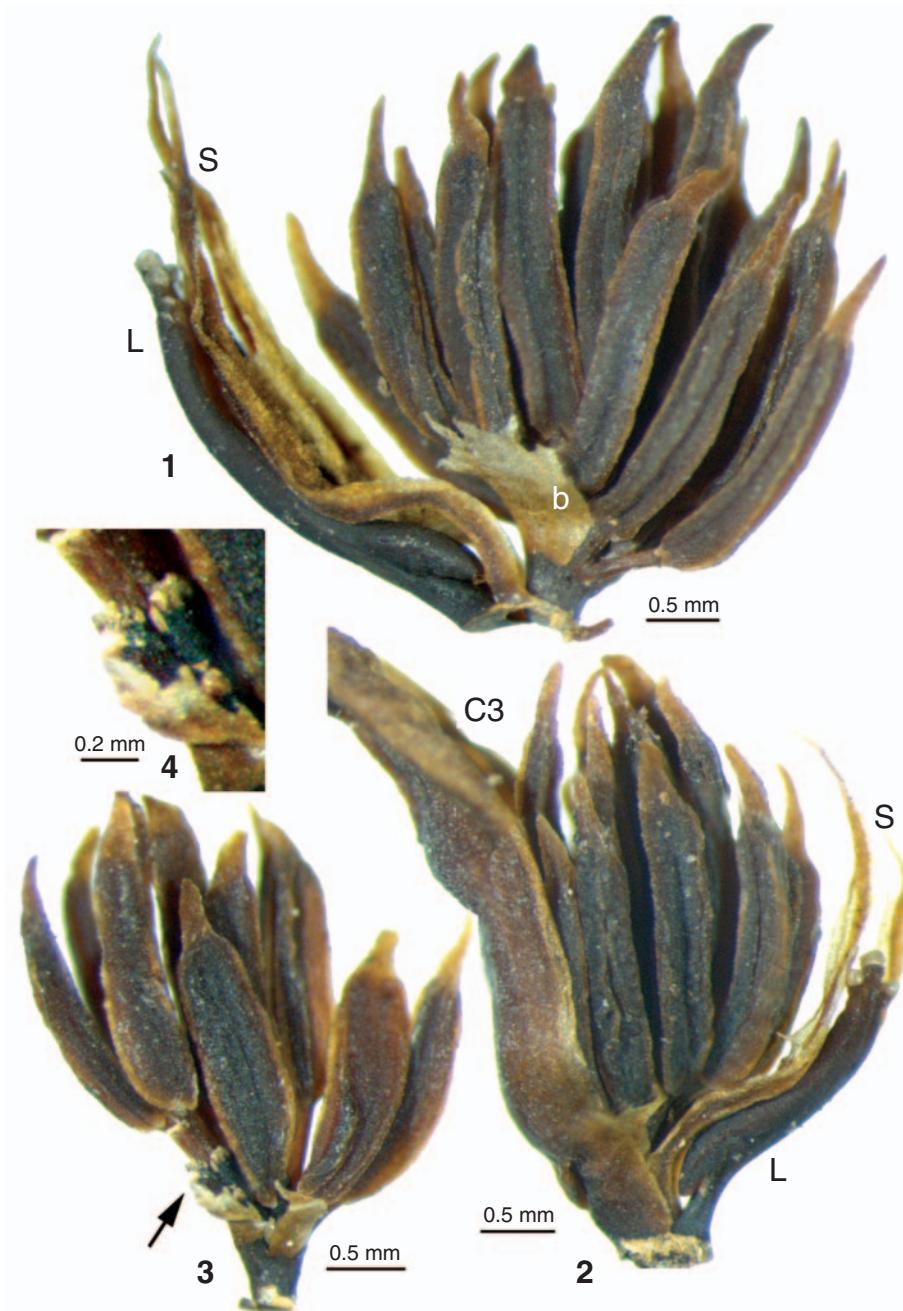


Plate X. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, staminate structures in bud: 1, 2, showing bracts (b), leaf (L), stipule (S) and the third cataphyll (C3); 3, 4, bract subtending a distinct group of pruned stamens (arrow).



Plate XI. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, staminate structures in bud : 1, 2, filiform appendages (arrows) associated with a defective stamen; 3, also showing leaf with a large stipule.



Plate XII. *Cercidiphyllum magnificum* Nakai, Kew, staminate structures in bud: 1, bracts of unequal length; 2, bracts whorled, nearly equal; 3, median bract raised above the smaller lateral bracts (S – leaf stipule).

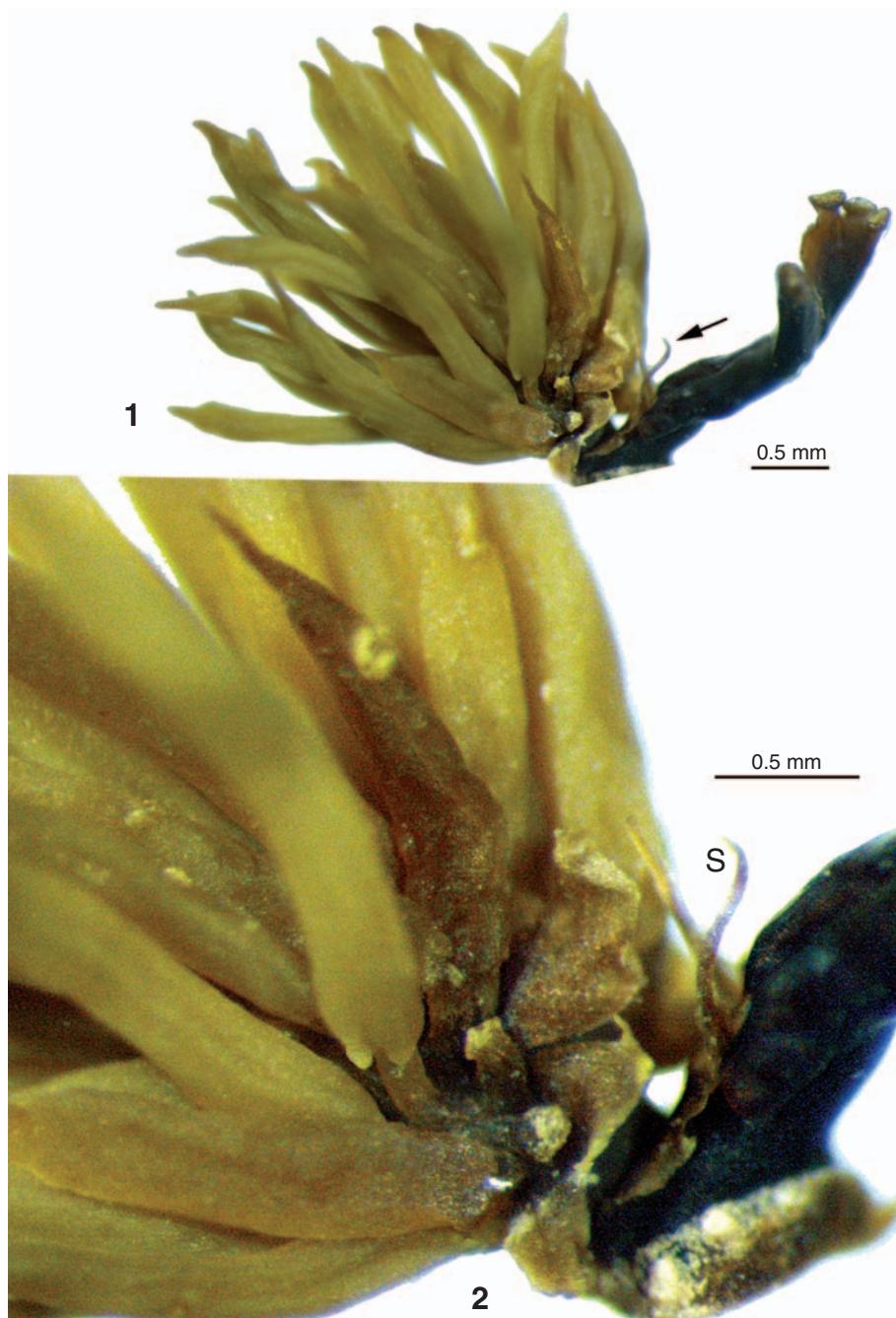


Plate XIII. *Cercidiphyllum magnificum* Nakai, Kew, staminate structure in bud: 1, 2, enclave (arrow) with additional bracts subtending pruned stamens (S – stipule).

