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Floral structure of extant *Quintinia* (Paracryphiales, Campanulids) compared with the late Cretaceous *Silvianthemum* and *Bertilanthus*

Friis, Else Marie ; Pedersen, Kaj Raunsgaard ; Endress, Peter K

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FLORAL STRUCTURE OF EXTANT *QUINTINIA* (PARACRYPHIALES, CAMPANULIDS) COMPARED WITH THE LATE CRETACEOUS *SILVIANTHEMUM* AND *BERTILANTHUS*

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Flowers of extant *Quintinia* are described in detail on the basis of field observations and serial microtome sections and compared with flowers of the Late Cretaceous *Silvianthemum suecicum* and *Bertilanthus scanicus* on the basis of new analyses of the fossil material. The analyses of both extant and fossil material also include synchrotron-based X-ray tomographic microscopy. The study shows that *Quintinia* and *Silvianthemum/Bertilanthus* have more features in common than previously recognized and strongly reinforces their earlier assumed close relationships. Among important characters linking the three genera are similar secretory hairs on the floral surface and pedicel; short sepals; free, quincuncial petals; broad anthers with small pollen sacs; 4-aperturate pollen (in *Silvianthemum* and *Quintinia*); postgenital union of the 3–4 apocarpous styles (in *Silvianthemum* and *Quintinia*); connection of the apocarpous carpel parts with the floral base; downward tapering ovary and locule(s); placentation on incomplete septa; and flask-shaped epidermal cells with a thin and long papilla on the carpels. Features observed in *Quintinia*, particularly the presence of bitegmic ovules and free petals, suggest that the apparent phylogenetic position with extant Paracryphiales (campanulids) needs further analysis. Bitegmic ovules are not known from other Paracryphiales or campanulids, and the presence of free petals is unusual in campanulids.

Keywords: asterid, *Bertilanthus*, fossil flowers, Late Cretaceous, Paracryphiales, *Quintinia*, *Silvianthemum*, synchrotron-based X-ray tomographic microscopy (SRXTM).

Introduction

A close relationship between extinct *Silvianthemum suecicum* Friis from the Late Cretaceous of Sweden and extant *Quintinia* A. DC. was first suggested on the basis of structural similarities of their flowers (Friis 1990; Friis et al. 2011) and supported by cladistic analyses (Backlund 1996; Martínez-Millán 2010). In the study by Backlund (1996), *Quintinia* appears as sister to a clade of *Silvianthemum* plus a large part of campanulids. In a structural cladistic analysis of asterids by Martínez-Millán (2010), *Silvianthemum* Friis is sister to *Quintinia*.

Quintinia contains ~25 extant species (Dickison and Lundberg, forthcoming), including species previously placed in *Dedea* Baill. (Baillon 1879; Schlechter 1906, 1914) and in *Curraniodendron* Merr. (Merrill 1915, 1923; Engler 1930) from Australia, New Zealand, Vanuatu, New Caledonia, New Guinea, and the Philippines (Dickison and Lundberg, forthcoming). A further fossil taxon from the Late Cretaceous of Sweden, *Bertilanthus scanicus* Friis et Pedersen, was linked to *Silvianthemum* and *Quintinia* by a number of unique floral features (Friis and Pedersen 2012). A sister relationship between *Silvianthemum-Bertilanthus* Friis and *Quintinia* would imply that the clade including extant *Quintinia* had a much wider distribution in the past (Friis 1990; Friis and Pedersen 2012) and perhaps an origin in the Northern Hemisphere.

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Quintinia was classified in Saxifragaceae (Engler 1930), Saxifragales (Takhtajan 1969), or Hydrangeales (Takhtajan 1987) in premolecular systems. It appeared as sister to *Paracryphia* Baker f. (and this clade sister to Dipsacales) in the studies by Bremer et al. (2002, 2004). This topology has not changed and is strongly supported in studies with larger data sets (Winkworth et al. 2008; Tank and Donoghue 2010). *Quintinia* is currently placed in Paracryphiales (Paracryphiaceae or Quintiniaceae; Lundberg 2001; Stevens 2001–; Winkworth et al. 2008; APG III 2009; Tank and Donoghue 2010). Inclusion of *Silvianthemum-Bertilanthus* in the same group would further imply the presence of two advanced campanulid asterids in the Late Cretaceous (Santonian-Campanian) of Europe.

This is the first detailed study of flowers of *Quintinia* based on field observations and serial microtome sections. In addition, the application of synchrotron-based X-ray tomographic microscopy (SRXTM) and additional fossil material have provided much new information on structural details in *Silvianthemum*, allowing a more detailed comparison between *Silvianthemum-Bertilanthus* and *Quintinia*. There is currently no data set available that is sufficiently comprehensive to support a more detailed phylogenetic assessment of *Silvianthemum* and *Bertilanthus*.

This study thus provides new material for two separate questions concerning *Quintinia*: (1) its apparent relationship with fossil *Silvianthemum/Bertilanthus* and (2) its apparent relationship with extant Paracryphiales (campanulids). The study primarily focuses on the first question and also provides new aspects for the second question.

Material and Methods

Flowers of extant *Quintinia* studied here were collected by P. K. Endress in 1977 and 1990: *Quintinia fawkneri* F. Muell. (PK Endress 9220; December 12, 1990; Mt. Lewis, North Queensland, Australia), *Quintinia quatrefagesii* F. Muell. (PK Endress 9081; November 15, 1990; Mt. Lewis, North Queensland, Australia), *Quintinia cf. sieberi* A. DC. (PK Endress 4332; September 25, 1977; Mt. Tambourine, Jolanah National Park, South Queensland, Australia), and *Quintinia verdonii* F. Muell. (PK Endress 4370; October 5, 1977; Coffs Harbour, Bruxner Park, New South Wales, Australia).

