



Cunoniaceae in the Cretaceous of Europe: Evidence from Fossil Flowers

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Fossil flowers of the Cunoniaceae from Late Cretaceous sediments of southern Sweden are described in detail. The flowers are small, bisexual, actinomorphic, tetramerous with broadly attached valvate sepals; they have narrowly attached petals; eight stamens in two whorls; a massive, lobed nectary; a semi-inferior, syncarpous gynoecium with axile placentation; numerous ovules; separate styles; and peltate, probably secretory, trichomes. They share many features with extant representatives of both the Cunoniaceae and Anisophylleaceae. However, the gynoecium structure in particular indicates a closer relationship to the Cunoniaceae. The floral characters are not specific for any extant genus of the family and therefore a new genus and species, *Platydiscus peltatus* gen. et sp. nov., is formally described. This is the first record of cunoniaceous floral structures from the Northern Hemisphere and the oldest record of Cunoniaceae flowers worldwide.

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Key words: Anisophylleaceae, Cunoniaceae, fossil flowers, Late Cretaceous, Oxalidales, *Platydiscus peltatus* gen. et sp. nov., Santonian-Campanian, southern Sweden.

INTRODUCTION

The present phylogenetic diversity and biogeographic distribution of angiosperms is the result of a long, complex history of changing biotic and abiotic factors. The fossil record provides a framework for unravelling part of this history, and extensive information, particularly on Tertiary and Quaternary angiosperms, has accumulated over 100 plus years of thorough studies. It has long been recognized that extensive floristic interchanges took place during the Tertiary between the floras of North America, Europe and Asia, and detailed biogeographic patterns for individual taxa have already been mapped (e.g. Manchester, 1999). In contrast, information is fragmentary regarding the Cretaceous period during which major angiosperm radiation took place and the starting points for many modern floras were established.

Recently, Cretaceous mesofossil floras with small, structurally preserved angiosperm reproductive organs have provided a new source for studying the systematic diversity and distribution of angiosperms. During the past two decades, different localities within Europe, Asia and North America have yielded a wealth of new information (e.g. Friis and Skarby, 1981; Friis *et al.*, 1992; Keller *et al.*, 1996; Gandolfo, 1998; Frumin and Friis, 1999b; Takahashi *et al.*, 1999b). Although these floras are mainly concentrated in the Northern Hemisphere and their study is still in the initial phase, results so far indicate that the Cretaceous vegetation was clearly distinct from that of the Tertiary, and that distribution patterns may in some cases have been

different from those inferred from the study of Tertiary and modern vegetation alone.

In this work we describe a new fossil taxon based on flowers from the Late Cretaceous (Santonian/Campanian) of southern Sweden. The floral remains show affinities to extant members of the Cunoniaceae; a morphologically diverse family that today is predominantly of Gondwanan distribution. This is the first floral record of the family in the Northern Hemisphere and it confirms previous suggestions based on wood fossils (Hoffman, 1952; Gottwald, 1992) that the Cunoniaceae were present in Europe early in the history of the family.

While determining the systematic position of the fossils, J.S. and E.M.F. found that they share floral features with both the Cunoniaceae and the Anisophylleaceae. At the same time, but independently, M.M. and P.E. started a project that compares the floral structures of the Anisophylleaceae and Cunoniaceae, and discusses the problem of their systematic position (Matthews *et al.*, 2001). It turned out to be most fruitful to join forces between the two projects and the resulting papers are good examples of how the integration of neobotanical and palaeobotanical approaches can influence discussions on phylogenetic relationships of certain groups even in the era of molecular systematics.

MATERIALS AND METHODS

The mesofossils examined in this study were isolated from deposits of Late Santonian—Early Campanian age exposed in the Höganäs AB kaolin quarry at the Åsen locality in the Kristianstad Basin in Scania, Sweden (56°9'N, 14°30'E). The sediments consist of unconsolidated

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sands and clays, from which plant fossils were extracted by sieving bulk samples in water. See Friis *et al.* (1988) for specific details of the site and methodology.

The material studied in this paper was extracted from four samples (GI 32116; GI 32117; GI 32172; and Åsen 2; the latter collected by S. Lindbom). The fossils are charcoalified (fusitized), with their original three-dimensional form more-or-less intact. See Friis *et al.* (1988) for discussion of this preservation. The fossil material comprises a few more-or-less complete floral buds/preanthetic flowers [S106204, S106207, S106208, S106348, S107058, S107135-01/S107135-02; all specimens and preparations of fossil material are deposited in the collections of the Swedish Museum of Natural History (S)] and a number of anthetic or post-anthetic flowers with varying degrees of preservation of their floral organs (S106197–S106199, S106275, S106347, S107007, S107029, S107055–S107057, S107159, S107060, S107087, S107088, S107094, S107130, S107134, S107136–S107144). The buds found in the fossil material could be unequivocally linked to the mature or nearly mature flowers due to their identical floral organization. In addition they share the same kind of indumentum (see Results).

All the specimens extracted are relatively small (< 4 mm in length) as is typical for most floral remains from this locality (Friis and Skarby, 1981; Friis, 1985; Schönenberger and Friis, 2001) and for most mesofossils from other Cretaceous deposits within Europe, North America, and central and eastern Asia (e.g. Nixon and Crepet, 1993; Friis *et al.*, 1994; Eklund and Kvacek, 1998; Frumin and Friis, 1999a; Herendeen *et al.*, 1999; Takahashi *et al.*, 1999a). The charcoalification process causes specimens to shrink to some extent (Lupia, 1995), thus measurements given in this text are approximations to the living state of these plants.

In preparation for scanning electron microscopy (SEM), specimens were mounted and sputter-coated with gold before being viewed with a Phillips 515 scanning microscope. Four of these specimens were then embedded in 2-hydroxyethyl methacrylate (Kulzer's Technovit 7100; Heraeus Kulzer GmbH, Wehrheim, Germany) according to Igersheim (1993) and, in particular, to Igersheim and Cichocki (1996), who describe the embedding and sectioning of charcoalified specimens in detail. Serial 3–6 µm sections were made using a rotary microtome (S107058, section slides S107058-01–S107058-15; S107087, section slides S107087-01–S107087-24; S107088, section slides S107088-01–S107088-12; S107094, section slides S107094-01–S107094-36).

RESULTS

Floral organization and morphology

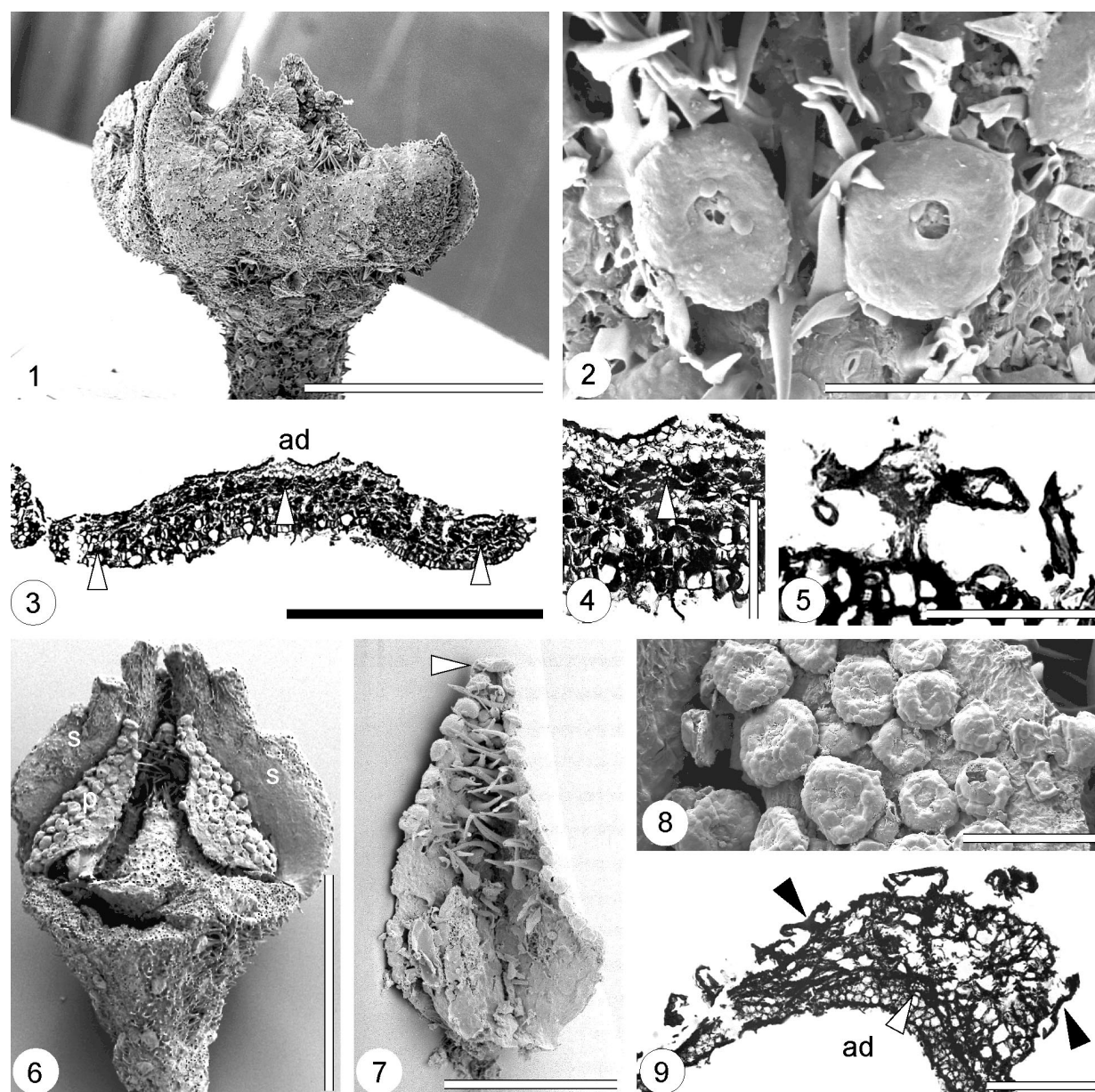
The flowers are actinomorphic, bisexual and tetramerous (Figs 10–12 and 42). As seen from above, the flowers are square in outline. Mature (anthetic) flowers are 3–4 mm long (without stamens) and 3–3.6 mm wide (without sepal and petal lobes). The perianth consists of distinct sepals and petals which are arranged in alternating whorls. The androecium has eight stamens and the gynoecium is