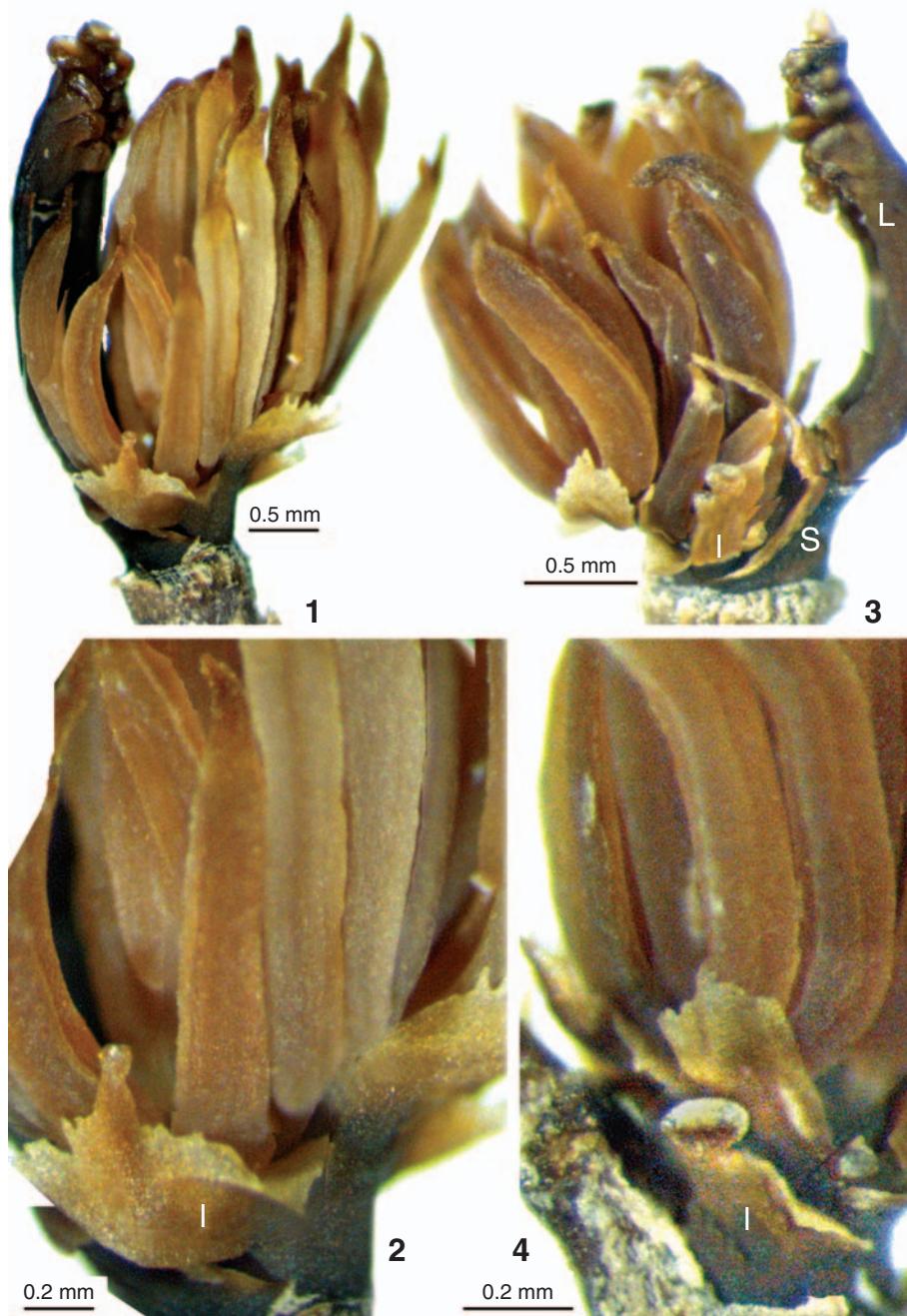


Plate XIV. *Cercidiphyllum magnificum* Nakai, Kew, staminate structures in bud: 1, 2, transition from leaf-like to ordinary bract, apical gland present; 3, leaf-like bract subtending pruned stamens, 4, leaf-like bract with large apical gland (L – leaf, I – leaf-like bract, S – leaf stipule).

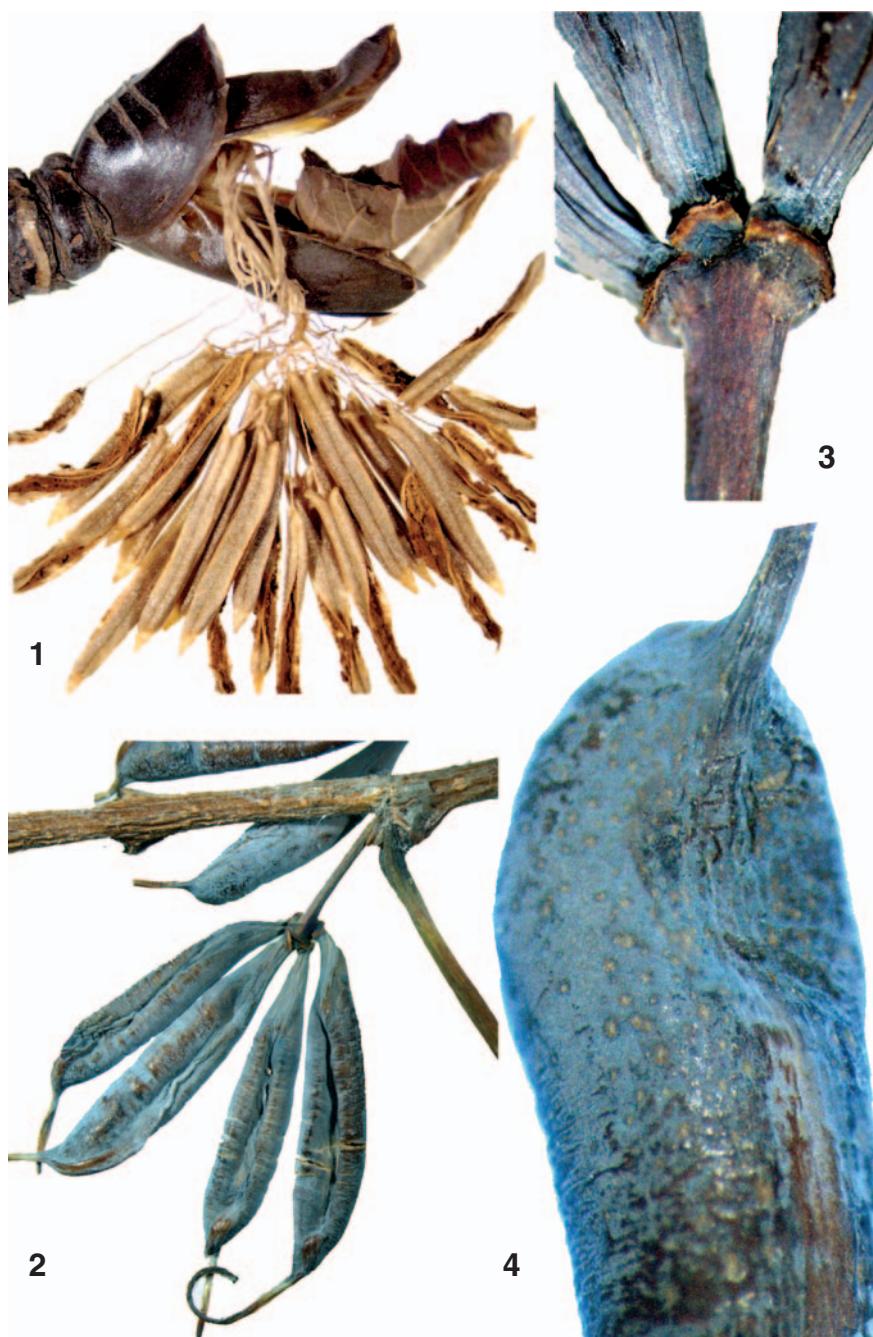


Plate XV. *Cercidiphyllum magnificum* Nakai, BIN: 1, staminate flower at anthesis; *Cercidiphyllum japonicum* Sieb. et Zuc., MSU: fruit stalk with four follicles turned their opening sutures to one side, 3, subtending bracts in mature fruit, 4, ridges and lenticels on the fruit wall.



Plate XVI. *Cercidiphyllum magnificum* Nakai, 1 – 3, BIN, four-carpellate pistillate buds at anthesis, 4, 5, *C. japonicum* Sieb. Et Zuc., MBG, six-carpellate gynoecium with four subtending bracts.