The fossil specimens of *Silvianthemum* and *Bertilanthus* discussed here are from the Late Cretaceous (Late Santonian–Early Campanian) mesofossil assemblages collected at the Åsen locality, southern Sweden (for further details, see Friis 1990; Friis and Pedersen 2012). *Silvianthemum* occurs in both the Late Santonian and the Early Campanian part of the sequence, while *Bertilanthus* is restricted to the Early Campanian part. The study includes all published material of *Silvianthemum* and *Bertilanthus* as well as more than 100 new specimens of *Silvianthemum* (S106024–S106026, S106318–S106322, S127615, S127616, S127618, S171503, S171544, S171567–S171581, S171614, S171615, S172536–S172548; specimens mounted for SEM and SXRTM have separate numbers, while several unmounted specimens may be stored in box-slides under the same number).

Specimens for SEM were mounted on aluminum stubs using nail polish, sputter-coated with gold, and studied using a Hitachi S-4300 field emission SEM at 2 kV. Gold coating of specimens studied earlier is heavier than for specimens coated more recently. Heavy coating is particularly distinct for the holotype for *Silvianthemum* (fig. 6D–6H).

The holotype for *Silvianthemum suecicum* (S100376), three other specimens of *Silvianthemum* (S171503, S171556, S171578), as well as three specimens of *Q. quatrefagesii* (flower bud, anthetic flower, postanthetic flower) were studied using SRXTM at the TOMCAT beamline of the Swiss Light Source at the Paul Scherrer Institute, Switzerland, using objective $\times 10$ at 10 keV, following the technique outlined by Donoghue et al. (2006). Vertical stacking was applied for several specimens and lateral stacking for the anthetic flower of *Q. quatrefagesii*. The holotype (gold coated) of *Silvianthemum* was retained on the SEM stub during SRXTM, while the other specimens were mounted uncoated on brass stubs with nail polish. After SRXTM, the uncoated fossils were remounted on SEM stubs and gold coated for SEM.

Slice data derived from the SRXTM (Hintermüller et al. 2010) were analyzed and manipulated using Avizo software (ver. 6.3 and 7) for computed tomography. Volume rendering (vortex and volume rendering) providing transparent and surface reconstructions was also used for virtual sections that consist of several consecutive slices. Contrast was enhanced for SEM micrographs by making the background black using Photoshop software.

For serial microtome sectioning of *Quintinia*, two techniques were applied. Flowers of *Q. fawkneri* and *Q. quatrefagesii* were embedded in Kulzer's Technovit (2-hydroethylmethacrylate) and sectioned using a Microm HM 355 rotary microtome with a conventional knife D. The sections were

stained with ruthenium red and toluidine blue and mounted in Histomount. Flowers of *Q. sieberi* and *Q. verdonii* were embedded in paraplast and the sections stained with astra blue and safranin.

All specimens of extant *Quintinia* used in this study are stored at the Institute of Systematic Botany, University of Zurich, Switzerland (Z). All specimens of fossil *S. suecicum* and *Bertilanthus scanicus* are stored in the paleobotanical collections of the Swedish Museum of Natural History, Stockholm, Sweden (S).

Results

Quintinia

Short description. The flowers are small (less than 5 mm in diameter), bisexual or unisexual. They commonly have 5 sepals, 5 petals, 5 stamens (alternating with the petals), and 3–4 carpels (*Quintinia quatrefagesii*: 3; *Quintinia sieberi* and *Quintinia verdonii*: 3 or 4; *Quintinia fawkneri*: 4). Sepals, petals, and stamens are free; stamens are also free from the perianth; and carpels are united in the inferior ovary. The floral base forms a shallow floral cup above the ovary. Numerous ovules are borne on parietal placentae. A nectary is present on the ovary roof.

Detailed description and comments. The descriptions are based on *Q. quatrefagesii*. If other species are used, they are specifically mentioned. The flowers are scent-less (weakly sweetish scented in *Q. verdonii*) and protogynous. They are mostly 5-merous (except gynoeceum), but 4-merous flowers also occur, and they are rarely 5-merous also in the gynoeceum (Schlechter 1914).

The sepals are short and narrow (fig. 1A, 1B). They have only one vascular bundle. They do not cover the floral bud (fig. 1A, 1B). Aestivation is open. The sepal tissues are not tanniferous.

The petals are white; they are acute (or rounded in other species) and have a broad base and one vascular trace. Aestivation is quincuncial in *Q. quatrefagesii* (fig. 1B) but cochlear in *Q. cf. sieberi* and *Q. verdonii*. The upper surface has a papillate epidermis (fig. 2A–2C), and near the base it bears unicellular hairs in *Q. quatrefagesii* (fig. 2A). The petal tissues are strongly tanniferous (fig. 2B, 2C).

The stamens have relatively short, stout filaments (fig. 1C). The anthers are more or less basifixed (or dorsifixed at the base), sagittate, and introrse (*Q. quatrefagesii*, *Q. sieberi*, *Q. verdonii*). They are broad and inflexed over the floral center (fig. 2D). The four pollen sacs are relatively small compared with the other parts of the anther (figs. 1C, 2A–2C, 4A–4C). Conspicuous elongate, nontanniferous parenchyma cells are present in the region between the thecae and the connective in *Q. quatrefagesii* (fig. 4A) and *Q. verdonii* (fig. 4B). Tanniferous tissue is concentrated in the periphery of the filament and connective (figs. 2A–2D, 4A–4C). Enlarged, somewhat radially elongate epidermal cells with especially dark tanniferous content are present in the median dorsal region of the anthers in *Q. quatrefagesii*, *Q. sieberi*, and *Q. verdonii* (fig. 4A–4C).