comprised of four semi-inferior carpels, i.e. the lower part of the ovary is congenitally fused with the floral base. Simple unicellular and peltate multicellular trichomes cover the peduncle and the floral base (Figs 1 and 2). The multicellular trichomes consist of a short, few-celled, multiseriate stalk and a peltate, multicellular head (Fig. 5). The margin of the peltate head is more-or-less involute. The surface of the peltate head is often ruptured in the central region of the head indicating a secretory function of these trichomes (Figs 2 and 5).

Calyx. The sepals are ovate-triangular with a broad base attached to the rim of the floral cup. Calyx aestivation is valvate. Adaxially, the indumentum of the sepals consists of simple trichomes, while peltate trichomes are also present on the abaxial surface (Fig. 1). The sepals have three distinct histological layers: (1) an abaxial layer of medium large, regularly arranged epidermal cells; (2) a relatively thick parenchyma with large, loosely arranged cells; and (3) an adaxial tissue of two–three layers of small, tightly packed cells (Figs 3 and 4). The sepals are vascularized by three main and approx. ten minor strands.

Corolla. In young floral stages the petals are trullate with a relatively narrow base (Figs 6 and 7). Corolla aestivation is probably imbricate. Relatively large simple, unicellular trichomes with inflated bases are present on the adaxial surface (Fig. 7). The abaxial surface is covered with peltate trichomes similar to those found on the pedicel, on the outside of the floral base and on the sepals. On young petals these trichomes decrease in size from the middle of the petal towards the petal margins (Figs 6, 8 and 9). In the distal half of the petal the margins are lined by medium-sized peltate trichomes of the same type as those on the surface. The petal tip is crowned by a similar, but larger structure which is probably also secretory (Fig. 7). Histologically, the petals are comprised of two–four layers of small, tightly packed cells. On the central abaxial surface a 'rib-like' structure of large, loosely arranged cells extends from the base to the tip of the petal (Fig. 9). No entire mature petal has been preserved and only the narrow basal parts remain attached to the mature flowers (Figs 10–12 and 14–16). At anthesis this narrow region is about 1.2 mm long (Fig. 16). The distal part of the mature petals must have been relatively broad compared to their base as is indicated by the diverging petal margins preserved in one of the pre-anthetic flowers, and also by the shape of the younger petals (Figs 7 and 15). The petals as a whole were apparently clawed. Identical peltate trichomes to those observed on the young petals are also present on the mature specimens (Fig. 14).

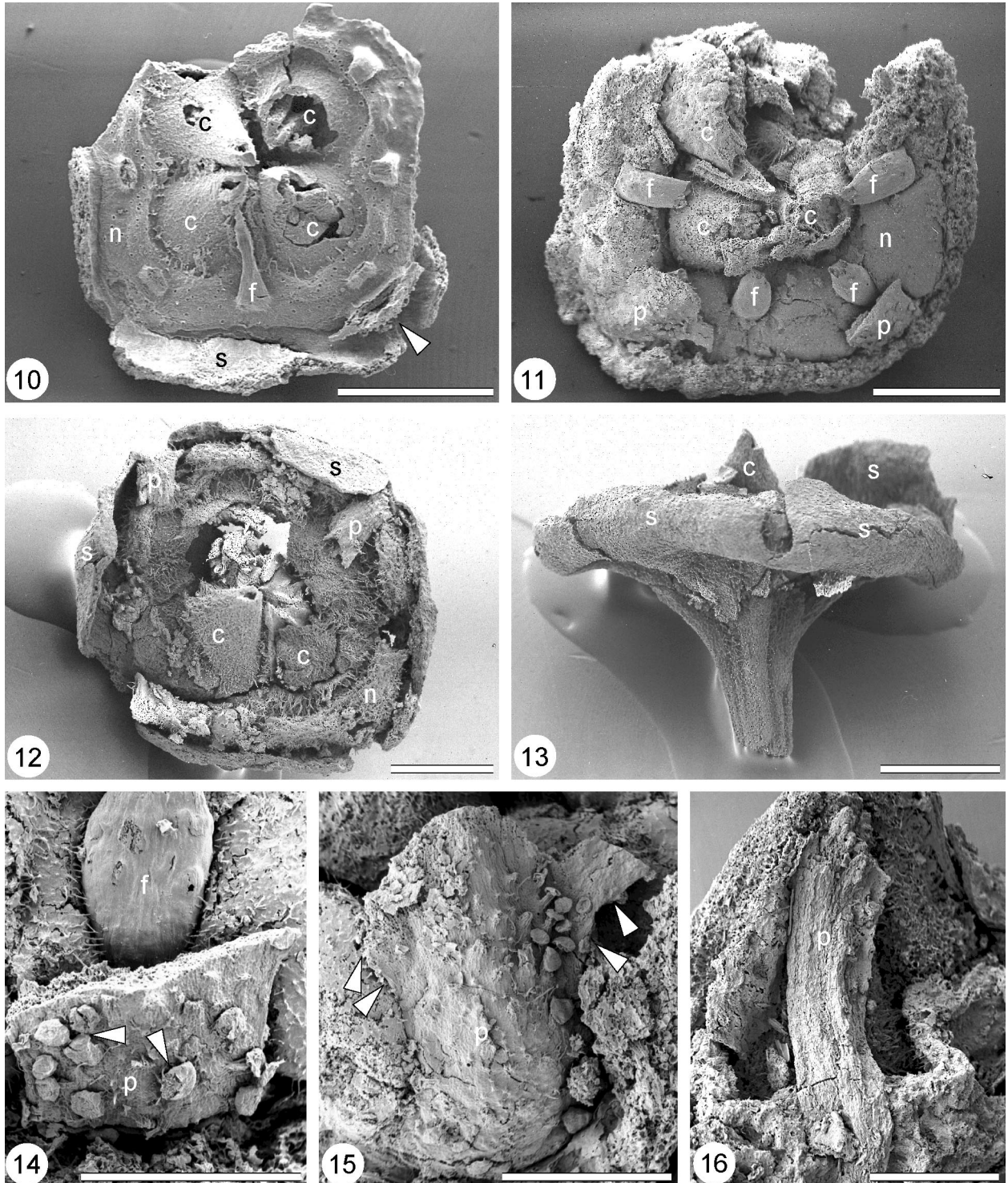
Androecium. The flowers have eight stamens (Figs 10, 11, 18 and 42) emerging from the upper rim of the floral base, which is fused with the lower half of the ovary. In pre-anthetic flowers, the filaments of the episepalous stamens are slightly wider than those of the epipetalous ones (Fig. 18). This suggests a basic stamen arrangement in two whorls. In mature flowers the eight stamens appear to be arranged in a single whorl (Fig. 10, but see Discussion). No anthetic anthers have been found. The best representation of anther structure comes from the transverse section