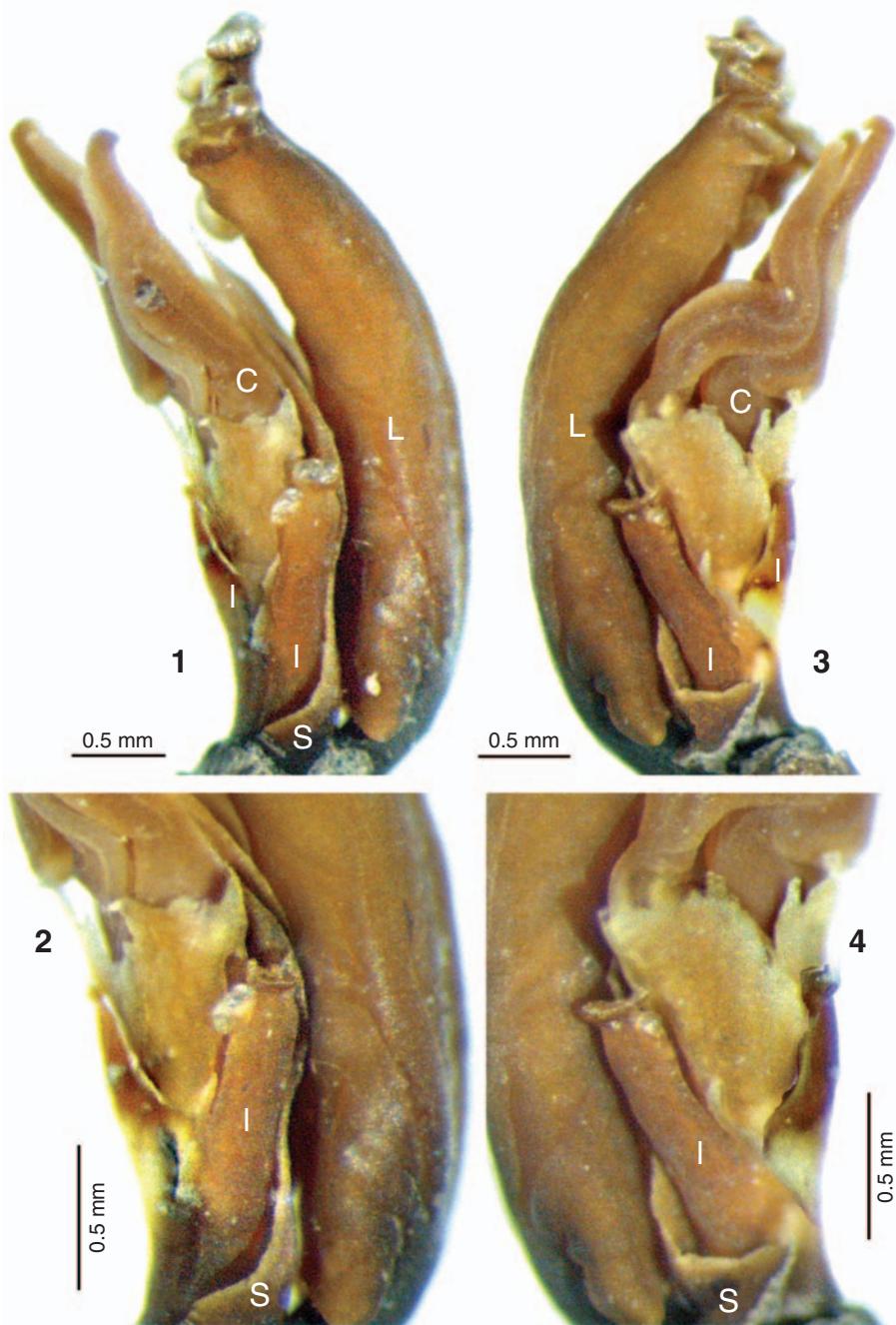


Plate XVII. *Cercidiphyllum magnificum* Nakai, Kew, pistillate structure in bud: 1–4, lateral aspects showing the involuted leaf-like bracts with apical glands (L – Leaf, S – stipule, I – leaf-like bract).



Plate XVIII. *Cercidiphyllum magnificum* Nakai, Kew, pistillate structure in bud: 1, with a single leaf-like bract of involuted blade, apical gland and small stipule; 2, with a lateral and median leaf-like bracts at different levels; 3, 4, with a transitional leaf like – ordinary bract (arrow) of a partly fused blade and stipule (b – bract, L – leaf, l – leaf-like bract, S – leaf stipule, s – leaf-like bract stipule).

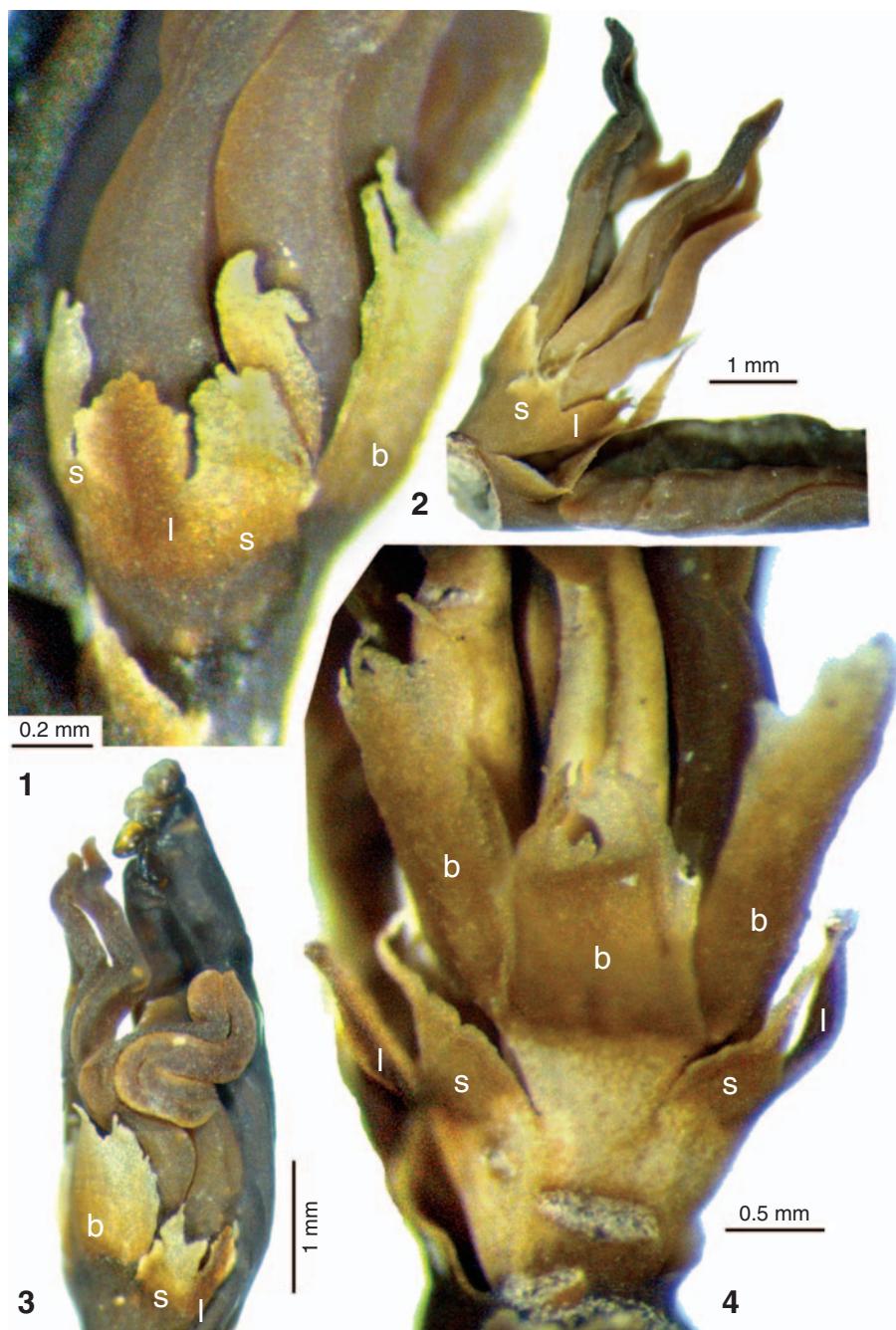


Plate XIX. *Cercidiphyllum magnificum* Nakai, Kew, pistillate structure in bud, leaf-like bracts; 1, glands lost, stipules expanded; 3, 4, blades further reduced; 4, stipule tips filiform.