Pollen grains are tetracolporate in *Q. quatrefagesii* (fig. 1G) and (3)4(5)-colporate in *Q. sieberi* (Kodela 2006).

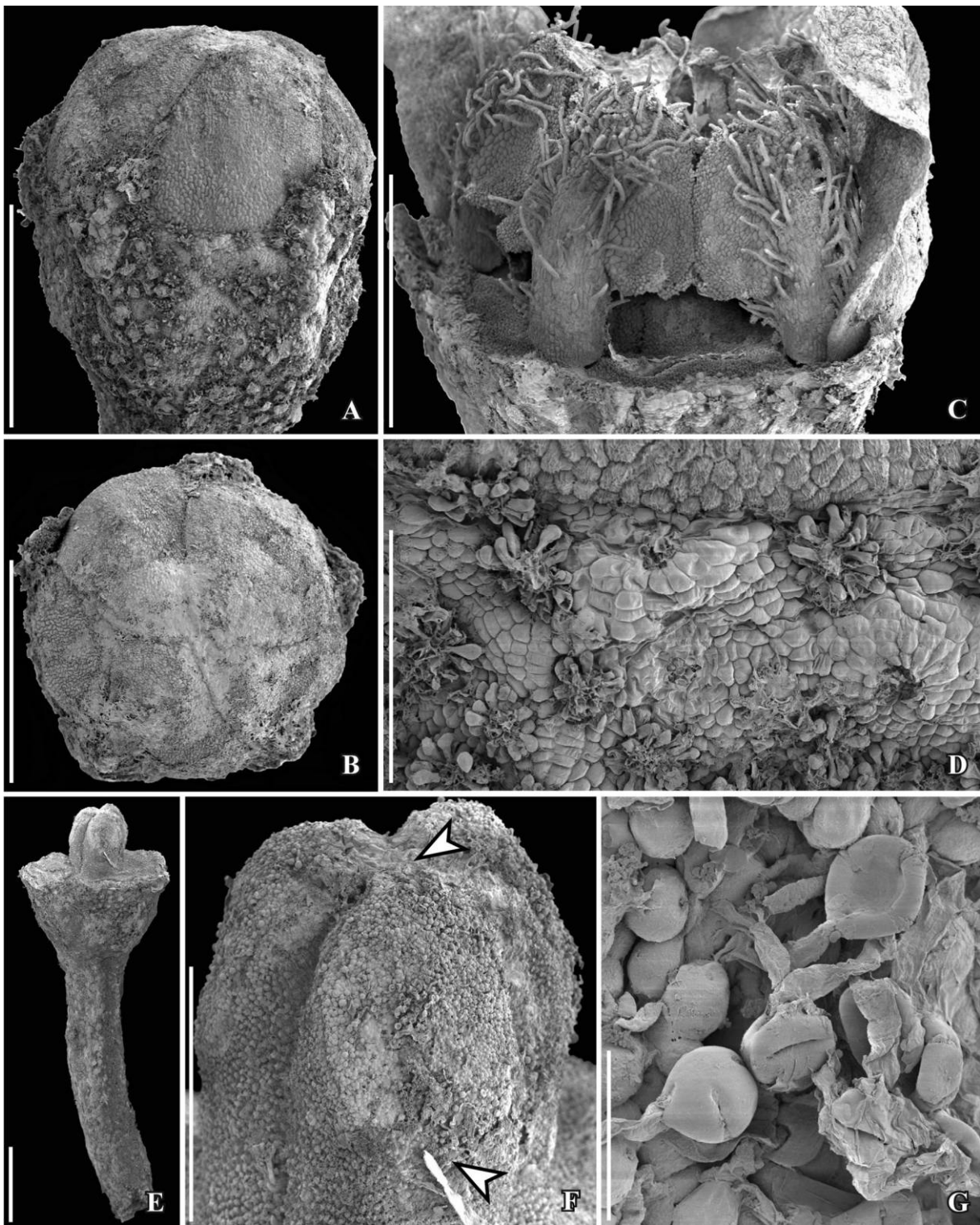


Fig. 1 *Quintinia quatrefagesii*. SEM micrographs. *A, B*, Flower bud in lateral and apical view showing narrow sepals that do not cover petals (*A, B*); free, quincuncial petals (*B*); and densely spaced secretory hairs on surface of hypanthium and sepals (*A*). *C*, Anthetic flower with part of perianth removed to show stamens. Note long hairs on dorsal surface of filament. *D*, Surface of hypanthium with slightly sunken secretory hairs. *E*, Preanthetic flower with perianth and androecium detached, showing long pedicel, ovary, and the broad styles. *F*, Detail of styles in *E* showing stigmatic region extending far down on the dorsal side of the carpels (extent marked with arrowheads). *G*, Pollen grains from stigmatic surface showing smooth surface and four apertures. Scale bars = 1 mm (*A-C, E*), 200 μm (*D*), 500 μm (*F*), 25 μm (*G*).