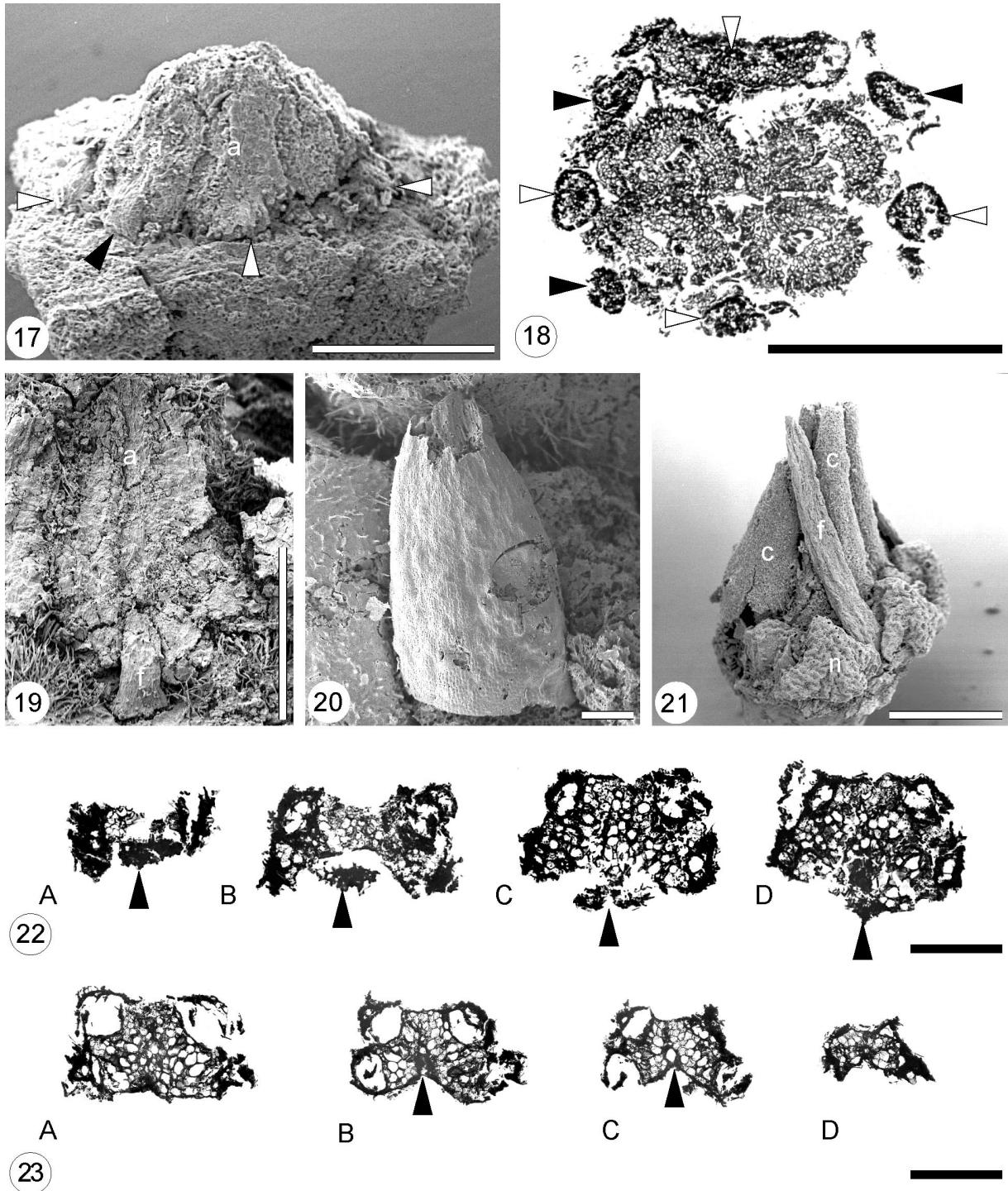
FIGS 1–9. Morphology and anatomy of floral buds. Fig. 1. Lateral view of floral bud with valvate aestivation of calyx, apically damaged; S107135; bar = 1 mm. Fig. 2. Multicellular peltate and unicellular simple trichomes on sepal; S107135; bar = 100 μ m. Fig. 3. Transverse section of sepal; arrowheads indicate main vascular bundles; S106201; bar = 0.5 mm. Fig. 4. Close-up of same transverse section as in Fig. 3 to show the anatomical structure; arrowhead indicates median vascular bundle; S106201; bar = 100 μ m. Fig. 5. Longitudinal section of multicellular peltate trichome; S106201; bar = 50 μ m. Fig. 6. Lateral view of floral bud; two sepals, one petal, and part of androecium are lacking; S106348; bar = 1 mm. Fig. 7. Petal removed from specimen in Fig. 6; unicellular trichomes with swollen base on adaxial side; petal margin lined with multicellular peltate trichomes; arrowhead indicates multicellular, probably secretory, tip of petal; S106348; bar = 0.5 mm. Fig. 8. Abaxial side of same petal as in Fig. 7; surface is covered with multicellular peltate trichomes decreasing in size towards the petal margin; S106348; bar = 100 μ m. Fig. 9. Transverse section of petal with three to four layers of relatively small cells adaxially and a multi-layered ‘rib-like’ structure on the abaxial side; white arrowhead indicates vascular bundle; black arrowheads indicate multicellular peltate trichomes; S106201; bar = 100 μ m. Abbreviations in all figures: a, anther; ad, adaxial; c, carpel; f, filament; fl, foot layer; h, hilum; il, infratectal layer; n, nectary; p, petal; pl, placenta; r, raphe; s, sepal; t, tectum.

series of a young bud (Figs 22 and 23). In this specimen the anthers are dithecal, tetrasporangiate, apparently dorsifixed in the lower part of the anther, and slightly sagittate (Fig. 22). The connective tissue is relatively extensive compared to the size of the pollen sacs and is broader on the dorsal side of the anther. This indicates an introrse

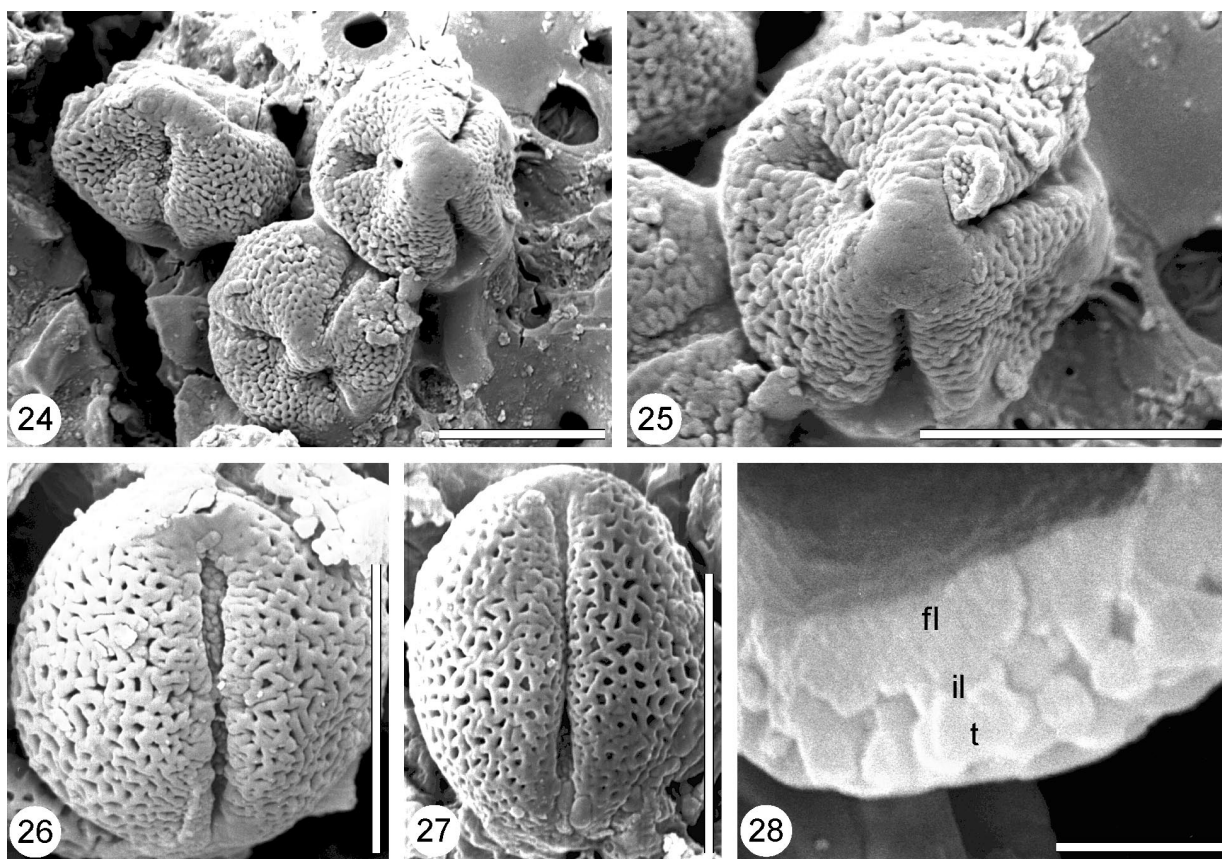
dehiscence of the thecae (Fig. 23). In the upper part of the connective tissue a dorsal furrow is present (Fig. 23B and C). The filaments are short in bud (Figs 11, 19 and 20) but are linear and about 2.2 mm long at anthesis (Fig. 21). The transition between the anther and filament is relatively narrow, as indicated by the tapering end of the filaments.