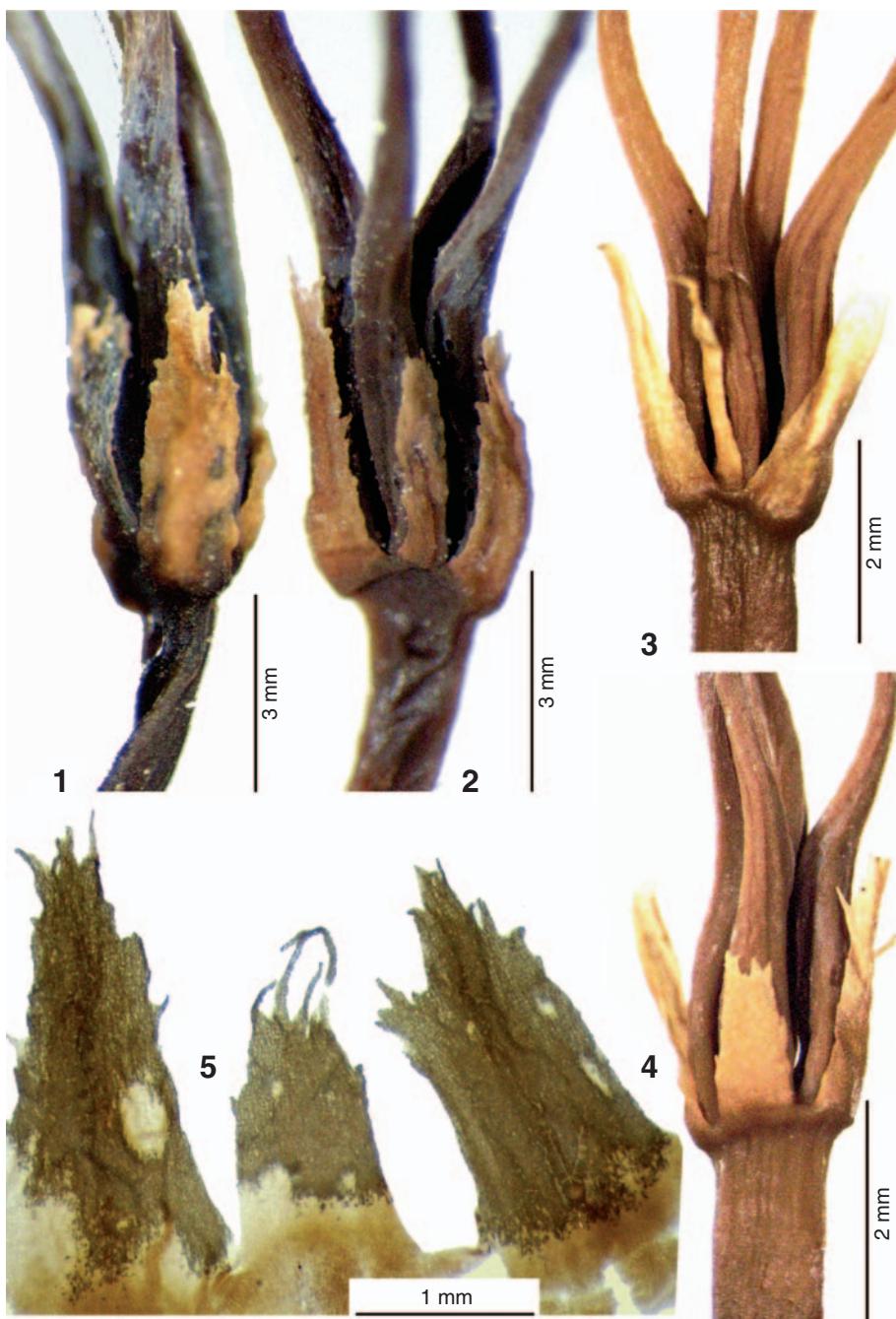


Plate XX. *Cercidiphyllum magnificum* Nakai, BIN, pistillate structures at anthesis: 1 – 5, bract morphology.



Plate XXI. *Cercidiphyllum magnificum* Nakai, BIN, pistillate structures at anthesis: 1, 2, with lateral bracts at different levels (black arrows) and reduced median bracts, one with a minute axillary appendage (Fig. 1, white arrow); 3, 4, linear median bracts with minute stipules at base (S), 5, 6, two aspects with differently developed median bracts.

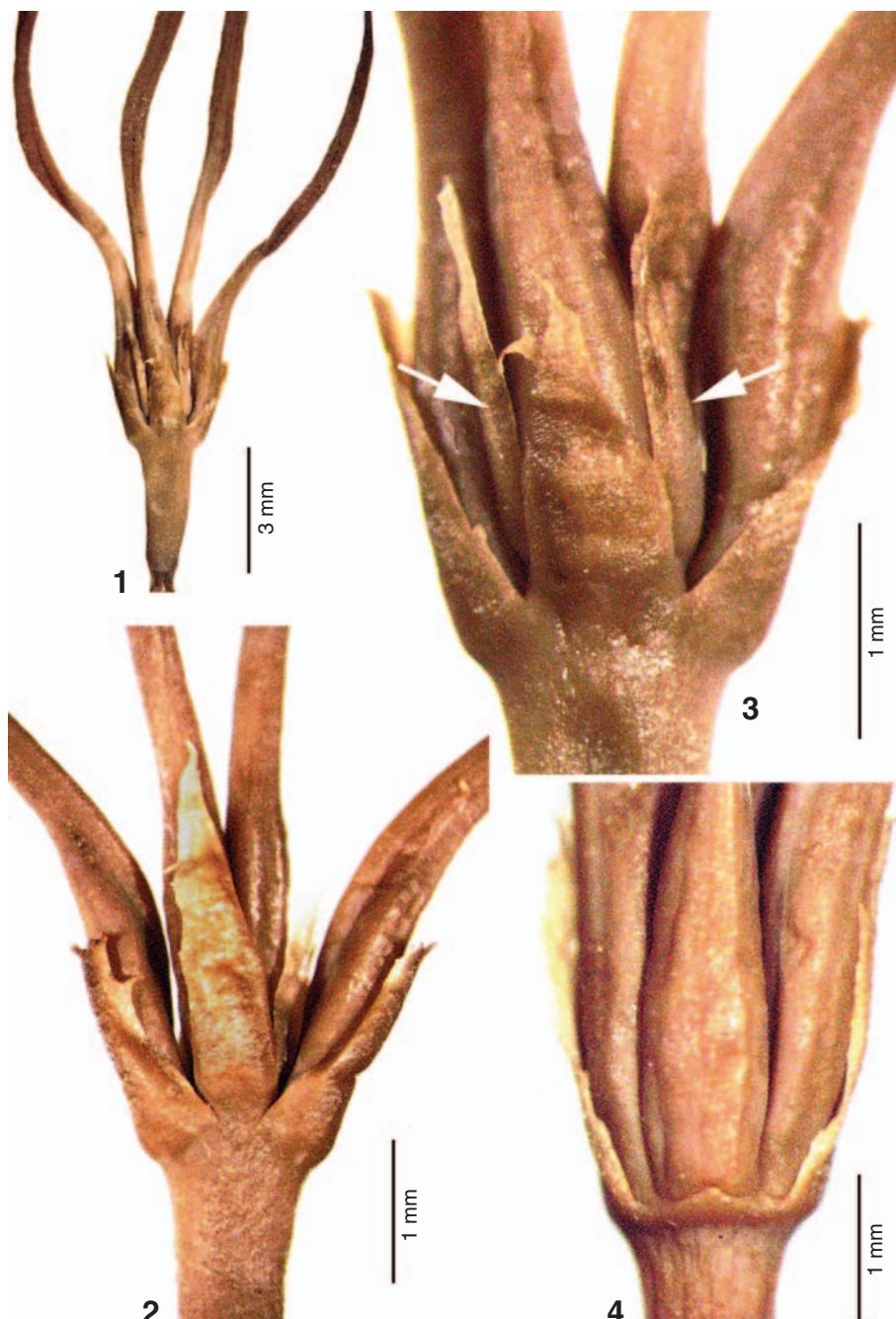


Plate XXII. *Cercidiphyllum magnificum* Nakai, BIN, pistillate structures at anthesis: 1 – 3, with median bracts well developed on both sides and with supernumerary empty bracts (arrows) on flanks of a median carpel; 3, with a median bract reduced.

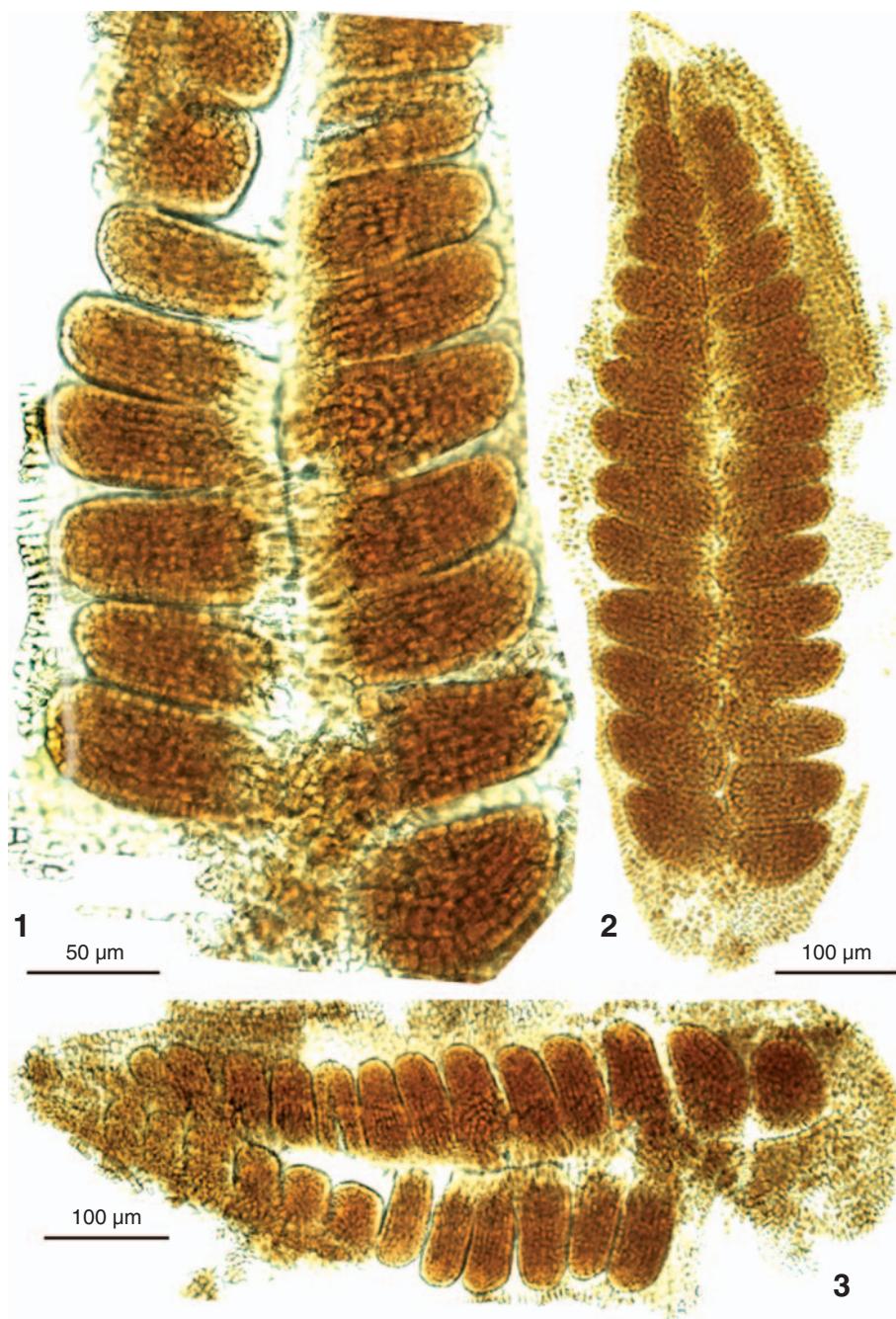


Plate XXIII. *Cercidiphyllum magnificum* Nakai, Kew: 1-3, placentas from carpels in bud showing endodermal lining of the locules and pectinate arrangement of the primordial lobes.