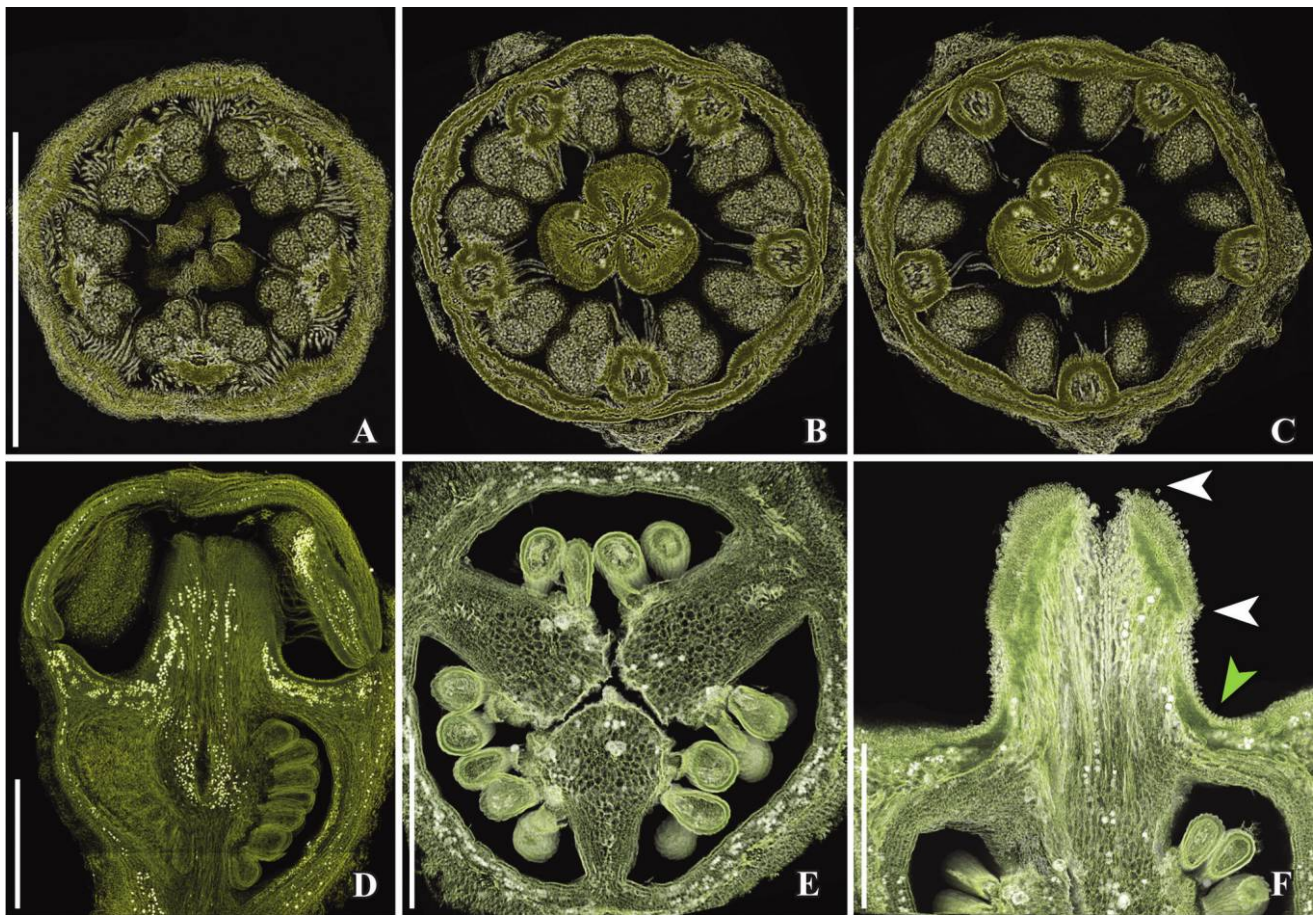


Fig. 2 *Quintinia quatrefagesii*. Synchrotron-based X-ray tomographic microscopy reconstructions showing internal structures of flower bud (A–D) and preanthetic flower (E, F) in cut voltex slices. A–C, Transverse sections through apical part of flower bud showing perianth and androecium. Homogeneous green areas in the outer parts of petals; dorsal part of connective and outer part of filament show position of tanniferous tissue. D, Longitudinal section through central part of flower bud showing extent of plicate and symplicate zones and ovule position. White dots show position of crystals. E, Transverse section of ovary showing parietal placentation. F, Longitudinal section through styles and apical part of ovary showing the dorsal stigmatic area (between white arrowheads), papillate zone below the stigmatic zone (green arrowhead), and uppermost ovules. Scale bars = 1 mm (A; applies to A–C), 500 μm (D, E), 200 μm (F).

The gynoecium is syncarpous in the ovary and apocarpous—but with postgenitally united carpels—in the style (figs. 2B–2F, 3, 4D–4F, 5A). All four species have a synascidiate zone. In *Q. quatrefagesii*, the syncarpous part is about half symplicate and half synascidiate (fig. 3A). The placental area is in the symplicate zone (figs. 2D, 3A, 5A). In *Q. fawkneri*, the symplicate zone appears to be longer than the synascidiate zone (fig. 3B). The stigma extends far down along the dorsal side of each carpel in *Q. quatrefagesii* (more than half the length of the [short] style; figs. 1E, 1F, 2F, 5A). The stigma is characterized by radially extended epidermal cells on the style (fig. 5A, 5C). The cell layer below the epidermis of the stigma is small celled. The stigma is wet in *Q. quatrefagesii* (already in old bud) and *Q. fawkneri* (observed in the field). Remains of secretion are also present in the microtome sections (fig. 5C). A distinctive radiating pollen tube transmitting tract is connected to the stigmatic zone and extends along the style (fig. 5C). In *Q. fawkneri* and *Q. verdonii*, the stigmatic zone also has somewhat radially elongate epidermal cells, but the zone

is short as compared with the style length (figs. 3B, 3C, 5B). The epidermal cells of the gynoecium below the stigmatic region are flask shaped, with a thin and long papilla (figs. 1F, 5A, 5C). They occur on the style and on the wide ovary roof. Tanniferous tissue is abundant in the style and ovary in *Q. quatrefagesii* and other species. Files of large cells each with an oxalate druse are present in the style in *Q. fawkneri* and *Q. quatrefagesii* (fig. 2B–2D).