FIGS 10–16. Floral morphology and anatomy. Fig. 10. Pre-anthetic flower seen from above, showing tetramerous arrangement of floral organs; sepals, petals, and stamens broken at different levels; S107055; bar = 1 mm. Fig. 11. Pre-anthetic flower (holotype) seen from above; nectary is well-developed; flower is damaged on one side and one carpel is lacking; S107143; bar = 1 mm. Fig. 12. Presumably anthetic flower (indicated by the presence of many pollen grains on the surface of the nectary and the gynoecium, see Figs 25 and 26); S107029; bar = 1 mm. Fig. 13. Lateral view of same specimen as in Fig. 12; S107029; bar = 1 mm. Fig. 14. Petal base of pre-anthetic specimen in Fig. 11; arrowheads indicate multicellular peltate trichomes; S107143; bar = 0.5 mm. Fig. 15. Petal base of pre-anthetic specimen in Fig. 11; arrowheads indicate diverging petal margins; S107143; bar = 0.5 mm. Fig. 16. Elongate, claw-like petal base of presumably anthetic flower; S107136; bar = 0.5 mm. See Figs 1–9 for abbreviations.



FIGS 17–23. Androecium morphology and anatomy. Fig. 17. Lateral view of pre-anthetic bud; perianth not preserved; anthers are compressed and abraded; white arrowheads indicate filaments of episepalous stamen whorl; black arrowhead indicates filaments of epipetalous stamen whorl; S107058; bar = 0.5 mm. Fig. 18. Transverse section of specimen shown in Fig. 17 at the level of the filaments; white arrowheads indicate episepalous stamen whorl; black arrowheads indicate epipetalous stamen whorl; S107058; bar = 0.5 mm. Fig. 19. Lateral view of pre-anthetic stamen; anther is strongly compressed; S106204; bar = 0.5 mm. Fig. 20. Filament of pre-anthetic flower; filament tapers towards its apex; S107143; bar = 100 μ m. Fig. 21. Lateral view of presumably anthetic flower with an elongate filament still attached; S107137; bar = 1 mm. Fig. 22. A–D, Transverse section series of lower half of anther from a relatively young floral bud; arrowheads indicate filament; A, lowest section: thecae are separate from each other; filament is free; B, thecae are united, filament is free; C, at level where filament becomes attached to the connective; D, filament is united with connective; S106201; bar = 100 μ m. Fig. 23. A–D, Transverse section series of upper half of anther from same bud as in Fig. 22; A, lowest section, at level just above joint of filament and connective, anthers are tetrasporangiate; B and C, connective tissue is more developed on dorsal side of anther indicating introrse dehiscence; arrowheads indicate dorsal furrow of connective; D, anther apex; theca are united; S106201; bar = 100 μ m. See Figs 1–9 for abbreviations.



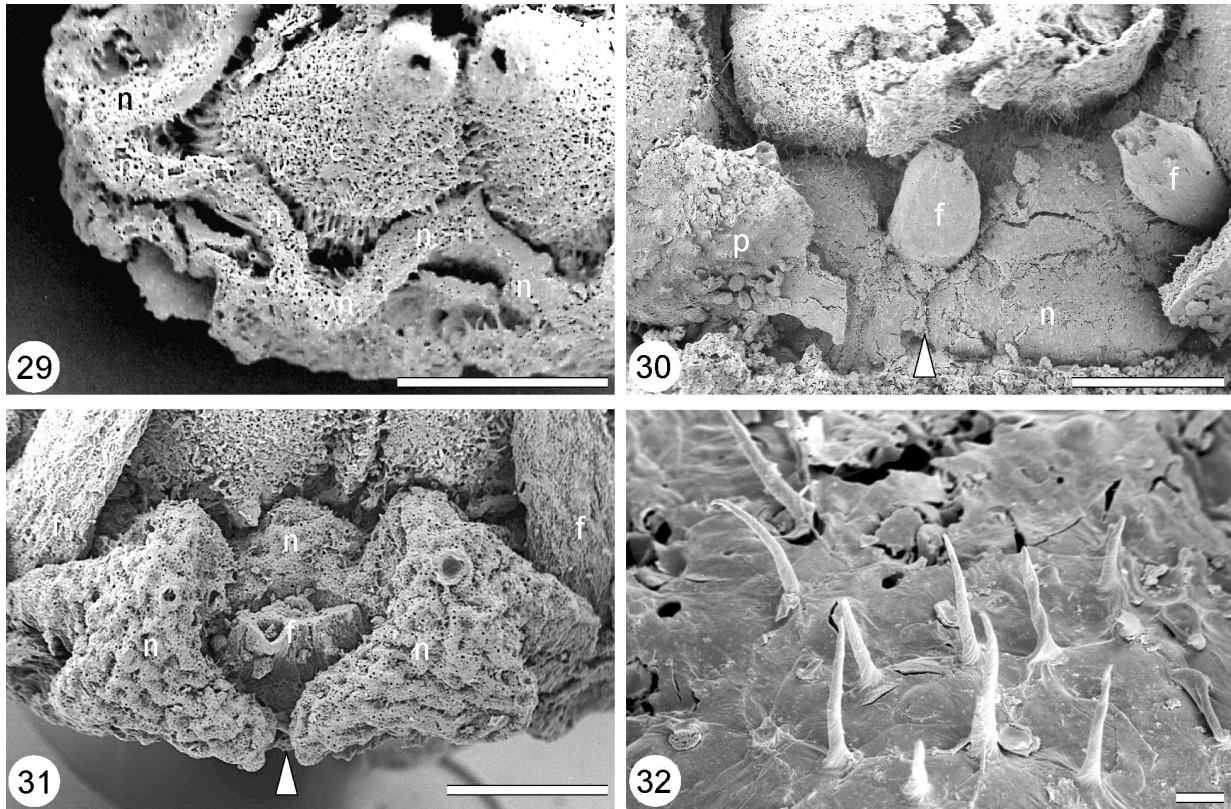
FIGS 24–28. Pollen structure. Fig. 24. Group of triaperturate pollen; S107029; bar = 10 μm . Fig. 25. Polar view of single pollen grain; reticulum with lumina decreasing towards the pole; S107029; bar = 10 μm . Fig. 26. Equatorial view of spheroidal pollen grain; reticulum with lumina decreasing towards the colpi; S106197; bar = 10 μm . Fig. 27. Equatorial view of prolate pollen grain; S107197; bar 10 μm . Fig. 28. Pollen wall of fractured grain with foot layer, infratectal layer and tectum; S106197; bar = 1 μm . See Figs 1–9 for abbreviations.

Pollen. Identical pollen grains were found on the superior regions of the gynoecium and on the nectaries of two specimens (S106197, S107029). Similar pollen has not been observed on the outer surfaces of these two specimens or on any other fossils from the same samples. It is therefore most likely that the pollen was produced by the flowers on which it was found. The pollen grains appear prolate to spherical (11–13 $\mu\text{m} \times 12$ –14.5 μm ; measured on SEM-micrographs) and are generally collapsed (Figs 24–27). They are triaperturate with long colpi. The colpi are narrower in the equatorial region of the pollen which may indicate a tricolporate structure of the apertures. The grains are semitectate and finely reticulate with lumina decreasing in size towards the poles (Fig. 25) and, to a lesser degree, also towards the colpi (Figs 26 and 27). In the pole region the tectum surface is foveolate to almost psilate (Fig. 25). The pollen wall in fractured grains is about 1.2 μm thick and consists of an inner foot layer about 0.6 μm thick, an infratectal layer about 0.2 μm thick, and a tectum about 0.4 μm thick (Fig. 28). An endexine could not be distinguished.