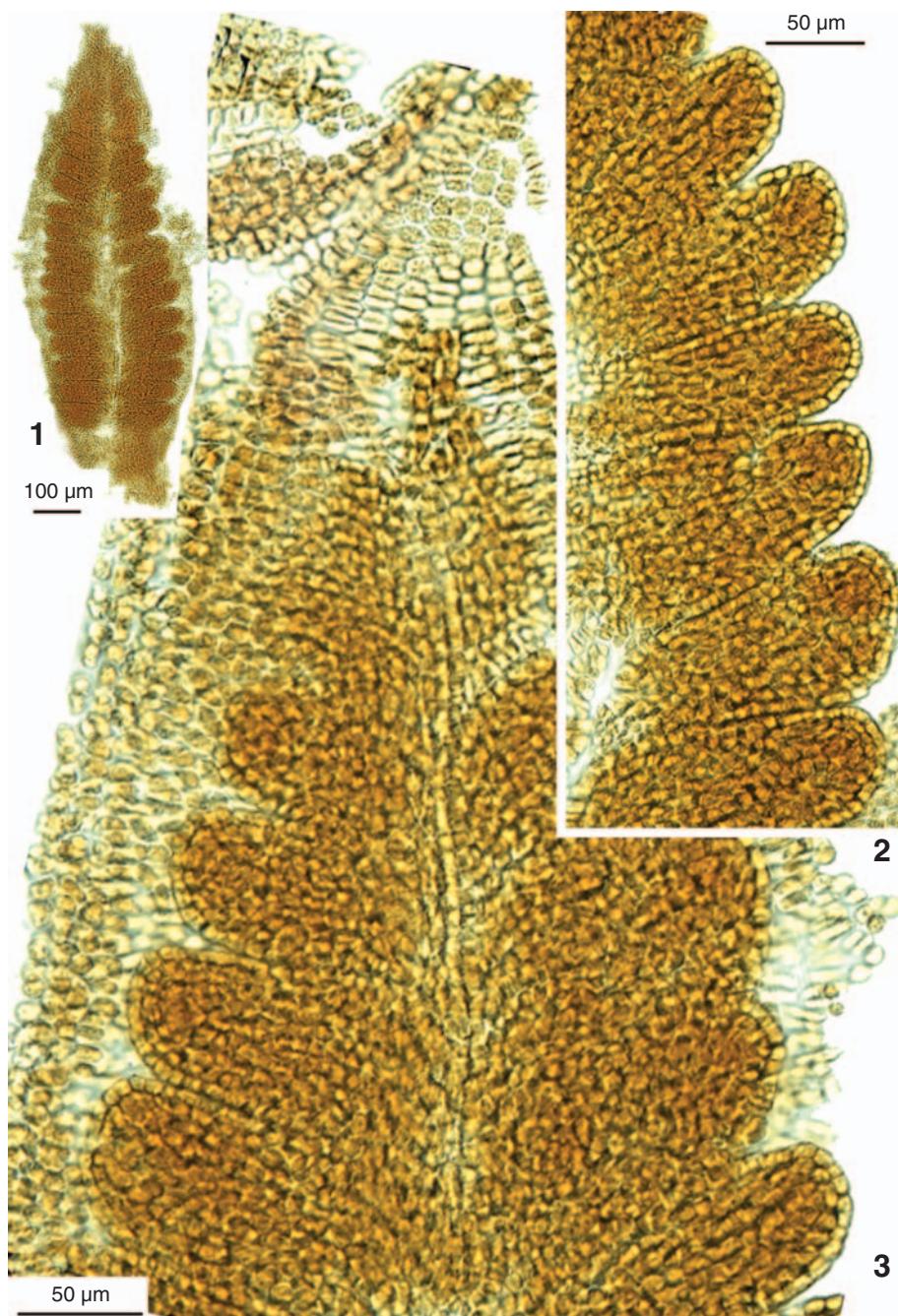


Plate XXIV. *Cercidiphyllum magnificum* Nakai, Kew: 1 – 3, placentas from carpels in bud, showing incipient differentiation of the inner integument and nucellus.

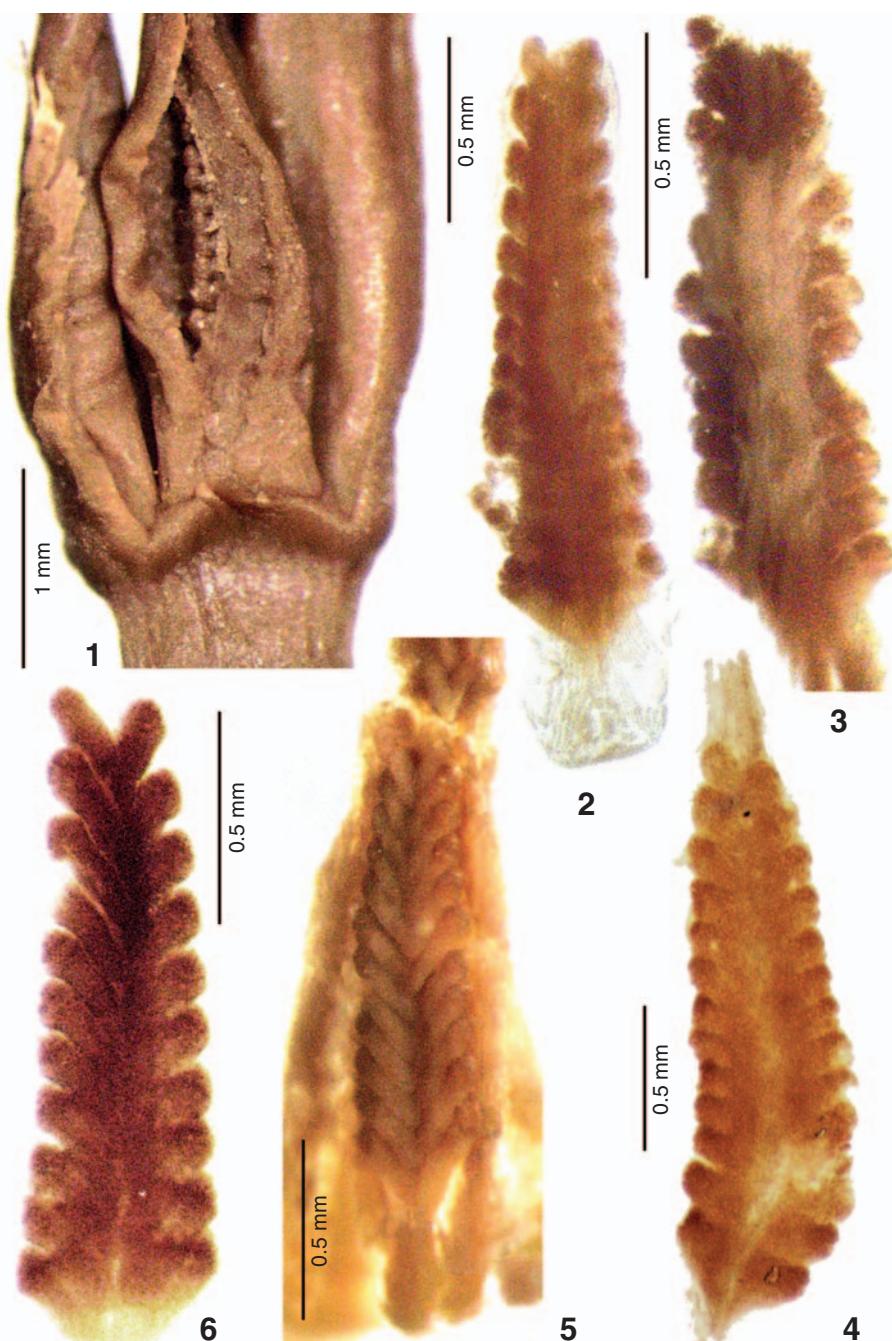


Plate XXV. *Cercidiphyllum magnificum* Nakai, BIN, placenta from carpels at anthesis: 1, seen through slit abaxial wall, 2, abaxial and adaxial aspects with a thick abaxial ridge, apically protruding in (4).