The carpels are free on top and postgenitally united in the style in *Q. quatrefagesii* (figs. 2B, 2C, 4D), *Q. cf. sieberi*, and *Q. verdonii*. Fusion of the carpels with the floral base (floral cup) begins higher up than fusion between the carpels. In *Q. quatrefagesii* and other species (*Q. verdonii*), in the upper part of the syncarpous zone, there are long intercarpellary slits (fig. 4E, 4F), which disappear lower down. In the symplicate zone, the three placentae in *Q. quatrefagesii* and *Q. sieberi* are protruding but are not connected in the middle of the ovary in the symplicate zone; thus, they are technically parietal (figs. 2E, 3A, 3C, 4F). However, in *Q. fawkneri* (fig. 3B) and *Q.*

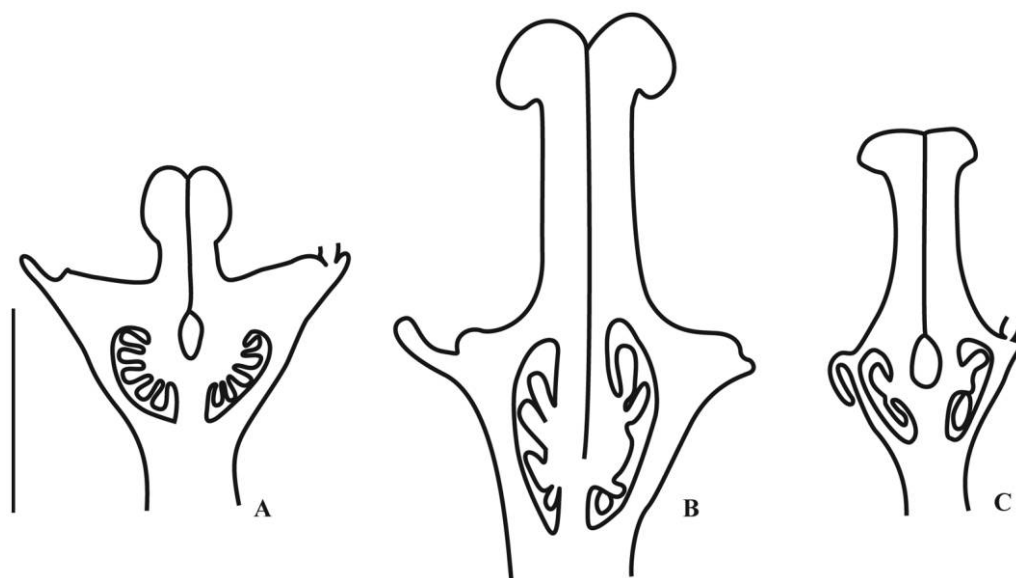


Fig. 3 *Quintinia*. Schematic median longitudinal sections of gynoecia (in tricarpellate gynoecia, two carpels are drawn in median section). The longitudinal line in the middle of the gynoecium shows the extent of the plicate and symplicate zones; the opening in the upper center of the ovary shows the free space caused by the incomplete septa. A, *Quintinia quatrefagesii* (advanced bud). B, *Quintinia fawkneri* (postanthetic). C, *Quintinia verdonii* (anthetic). Scale bar = 2 mm.

verdonii, in the symplicate zone the placentae are partially contiguous. Thus, here the placentae are at the borderline between parietal and axile in the symplicate zone. The zone with the inferior ovary and the locule(s) tapers downward.

The vascular pattern of the gynoecium is simple, with a dorsal and two lateral strands. In the zone of the inferior ovary, several vascular bundles of the outer floral organs also pass close to the gynoecium.

The ovules are small, not filling the locules (figs. 2D–2F, 4F, 5A). In *Q. quatrefagesii*, there are ~20 ovules per carpel in 2–3 rows on each carpel margin; in *Q. sieberi*, there are ~12 ovules per carpel; and in *Q. verdonii*, there are ~6 ovules per carpel. In *Q. quatrefagesii*, ovule position is perpendicular to the placenta surface so that the upper ovules are more or less upright, the middle ones horizontal, and the lower ones pendant (fig. 3A); in *Q. verdonii*, the upper ovules are upright, the lower pendant (fig. 3C); in *Q. fawkneri*, the ovules are upright, except for some of the lowermost ones (fig. 3B). The ovules in all four species are anatropous, incompletely tenuinucellar (for definition, see Endress 2011b), and have two long integuments (fig. 4H). At anthesis, the nucellus disintegrates except below the short embryo sac (fig. 4H). Both integuments are 2–3- or 3-cell-layers thick (fig. 4G, 4H). The micropyle is formed by the inner integument and is appressed to the placenta (fig. 4H). An endothelium is not or only weakly differentiated. In *Q. quatrefagesii*, *Q. sieberi*, and *Q. verdonii*, the epidermis of the outer surface of the ovule (outer integument and raphe) is large celled and tanniferous (fig. 4G, 4H); also, some cells of the inner epidermis of the inner integument are tanniferous (fig. 4G, 4H). In *Q. fawkneri*, the epidermis of the outer ovule surface is also tanniferous.

Nectar is released through stomata (nectar pores) on a shallow disk on the extensive roof of the ovary (nectar observed

in the field in *Q. quatrefagesii* and *Q. fawkneri*); the nectary is dark green in *Q. fawkneri*.