Nectary. An exceedingly broad nectary is present (Figs 10 and 11). The nectary forms a lobed ring around the gynoecium (Fig. 29) which fills all the available space between the ovary and perianth. The filament bases appear

to be completely embedded in the nectary. Only a narrow gap remains between the nectary lobes on the abaxial side of the filaments (Figs 30 and 31). Thin, unicellular trichomes are present on the surface of the nectary (Fig. 32).

Gynoecium. The gynoecium is tetramerous, syncarpous, and the ovary is semi-inferior (Fig. 34). The lowermost part of the ovary is four-locular; it seems to be synascidiate, i.e. each carpel appears to be congenitally closed and the four carpels are congenitally united (Fig. 33A). This synascidiate region is short in anthetic flowers (Fig. 34). Above this zone, carpels are laterally united but their margins do not meet in the centre (symplicate region, Fig. 33B). In the synascidiate/symplicate region of the ovary, which corresponds to the inferior part of the gynoecium, the dorsal carpel walls are congenitally fused with the floral base. The superior regions of the carpels (above the insertion level of the other floral organs) are completely free from each other (plicate or asymplicate region, Fig. 33C). A central canal extends between the carpels down to the lower end of the symplicate region of the ovary (Figs 33B, 38 and 39). A ventral slit is present from the base of the symplicate region to the tip of each carpel (Figs 33B and 40). Placentation is axile (as seen in the synascidiate region of the ovary, Fig. 33A). In mature



FIGS 29–32. Nectary morphology. Fig. 29. Part of post-anthetic flower seen from top showing continuous (shrivelled) nectary tissue surrounding the gynoecium; S107130; bar = 0.5 mm. Fig. 30. Part of lobed nectary of pre-anthetic bud; arrowhead indicates region where nectary lobes abut on dorsal side of filament; S107143; bar = 0.5 mm. Fig. 31. Part of shrivelled nectary of post-anthetic flower; filament is broken close to its base; nectary is continuous on adaxial side of filament; arrowhead indicates gap between nectary lobes on abaxial side of filament; S107137; bar = 0.5 mm. Fig. 32. Unicellular simple trichomes on nectary surface; S107143; bar = 100 μ m. See Figs 1–9 for abbreviations.

flowers the involute placentae are enlarged and contain numerous rows of ovules (protruding-diffuse placentation, Figs 37–39). The densely packed ovules (more than 200 per carpel) are anatropous with their micropyle directed towards the placenta (Figs 35 and 36). The number of integuments and the structure of the nucellus could not be established from the fossil material. The superior region of each ovary is elongate and tapering into a hollow style (Figs 34 and 40). Mature stigmas have not been preserved but they were most likely terminal because no remnant of a stigmatic region could be found on the styles. The styles are erect, suggesting that the stigmas of the four carpels must have been positioned next to each other (Figs 34 and 40). The carpels are covered by a dense indumentum of simple unicellular trichomes (Fig. 41). The structure of mature fruits and seeds is unknown.

DISCUSSION

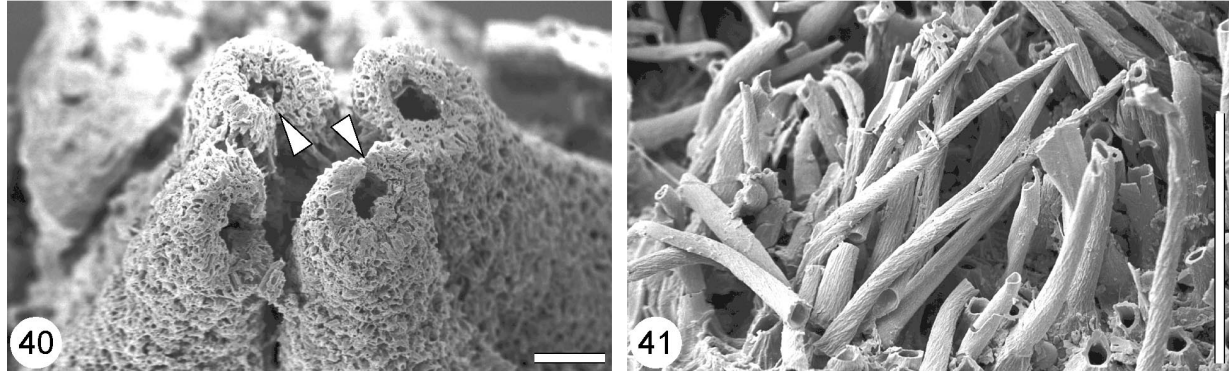
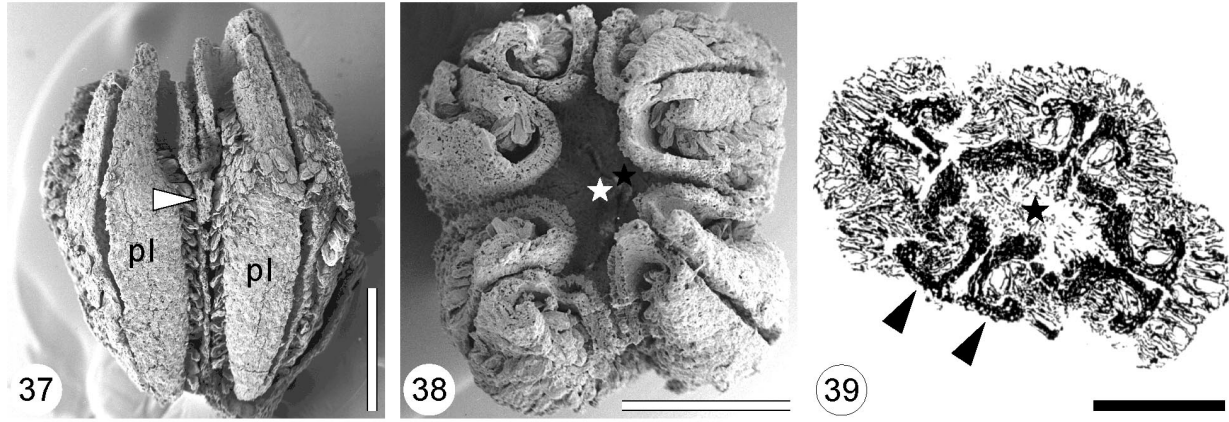
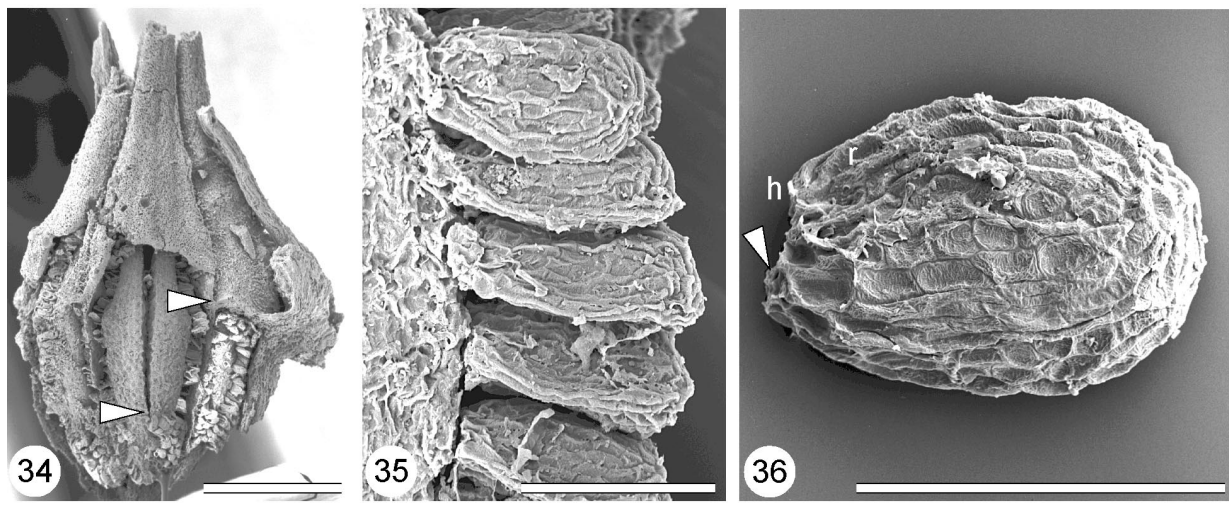
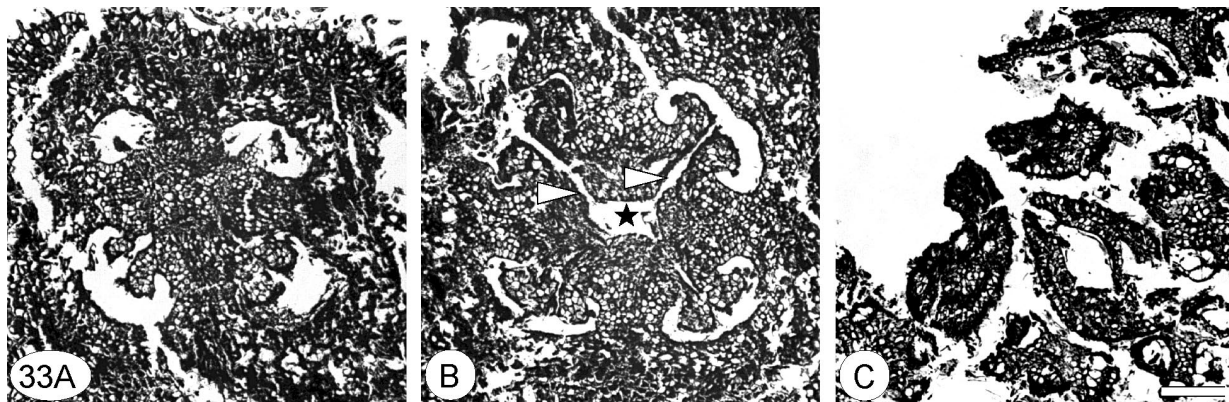
Comparison with extant plants