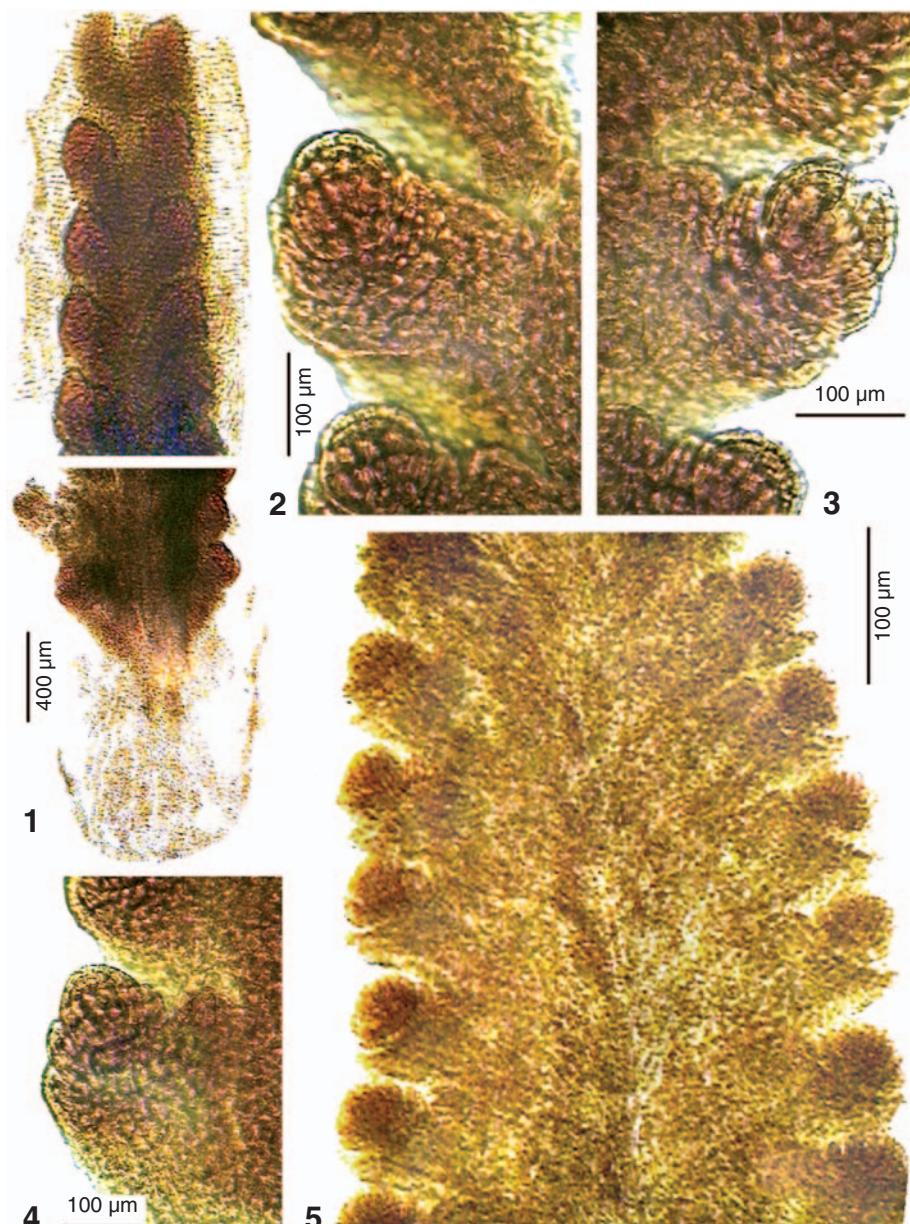


Plate XXVI. *Cercidiphyllum magnificum* Nakai, BIN, placenta from carpels at anthesis: 1, locule with placenta, the basal part sterile; 2 – 4, protruding nucelli and annular integuments; 5, vascularization.

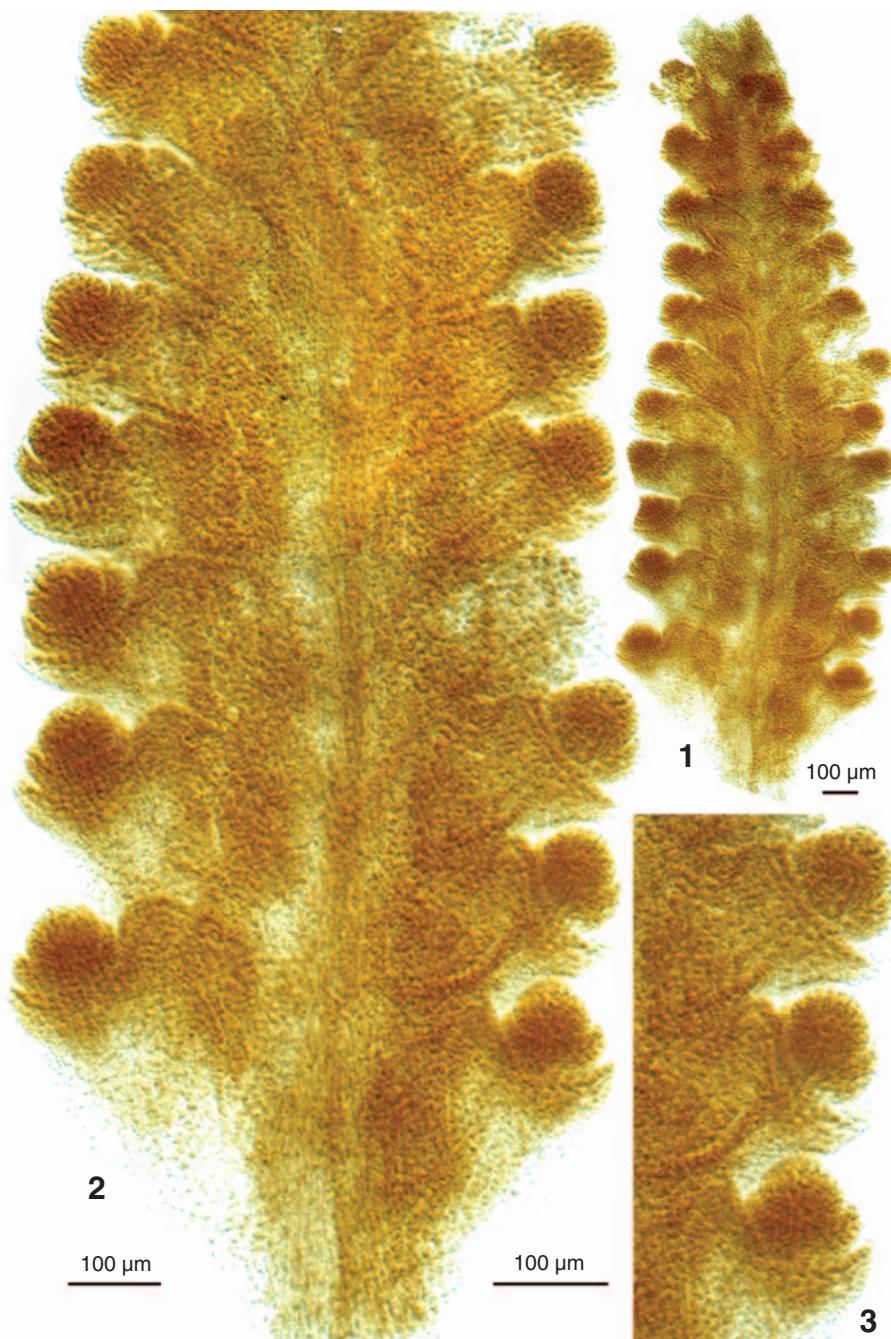


Plate XXVII. *Cercidiphyllum magnificum* Nakai, BIN, placenta from carpels at anthesis: 1, 2, asymmetric development of integumental lobes; 3, vascular supply of ovules.