Large, multicellular secretory hairs of an almost hemispherical overall shape are present on the outer floral surface, including the sepals, floral base, and pedicel (in the sepals also on the upper surface). In *Q. quatrefagesii*, these hairs have a group of small cells at the base and a group of upper, elongate, radiating secretory cells (figs. 1D, 5D). In *Q. quatrefagesii*, in addition, some hairs of this kind are in depressions on the uneven surface of the pedicel (fig. 1E). Such hairs are also present in *Q. sieberi*. Although the flowers are highly tanniferous, surprisingly the floral periphery at the level of the inferior ovary is partly not tanniferous. It may be assumed that the secretion by the hairs in this area is a compensatory protection against herbivores.

Silvianthemum suecicum

Short description. The flowers are small (less than 2 mm in diameter) and bisexual. They have 5 sepals, 5 petals, 8 stamens, and 3 (occasionally 4) carpels. Sepals and petals are free; carpels are united in the inferior ovary. Numerous ovules are borne on parietal placentae. A nectary is present on the ovary roof.

Detailed description and comments. The description is based on earlier published specimens (Friis 1990) as well as new material and information obtained from SRXTM. There is some structural variation (e.g., distribution of trichomes, number of carpels, distinctiveness of nectary) among the fossil specimens assigned to *Silvianthemum*. It is possible that this variation reflects the presence of more than one species, but the variation may also fall within the natural variation of a