The combination of small, bisexual, actinomorphic, tetramerous flowers with broadly attached, valvate sepals, narrowly attached petals, eight stamens, a massive nectary, a syncarpous gynoecium with axile placentation, and separate styles, found in the fossil flowers, is known from

two families among modern eudicots, namely the Cunoniaceae and Anisophylleaceae.

Traditionally, Cunoniaceae have been placed in the rosids, in or near the saxifragalean complex, either in Rosales (e.g. Engler, 1928; Schulze-Menz, 1964; Cronquist, 1981), in Saxifragales (e.g. Takhtajan, 1969) or in Cunoniales (e.g. Hutchinson, 1969). Similarities between Cunoniaceae and Dilleniales (Takhtajan, 1969) and Hamamelidae, respectively (Dickson, 1989), have also been discussed. However, recent molecular studies resolve Cunoniaceae to be a member of Oxalidales *sensu* APG (1998) in eurosids I (e.g. Morgan *et al.*, 1994; Savolainen *et al.*, 2000a; Soltis *et al.*, 2000; for more detailed references see Magallón *et al.*, 1999).

Anisophylleaceae have traditionally been placed close to, or within, Rhizophoraceae (e.g. Schimper, 1898; Melchior, 1964). More recent morphological and anatomical studies support an exclusion of Anisophylleaceae from Rhizophoraceae (e.g. Behnke, 1988; Tobe and Raven, 1988). Recent molecular studies have indicated that Rhizophoraceae are members of Malpighiales *sensu* APG (1998) (Setoguchi *et al.*, 1999; Savolainen *et al.*, 2000a; Schwarzbach and Ricklefs, 2000; Soltis *et al.*, 2000), while Anisophylleaceae are placed in Cucurbitales *sensu* APG (1998) (Setoguchi *et al.*, 1999; Savolainen *et al.*, 2000b; Schwarzbach and



Ricklefs, 2000). These new molecular results indicate that Cunoniaceae and Anisophylleaceae are not closely related; however, both are in the eurosid I clade. It will be interesting to see whether these classifications hold true when these two families are studied more intensively at the morphological and molecular level.

Important floral features of Cunoniaceae, Anisophylleaceae and the fossil taxon are summarized in Table 1, and selected characters are discussed in more detail below.

Perianth. The condition of four broadly attached sepals and four narrowly attached petals as found in the fossil flowers is closely matched in different members of the Cunoniaceae (Dickison, 1989; Barnes and Rozefelds, 2000; Matthews *et al.*, 2001) as well as in many members of the Anisophylleaceae (Tobe and Raven, 1988; Matthews *et al.*, 2001). In Cunoniaceae, the petals are often essentially linear and dissected (Dickison, 1975b), as is also the case in many members of Anisophylleaceae (Tobe and Raven, 1988; Matthews *et al.*, 2001). The petal tips of the fossil flowers are apparently secretory. Similar secretory structures are present on the tips of the bifid petals of *Gillbeea* in Cunoniaceae (Hoogland, 1960; Dickison, 1989; Endress, 1994). This condition is apparently also matched in some members of Anisophylleaceae (Tobe and Raven, 1987).

Androecium. The positions of the stamens and the epipetalous position of the carpels in the fossil flowers indicate clearly that the androecium is obdiplostemonous. Obdiplostemony is also present in some Cunoniaceae (Dickison, 1975b) and in Anisophylleaceae (see figures in Tobe and Raven, 1988; Matthews *et al.*, 2001).

The general structure of the anthers (Table 1) is similar in both modern families as well as in the fossil flower and does not provide any evidence for the systematic position of the fossil.

Pollen. The aperture configuration in the fossil pollen is probably tricolporate. Tricolporate, as well as tricolpate pollen grains are common in the Cunoniaceae and their pollen is further comparable to that of the fossils due to their small size (8.5–19 µm long). Many Cunoniaceae have a comparable finely reticulate tectum with the lumina of the reticulum decreasing slightly in size towards the poles and aperture margins (Erdtman, 1952; Hideux and Ferguson, 1976). Pollen grains of the Anisophylleaceae are slightly



FIG. 42. Floral diagram of fossil flower.

larger (16–29 µm long), but also include tricolporate/tricolporoidate finely reticulate to foveolate grains whose lumen size decreases slightly towards the poles and apertures (Vezev *et al.*, 1988). However, the similarity in general morphology and structure of the fossil pollen grains is not restricted to the pollen of Cunoniaceae and Anisophylleaceae, as pollen from several other eudicots, especially taxa included in the earlier Saxifragaceae *sensu lato* share these features (Hideux and Ferguson, 1976). Both Cunoniaceae and Anisophylleaceae also include other pollen types and it is interesting to note that the more rare aperture configurations, such as dicolporate and syncolpate types, occur in both families (Erdtman, 1952; Hideux and Ferguson, 1976; Vezev *et al.*, 1988).

Nectary. In both the Cunoniaceae and Anisophylleaceae an annular nectary disc, similar to that in the fossil flower, is present in most species (Engler, 1928; Dickison, 1975b; Matthews *et al.*, 2001). In the Anisophylleaceae, there is a tendency towards a more segmented structure of the nectary (Tobe and Raven, 1988; Matthews *et al.*, 2001), whereas in the Cunoniaceae the nectary is usually a massive ring surrounding the gynoecium as it is in the fossil flowers.

Gynoecium. In the fossil flowers the ovary is semi-inferior. This is a common floral feature in many taxa of the previous Saxifragaceae *sensu lato* (Bensel and Palsler,

FIGS 33–41. Gynoecium morphology and anatomy. Fig. 33. A–D, Transverse section series of gynoecium of relatively young floral bud; A, base of ovary; synascidiate region; B, symplicate (inferior) region, ventral slits open; star indicates central canal that is continuous with the exterior, arrowheads indicate ventral slits of two of the carpels; C, plicate (superior) region, only three carpels preserved; S106201; bar = 100 µm. Fig. 34. Lateral view of presumably anthetic flower; floral base and dorsal wall of one of the carpels partially broken; lower arrowhead indicates boundary between synascidiate and symplicate region, upper arrowhead indicates boundary between symplicate and plicate region of ovary; S107137; bar = 1 mm. Fig. 35. Row of anatropous ovules attached to placenta; S107134; bar = 100 µm. Fig. 36. Lateral view of single ovule, arrowhead indicates position of micropyle; S107134; bar = 100 µm. Fig. 37. Lateral view of presumably anthetic ovary, dorsal carpel walls and most ovules broken away revealing the broad placentae; arrowhead indicates approximate boundary between inferior and superior region of ovary; S106275; bar = 0.5 mm. Fig. 38. Same specimen as in Fig. 37 seen from above; star indicates central canal that is continuous with exterior; S106275; bar = 0.5 mm. Fig. 39. Transverse section of presumably anthetic ovary in symplicate region, dorsal carpel walls broken away but most of the ovules still attached to the placentae; arrowheads indicate the two involute placentae of one of the carpels; star indicates central canal; S107094; bar = 0.5 mm. Fig. 40. Styles of presumably anthetic flower seen from above, tips broken, styles hollow; arrowheads indicate ventral slits; S107138; bar = 100 µm. Fig. 41. Carpel surface with dense indumentum of unicellular simple trichomes; S107029; bar = 100 µm. See Figs 1–9 for abbreviations.