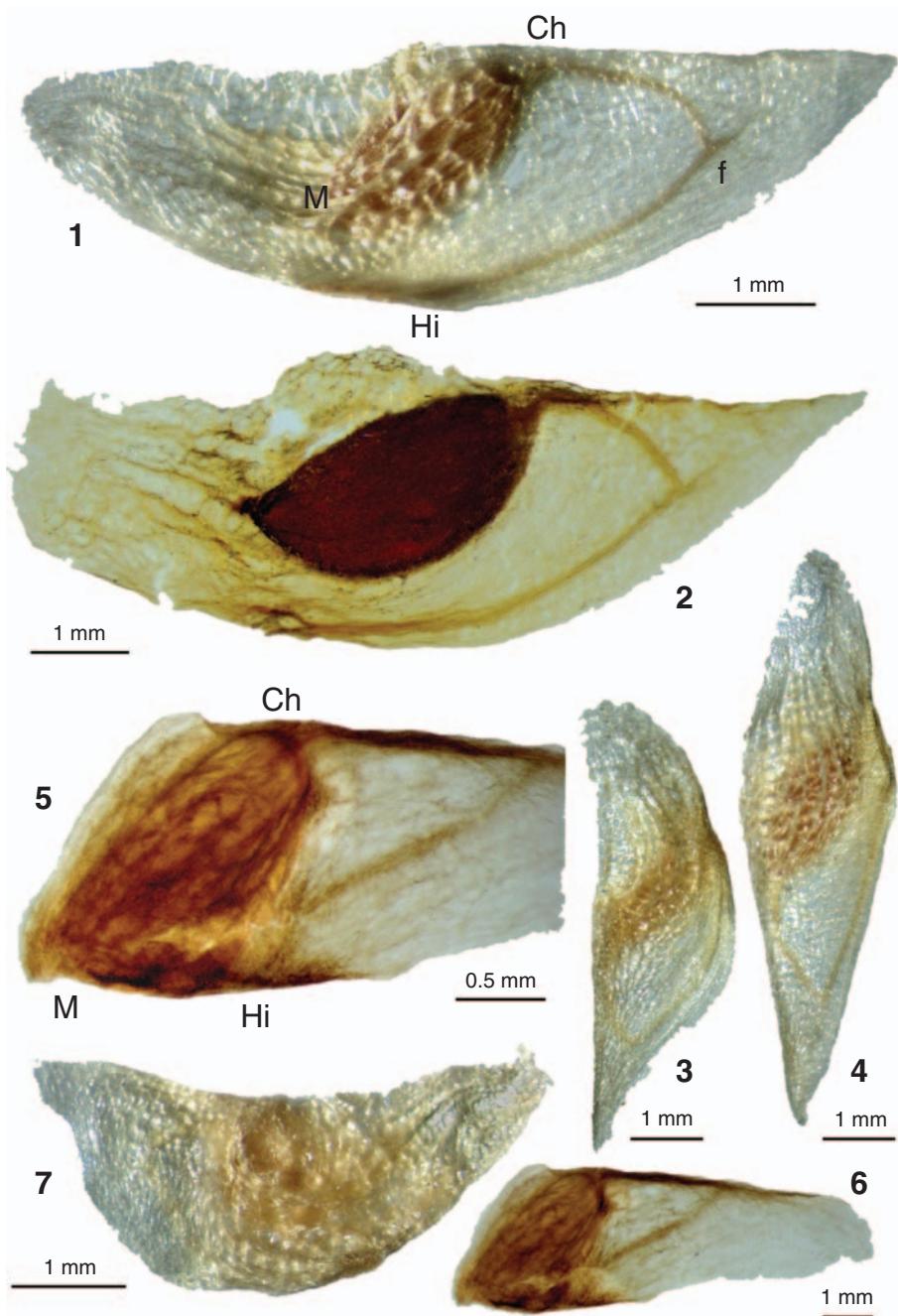


Plate XXVIII. *Cercidiphyllum japonicum* Sieb. et Zuc., MSU, seed shape variation: 1 – 4, hemitropous, 5 – 7, subanatropous.

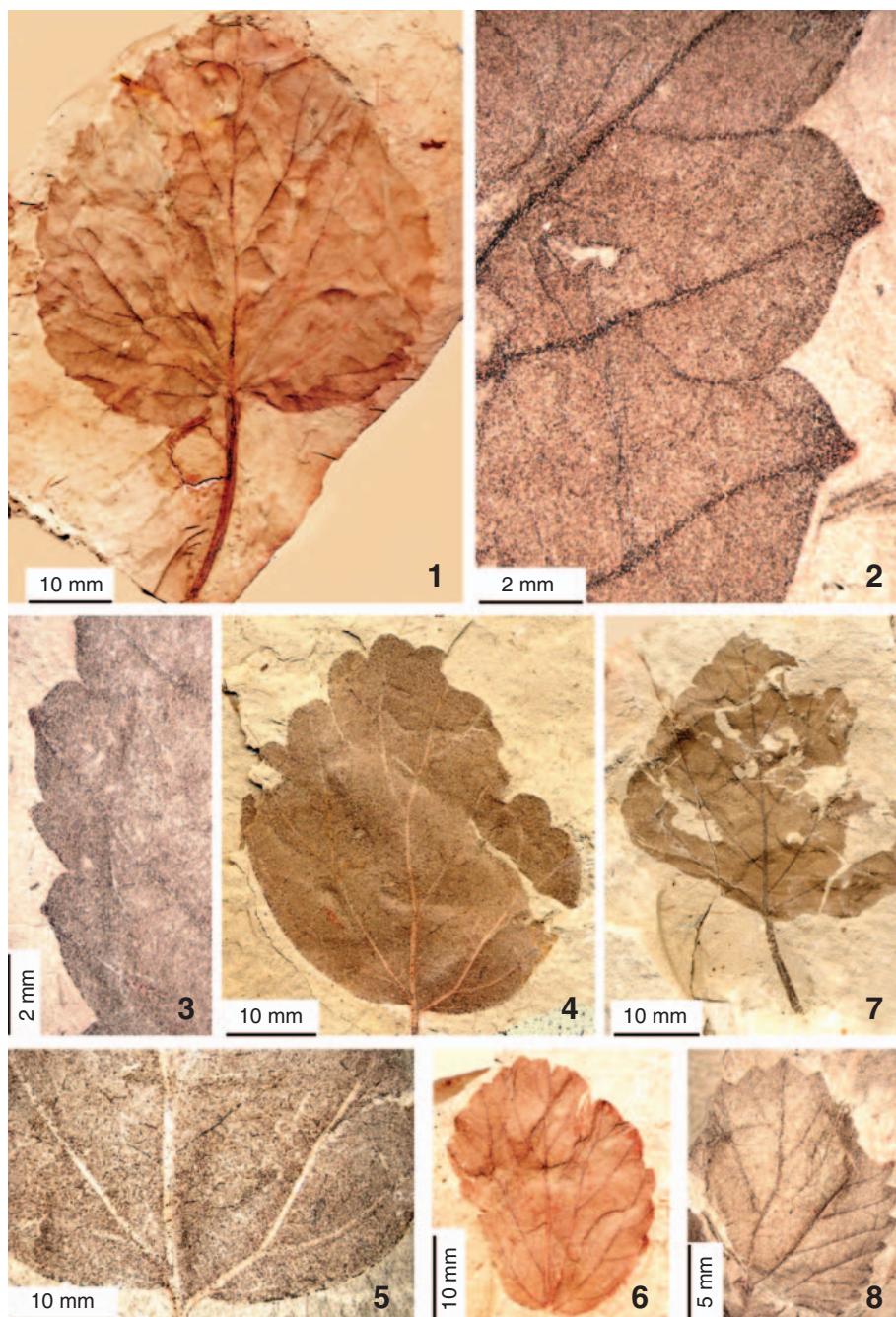


Plate XXIX. *Eocercidiphyllites glandulosus* Krassilov, Late Cretaceous (Turonian) of Gerofit, Arava Valley, Israel: 1, reniform leaf; 2, marginal glands; 3, marginal teeth with additional serration; 4–6, elliptical leaves; 7, deltoid leaf; 8, juvenile leaf of the reniform morphotype.

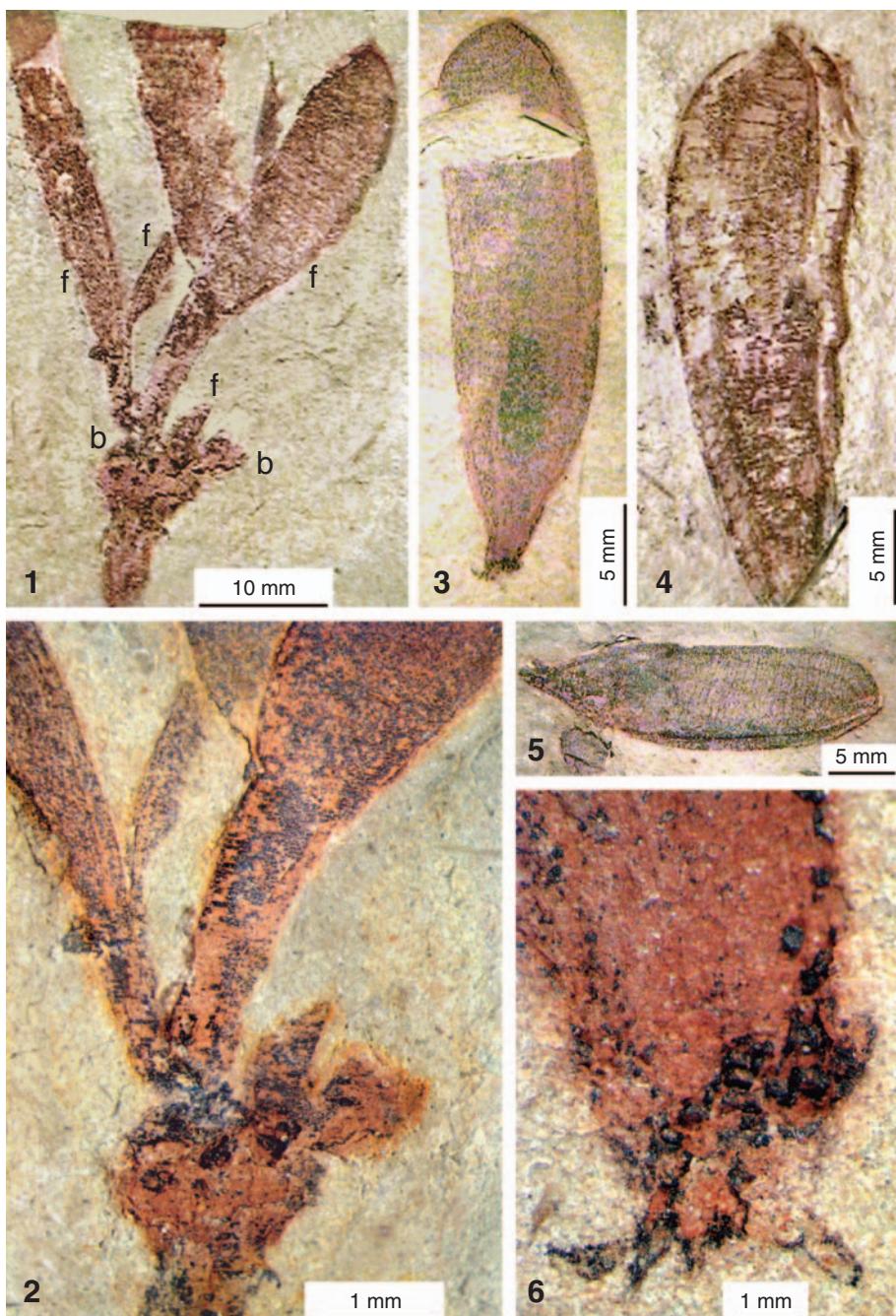


Plate XXX. *Eocercidianthus bracteatus* Krassilov, Late Creaceous (Turonian) of Gerofit, Arava Valley, Israel: 1, 2, pistillate structure of four follicles (f) and partly preserved subtending bracts (b); 3, 6, detached follicle with a persistent lobed scale (carpellar stipule) at base; 4, 5, detached follicles, one (4) with a gaping suture.