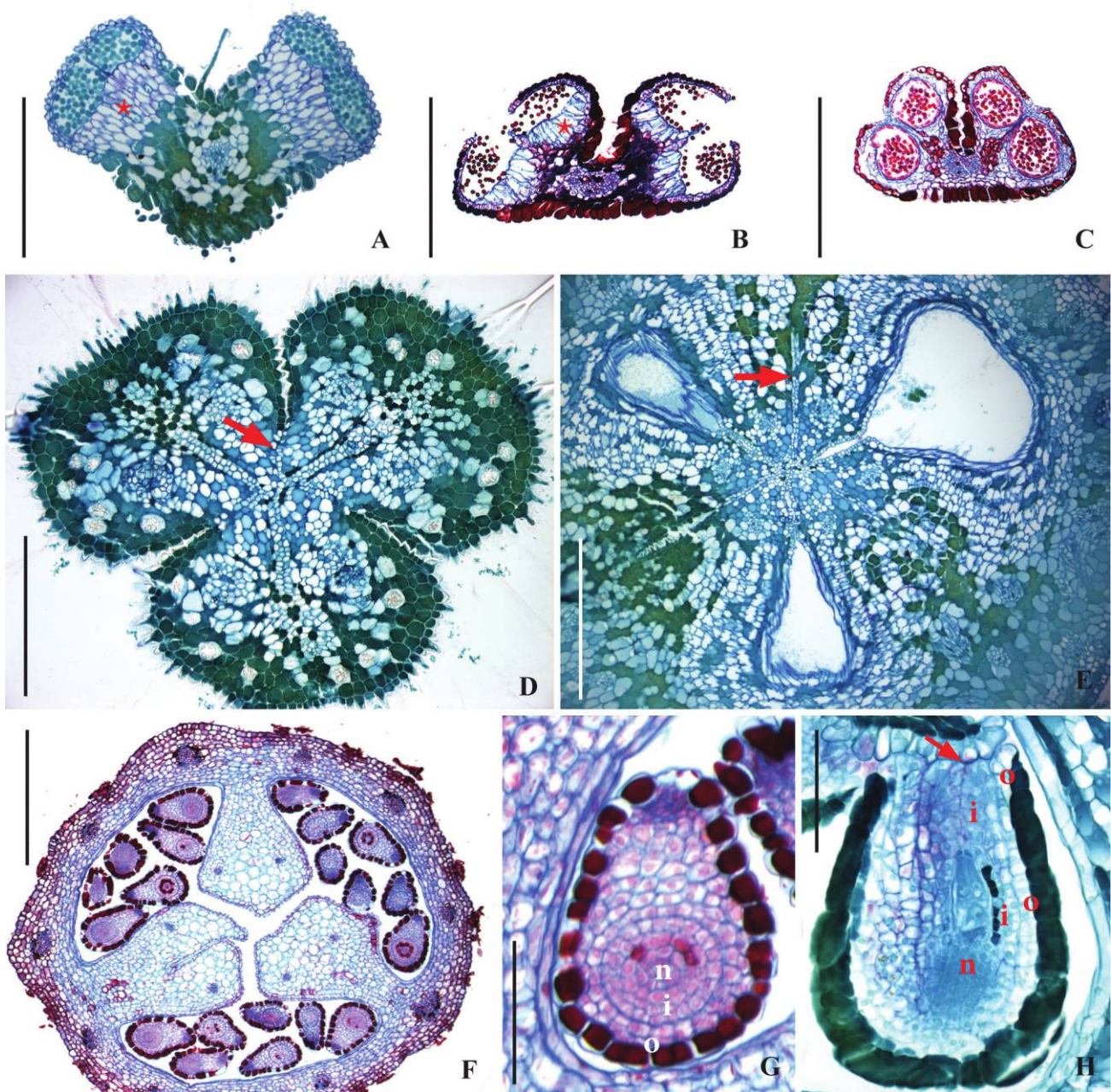


Fig. 4 *Quintinia*. A–C, LM micrographs of microtome sections. Transverse sections of anthers, ventral side up. Radially elongate cells between connective and theca in A and B indicated by red stars. A, *Quintinia quatrefagesii* (anthetic). B, *Quintinia verdonii* (anthetic). C, *Quintinia sieberi* (from advanced bud). D–F, Transverse sections of gynoecium. D, E, *Quintinia quatrefagesii*. D, Style, apocarpous but carpels postgenitally united (red arrow; ventral slits postgenitally fused). E, Transition from style to ovary, gynoecium (congenitally) fused with floral base, but carpel flanks still only postgenitally united (red arrow). F, *Quintinia sieberi*, ovary above placenta, with partial septa, and one of the septa still showing free carpel flanks. G, H, Ovules, with two integuments (i = inner integument; red arrow = micropyle; n = lower part of nucellus; o = outer integument). G, *Quintinia sieberi*, transverse section. H, *Quintinia quatrefagesii*, longitudinal section. Scale bars = 500 μm (A–C, E, F), 250 μm (D), 100 μm (G, H).

single species, and we therefore treat all specimens as a single species, *Silvianthemum suecicum*.

The sepals are short and narrow and apparently persistent (figs. 6A–6C, 6G, 8A, 8B). They have three vascular traces. The sepals do not cover the floral bud. Aestivation is open.

They are apparently glabrous. A larger gland-like structure occurs at the apex of the sepals (figs. 6C, 6F, 11A).

The petals are rounded. They have one vascular trace. Aestivation is quincuncial (fig. 6A–6C, 6G). Short unicellular trichomes are scattered on both surfaces (fig. 6A–6C). The outer

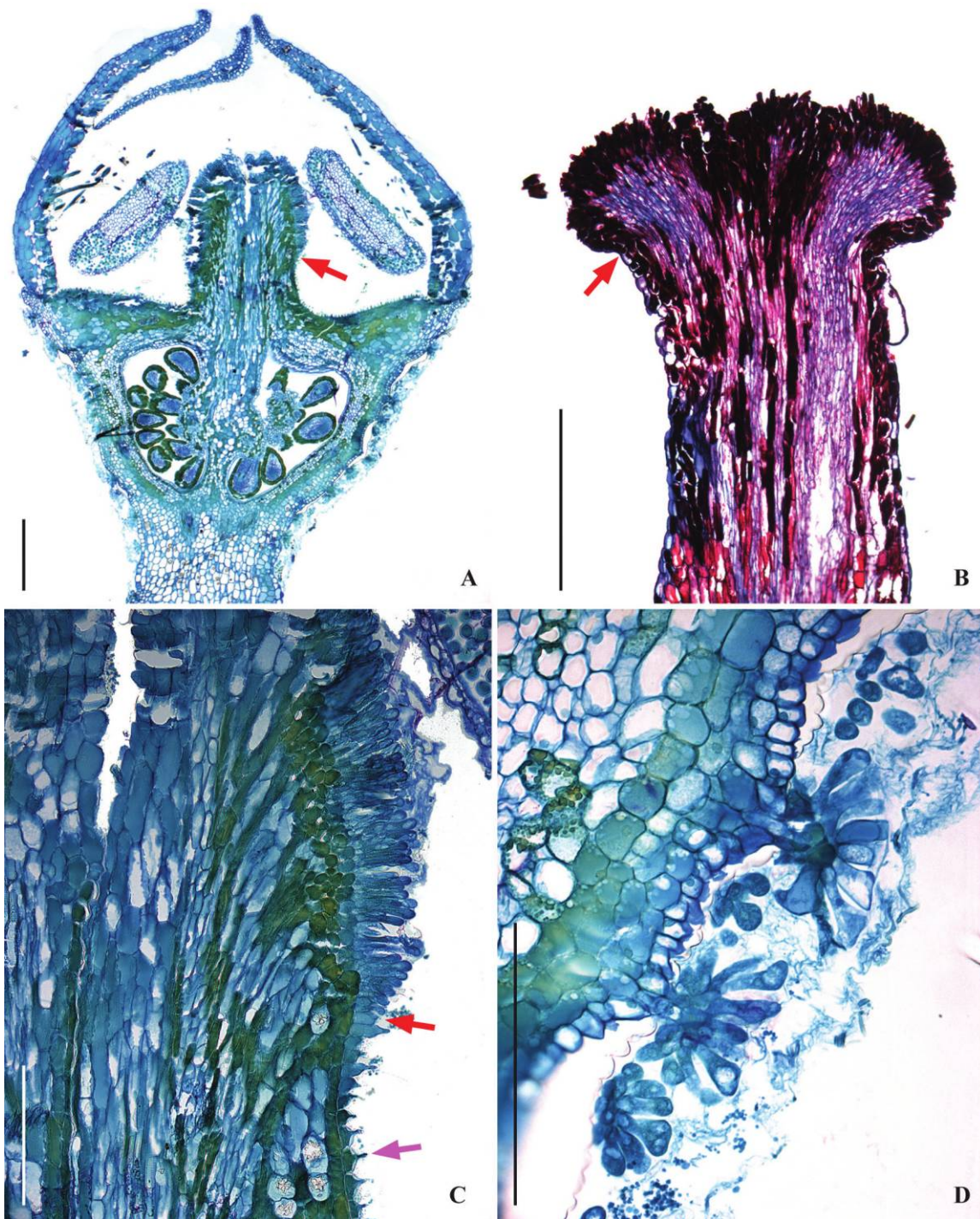


Fig. 5 *Quintinia*. LM micrographs of microtome sections. Longitudinal sections of flowers. *A*, *Quintinia quatrefagesii*, entire flower, showing long stigma (more than half as long as the style; lower end of stigma marked with red arrow), inferior ovary, and nectary disk on ovary roof. *B*, *Quintinia verdonii*, upper part of gynoecium, showing short stigma; lower end of stigma marked with red arrow. *C*, *Quintinia quatrefagesii*, stigma with long radial epidermal cells covered with secretion and pollen tube transmitting tissue with long, radiating cells (lower end of stigma marked with red arrow); below the stigma, epidermis with flask-shaped cells (purple arrow). *D*, *Quintinia quatrefagesii*, surface of lower part of flower (level of inferior ovary) with multicellular secretory hairs covered with secretion. Scale bars = 500 μm (*A*, *B*), 200 μm (*C*, *D*).