TABLE 1. Comparison of floral characters of the fossil flowers and modern *Cunoniaceae* and *Anisophylleaceae**

Character	Fossil flower	Cunoniaceae	Anisophylleaceae
Size	3–4 mm long and 3–3.6 mm wide	Mostly few mm	Few mm
Symmetry	Actinomorphic	Actinomorphic	Actinomorphic
Sexuality	Bisexual	Mostly bisexual	Bisexual or perfect but functionally unisexual
Calyx	K 4, valvate	K 4 or 5(–10), valvate or imbricate	K 3 or 4 (5), valvate
Sepal shape	Ovate-triangular	Ovate-triangular	Ovate-triangular
Sepal indumentum	Unicellular-simple, multicellular-peltate (secretory ?)	Simple-unicellular/uniseriate, multicellular-stellate, rarely secretory	Unicellular-simple, multicellular-simple, secretory
Corolla, aestivation	C 4, imbricate	C 4 or 5(-many) or apetalous, open to imbricate	C 3 or 4 (5), open
Petal shape	Clawed, mature shape of blade unknown	Various	Various
Petal indumentum	Unicellular-simple, multicellular-peltate, secretory (?)	Rarely unicellular-simple, one genus with secretory structures on petal tips	Occasionally unicellular-simple
Androecium	Obdiplostemonous	Some obdiplostemonous	Some obdiplostemonous
Anther	Introrse, dorsifixed, sagittate	Introrse, dorsifixed, sagittate or X-shaped	Introrse-latrorse, dorsifixed, sagittate or X-shaped
Pollen	Prolate-spheroidal, longest axis ~ 13 µm	Oblate-prolate, longest axis 8.5–19 µm	Prolate-subprolate, longest axis 16–29 µm
Pollen apertures	Probably tricolporate	Dicolporate, dicolpate, some tricolporate or tricolporoidate, some syncolpate	Tricolporoidate, some tricolporate, some syncolpate
Exine	Finely reticulate	Rugulate to reticulate	Punctate to finely reticulate
Nectary	Lobed ring around gynoecium	Often a lobed ring around gynoecium	Mostly a lobed ring around gynoecium, tendency towards segmentation of nectary
Gynoecium	G 4, semi-inferior	G 2(–5)(rarely more), superior to almost inferior	G (3–)4, inferior
Ovary	Carpels united in lower half, 4-loculed	United to distinct, 2(–5)-loculed	United, 3(–4)-loculed
Placenta	Axile, protruding-diffuse, involute	Axile to apical-axile, some protruding and involute	Axile
Ovules	Numerous, anatropous	(1)2-numerous, anatropous to hemitropous	1–2 ovules/carpel, pendant, anatropous
Styles	Distinct, hollow	Distinct, with narrow canal	Distinct, solid or with narrow canal
Stigmas	Terminal, small (?)	Terminal, small	Terminal, small to well-developed

* Data of Cunoniaceae: Engler, 1928; Erdtman, 1952; Hoogland, 1960, 1979; Dickison, 1974, 1975, 1989; Govil and Saxena, 1976; Hideux and Ferguson, 1976; Cronquist, 1981; Endress and Stumpf, 1991; Hufford and Dickison, 1992; Hoogland et al., 1997; Bradford, 1998; Barnes and Rozefelds, 2000; Matthews et al., 2001. Data of Anisophylleaceae: Ding Hou, 1958; Cronquist, 1981; Tobe and Raven, 1987, 1988; Dahlgren, 1988; Vezey et al., 1988; Matthews et al., 2001.

1975a,b,c,d; Dickison et al., 1994) and is also found in different members of Cunoniaceae (Hoogland, 1960; Dickison, 1974; Dickison, 1975a; Matthews et al., 2001). The degree of carpel union ranges from completely united at the level of the ovary to united only at the very base of the carpels or to no union at all (Dickison, 1975b). In the Anisophylleaceae, the ovary is always inferior, the carpels are completely united at the level of the ovary, and the styles are generally free (Tobe and Raven, 1988).

As in the fossil flowers, a central canal or opening is present in the symplicate region of the gynoecium of some species of Cunoniaceae and Anisophylleaceae (Matthews et al., 2001).

Placentation is axile in the fossil flowers and the placentae are exceedingly large with the ovules arranged in several rows. In Cunoniaceae, placentation is axile or sometimes apical-axile and in some species numerous (although not as many as in the fossils) ovules occur in different genera (Dickison, 1975b). Involute and relatively broad placentae are present in some members of Cunoniaceae (*Weinmannia*, *Geissois*, J. Schönenberger, pers. obs.; for *Weinmannia* see figures in Dickison, 1975b). Anisophylleaceae also have axile placentation, but only one or two ovules per carpel are present and the placentae are not involute (Tobe and Raven, 1988).

The styles of the fossil flowers are hollow and the stigmatic region was most probably restricted to the tip of the styles. Similar styles with a narrow canal and terminal stigmas are also present in Cunoniaceae and Anisophylleaceae (Matthews et al., 2001).

Indumentum. In addition to the simple unicellular trichomes present on most floral organs, the fossil flowers have conspicuous multicellular, peltate trichomes on the pedicel, outer surface of the floral base, sepals, and on the petals. In Cunoniaceae, similar glandular trichomes are present in different species (Dickison, 1975a; Al-Shammary and Gornall, 1994; Matthews et al., 2001). The carpels of Cunoniaceae appear in some species to be covered by a dense indumentum of simple trichomes similar to that of the fossil flowers (see Fig. 4.2 in Hoogland, 1979; Dickison, 1989). In Anisophylleaceae, simple unicellular trichomes are rare and multicellular glandular peltate trichomes are known only for the monotypic genus *Combretocarpus*, where they characteristically occur on the pedicel, the outer surface of the hypanthium, and on the abaxial surface of the sepals (Tobe and Raven, 1988).

Systematic affinities of the fossil flowers

Taking all characters into consideration, the fossil flowers described in this paper share many floral features with the representatives of both Cunoniaceae and Anisophylleaceae. However, the gynoecium structure of the fossil flowers in particular indicates a closer relationship to the former family. Cunoniaceae includes taxa with a similar ovary position and carpel union as observed in the fossil flowers. In contrast, all members of Anisophylleaceae have an inferior ovary and completely united carpels at the level of the ovary. The number of ovules per carpel is limited to one

or two in Anisophylleaceae, whereas in Cunoniaceae certain taxa have numerous ovules per locule. Involute placentae are present in some members of Cunoniaceae but are apparently absent in Anisophylleaceae. Finally, as in the fossil flowers, the nectary in Cunoniaceae generally consists of an annular disc. Similar nectaries are also present in Anisophylleaceae; however, there is a tendency towards a subdivision of the nectariferous tissue into several distinct parts in this family.

The character combination present in the fossil taxon justifies its inclusion in the Cunoniaceae. The characters are, however, not specific for any extant genus in the family. Therefore, a new genus and species are formally described below.

Comparison with other fossil flowers

A number of fossil reproductive organs of cunoniaceous affinity have been recovered from Tertiary deposits located in Australia (see below). Although some of these fossils are organically and three-dimensionally preserved, none have sufficient structural details intact to allow a full comparison with the fossil flowers described in this paper.

The Åsen mesofossil flora comprises a variety of other fossil flowers which have a general floral organization similar to that of the flowers described here, and also to extant taxa previously included in the broadly defined Saxifragales (Takhhtajan, 1969). They are small, bisexual and actinomorphic, with tetramerous or pentamerous perianth and androecium; they have small, unspecialized tricolpate or tricolporate pollen, a distinct nectary and an inferior or semi-inferior ovary with numerous small ovules and long, stout and free styles. *Scandianthus costatus* Friis & Skarby and *S. major* Friis & Skarby were tentatively compared to the extant genus *Vahlia* of the Vahliaceae, a family previously included in the Saxifragales (Friis and Skarby, 1982), but now referred to as the euasterid I complex *sensu* APG (1998). These species also show similarities to other former saxifragalean families such as Hydrangeaceae, Escalloniaceae and Saxifragaceae. *Scandianthus* differs from the fossil flowers in this study in having a unilocular ovary composed of two carpels with apical, pendant placentae. The flowers of *Scandianthus* are further distinguished, being pentamerous and having an indumentum of sparse, simple trichomes. The nectary is distinctly subdivided, with five lobes that are each bilobed. *Silvianthemum suecicum* Friis was compared to extant members of the Escalloniaceae (Friis, 1990) that were also previously included in the broadly defined Saxifragales, but it is now resolved to be a member of the euasterid II complex (APG, 1998). It is similar to the fossil flowers described here in having an indumentum of simple and glandular peltate trichomes. However, it differs with regard to the shape and size of its sepals and petals, and its possession of a unilocular ovary composed of three carpels with parietal placentation.