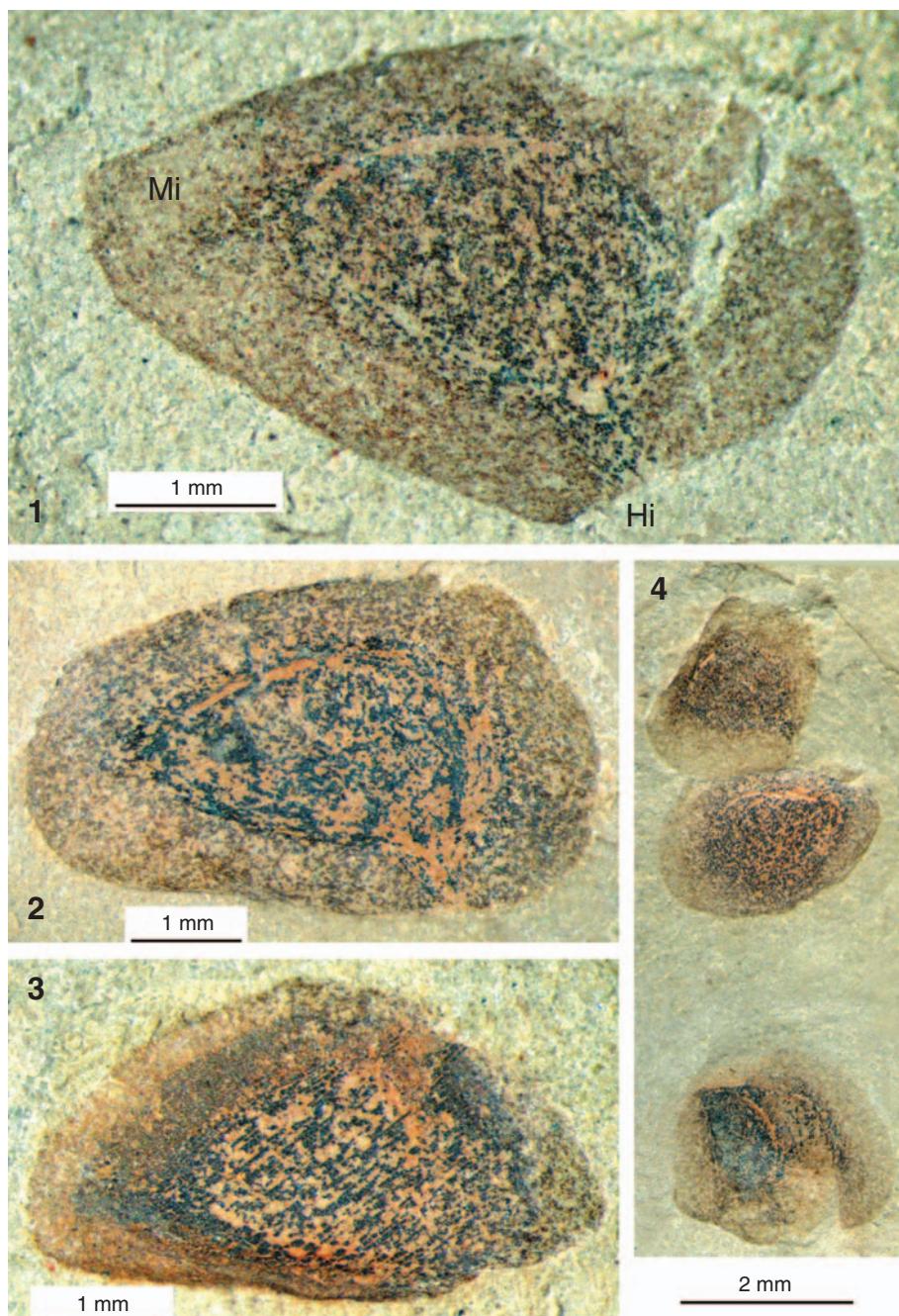


Plate XXXI. *Eocercidispermum campylum* Krassilov, Late Creaceous (Turonian) of Gerofit, Arava Valley, Israel:
1 – 3, seed shapes (Hi – hilum, Mi – micropyle); 4 – shed seeds on a bedding plane.

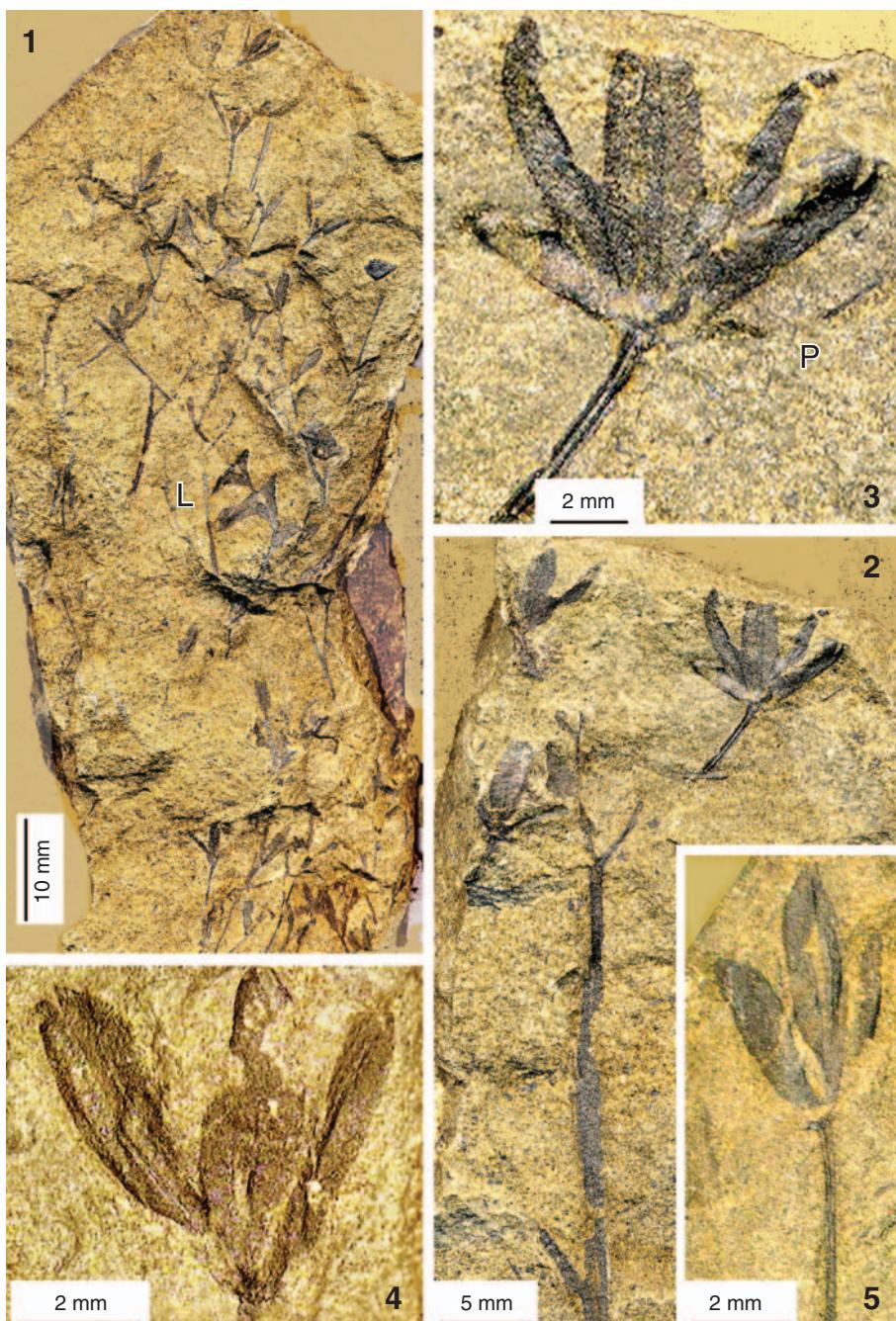


Plate XXXII. *Ternaricarpites floribundus* Krassilov et Volynetz, Early Cretaceous (Albian) of Primorye, Far East: 1, branching shoots with terminal fruits, one basal leaf (L) partly preserved; 2, branching stem with flower on a lateral branch, 3, perianth of leaf-like tepals (P – prophyll); 4, 5, fruits of ternate follicles, some split along the abaxial sutures.