Late Cretaceous mesofloras of North America have also yielded a number of fossil flowers with a general floral organization comparable to that of the fossil flowers from Åsen; however, none are identical or systematically closely related. *Tylerianthus crossmanensis* Gandolfo, Nixon &

Crepet shows closest similarity to extant Saxifragaceae and Hydrangeaceae (Gandolfo, 1998) and differs from our fossils in several respects, including the presence of a bicarpellate ovary.

Fossil history of Cunoniaceae

This new finding of Cunoniaceae flowers from the Cretaceous of southern Sweden documents the presence of the family in Europe, as has been suggested previously based on fossil wood from the Tertiary (Hoffman, 1952; Gottwald, 1992). However, in spite of these findings, Cunoniaceae are rare in the fossil record of the Northern Hemisphere. Thus, although the family may not have had its initial radiation in the Gondwanan region, it is clear that the major diversification of the family took place there. Tertiary records of Cunoniaceae in the Southern Hemisphere are extensive: most fossils are dispersed pollen and leaves; however, flowers, inflorescences/infructescences, and dispersed fruits have also been recovered (e.g. Carpenter and Buchanan, 1993; Blackburn and Sluiter, 1994; Macphail et al., 1994; Barnes and Hill, 1999a,b; Barnes and Jordan, 2000).

Southern Hemisphere records of the Cunoniaceae extend back to the Late Cretaceous. Poole et al. (2000) described fossil wood from the Late Cretaceous (Santonian/Campanian) of Antarctica as having a combination of anatomical characters most similar to extant Cunoniaceae. Aside from this account, Cunoniaceae from the Cretaceous were previously known only from relatively few palynological and vegetative records (Askin, 1992). Some records are based on the dispersed pollen of *Concolpites leptos* Partr., which was compared to that of extant *Gillbeea* (Macphail et al., 1994).

Cunoniaceae pollen is common in Paleocene and Eocene floras of central Australia, thus constituting a prominent component of many palynofloras. The frequency of Cunoniaceae pollen ranges from 16 to 80 % in the Paleocene and from 1 to 17 % in the Eocene (Macphail et al., 1994). While the importance of the Cunoniaceae decreased in the central areas of Australia from the latest Eocene onwards, the pollen record indicates that the family became well established and locally abundant in eastern and south-eastern Australia during the late Eocene (Macphail et al., 1994). The family then continued to diversify in these areas up to the present time (Blackburn and Sluiter, 1994; Carpenter et al., 1994).

Australian macrofossils of Cunoniaceae comprise leaves and reproductive organs assigned to the fossil genera *Phyllites* and *Weinmanniaphyllum* (Carpenter and Buchanan, 1993) or more commonly these are included in extant genera. Currently, species assigned to *Acsmithia*, *Callicoma*, *Ceratopetalum*, *Codia*, *Cunonia*/*Weinmannia*, *Eucryphia*, *Schizomeria* and *Vesselowskyia* have been described from the Tertiary of Australia (Ettinghausen, 1894; Holmes and Holmes, 1992; Carpenter and Buchanan, 1993; Blackburn and Sluiter, 1994; Carpenter et al., 1994; Barnes and Hill, 1999a,b; Barnes and Jordan, 2000). The presence of *Acsmithia*, *Callicoma*, *Ceratopetalum*, *Codia* and *Eucryphia* is based on fossil flowers, fruits, seeds,

inflorescences/infructescences and fossil leaves (Holmes and Holmes, 1992; Carpenter and Buchanan, 1993; Barnes and Hill, 1999a,b; Barnes and Jordan, 2000), while the presence of the remaining genera is based on leaf fossils only (Carpenter and Buchanan, 1993; Blackburn and Sluiter, 1994).

In New Zealand and South America, the Tertiary fossil record of Cunoniaceae is scarce and includes mostly dispersed pollen (e.g. Couper, 1953; van der Hammen et al., 1973; Mildenhall, 1980; Romero, 1986) (see references in Morley, 1999).

The fossil wood described from the Tertiary of Europe was assigned to the fossil genus *Cunonioxylon* established by Hoffman (1952) and shows a suite of wood characters closely comparable to those of extant *Weinmannia*, and particularly to wood of South American species. The type species, *Cunonioxylon weinmannioides* Hoffman, is from the Oligocene of Austria (Hoffman, 1952). The only other species currently known from the European Tertiary is *Cunonioxylon parenchymatosum* Gottwald described from the Eocene of Lower Saxony in Germany. This species shows complete agreement with wood of extant *Cunonia* (Gottwald, 1992).

Biogeography

Three other floral fossils with strong similarity to extant Gondwanan taxa have been described from the Late Cretaceous of Europe. These include flowers of *Silvianthum suecicum* from southern Sweden (Friis, 1990), and flowers of *Esgueiria adenocarpa* Friis, Pedersen & Crane and *E. miraensis* Friis, Pedersen & Crane from the Late Cretaceous of Portugal (Friis et al., 1992). Flowers of *Esgueiria*, assigned to the species *E. futabensis* Takahashi, Crane & Ando, have also been reported from the Late Cretaceous of Japan (Takahashi et al., 1999a). *Silvianthum* shows close similarity to extant *Quintinia* (Escalloniaceae) distributed today from the Philippines and New Guinea to Australia (Friis, 1990). Although *Esgueiria* could not be definitely included in any modern family, it shares many features with the African genus *Guiera* of the Combretaceae, and is believed to be closely related (Friis et al., 1992).

The discovery of an early member of the Cunoniaceae in the Late Cretaceous flora of southern Sweden is a further indication that families which now occur predominantly in the Southern Hemisphere were present in Europe in earlier times. It also suggests that there may have been more floristic interchange between the floras of the northern continents and the old Gondwanan continents during the Cretaceous than during later periods of the earth's history.

FORMAL DESCRIPTION

Order—Oxalidales *sensu* APG (1998)

Family—Cunoniaceae

Platydiscus Schönenberger & Friis, gen. nov.

The name *Platydiscus* refers to the broad nectary disc of the fossil flowers (from Greek 'platys': wide, broad; 'discos': disc).

Generic diagnosis—Flowers small, shortly (?) pedunculate, actinomorphic, tetramerous, perigynous; perianth of distinct sepals and petals; androecium obdiplostemonous; anthers dorsifixed, sagittate, dithecal, tetrasporangiate; pollen small, prolate to spherical, tricolporate (?), semitectate, finely reticulate; nectary disc thick, annular, lobed; gynoecium syncarpous, superior regions of carpels free from each other; styles hollow; placentation axile; ovules numerous, anatropous.

Comments on the new genus

Mature fruits and seeds as well as vegetative organs are unknown.

Type species—*Platydiscus peltatus* Schönenberger & Friis, spec. nov.

The specific epithet refers to the conspicuous peltate trichomes on the outer surface of the floral base, on the sepals, and on the petals.

Specific diagnosis—As for the genus with the following additions: calyx valvate; sepals ovate-triangular; corolla imbricate; petals with narrow base, clawed (trullate in young stages), ribbed, petal tips secretory; filaments linear; anther dehiscence introrse; connective with dorsal furrow; exine reticulate with decreasing lumina towards poles and colpi; gynoecium with central canal in symplicate region; carpels with ventral slits; placenta involute-protruding-diffuse; indumentum of multicellular, secretory, peltate trichomes with multiseriate stalk on outer surface of floral base and abaxial sides of sepals and petals; simple, unicellular trichomes on floral base, abaxial side of sepals, nectary, and free parts of carpels; unicellular trichomes with swollen base on adaxial side of petals.

Dimensions—Measurements are given for flowers that presumably were in anthetic stage when becoming fossilized (specimens S106197, S107029, S107136–S107138). Flower 3–4 mm long and 3–3.6 mm wide (without sepal and petal lobes); sepals approx. 2.5 mm broad at base, length unknown; petals approx. 0.5 mm at base, clawed part approx. 1.2 mm long, size of petal limb unknown; filaments approx. 2.2 mm long, size of anthers unknown; pollen 11–13 μm \times 12–14.5 μm ; inferior part of gynoecium approx. 1.3 mm long, superior part approx. 2.2 mm long.

Holotype—S107143 (sample GI 32116), Figs 11, 14, 15, 20, 30 and 32.

Type locality—Höganäs AB quarry at Åsen near Axeltorp, Scania, Sweden.

Type stratum—Fluviatile-lacustrine sequence.

Age—Late Cretaceous (Late Santonian—Early Campanian).

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