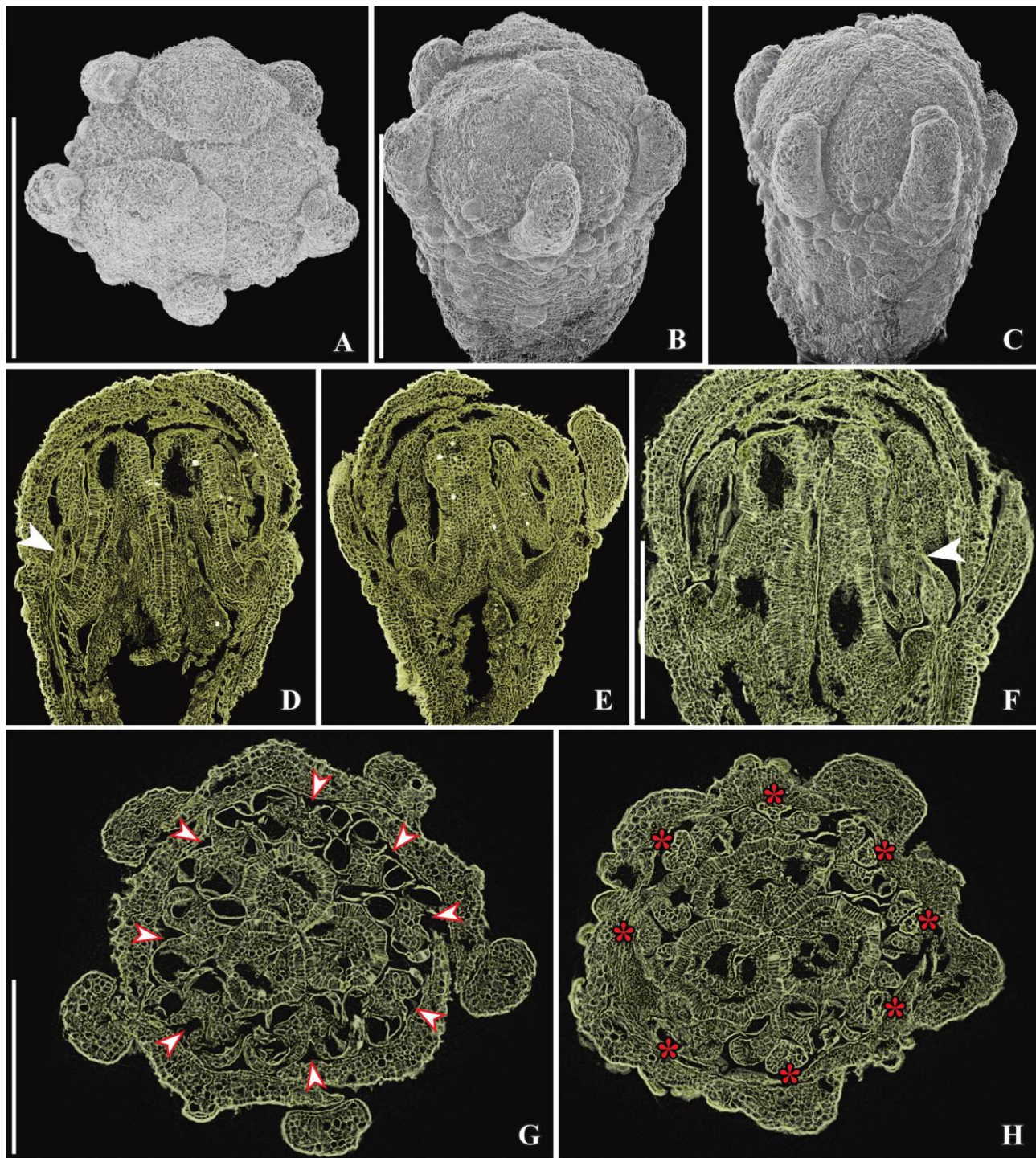


Fig. 6 *Silvianthemum suecicum*. Synchrotron-based X-ray tomographic microscopy reconstructions of holotype (S100376, sample GI32197) showing volume renderings of surface (A–C) and cut vortex slices with internal structures (D–H). A, Flower bud in apical view showing five narrow sepals with glands at the tips and five quincuncial petals. B, C, Oblique (B) and lateral (C) views of flower bud showing shape of sepals and petals and distribution of peltate trichomes. D, Longitudinal section of flower bud through central part of flower bud showing dorsifixed stamen (arrowhead indicates filament) and two apocarpous styles with radiating cells. E, Longitudinal section of flower bud more or less perpendicular to section in D showing a single style and section through perianth parts. F, Longitudinal section of flower bud showing one stamen with distinct dorsifixed anther (arrowhead). G, Transverse section of flower bud showing the pentamerous perianth with narrow sepals and eight stamens with broad connective (arrowheads). H, Transverse section of flower bud below the level of anther attachment showing the triangular filaments (red asterisks). Scale bars = 1 mm (A, B; applies to A–E), 500 μ m (F), 500 μ m (G; applies to G, H).

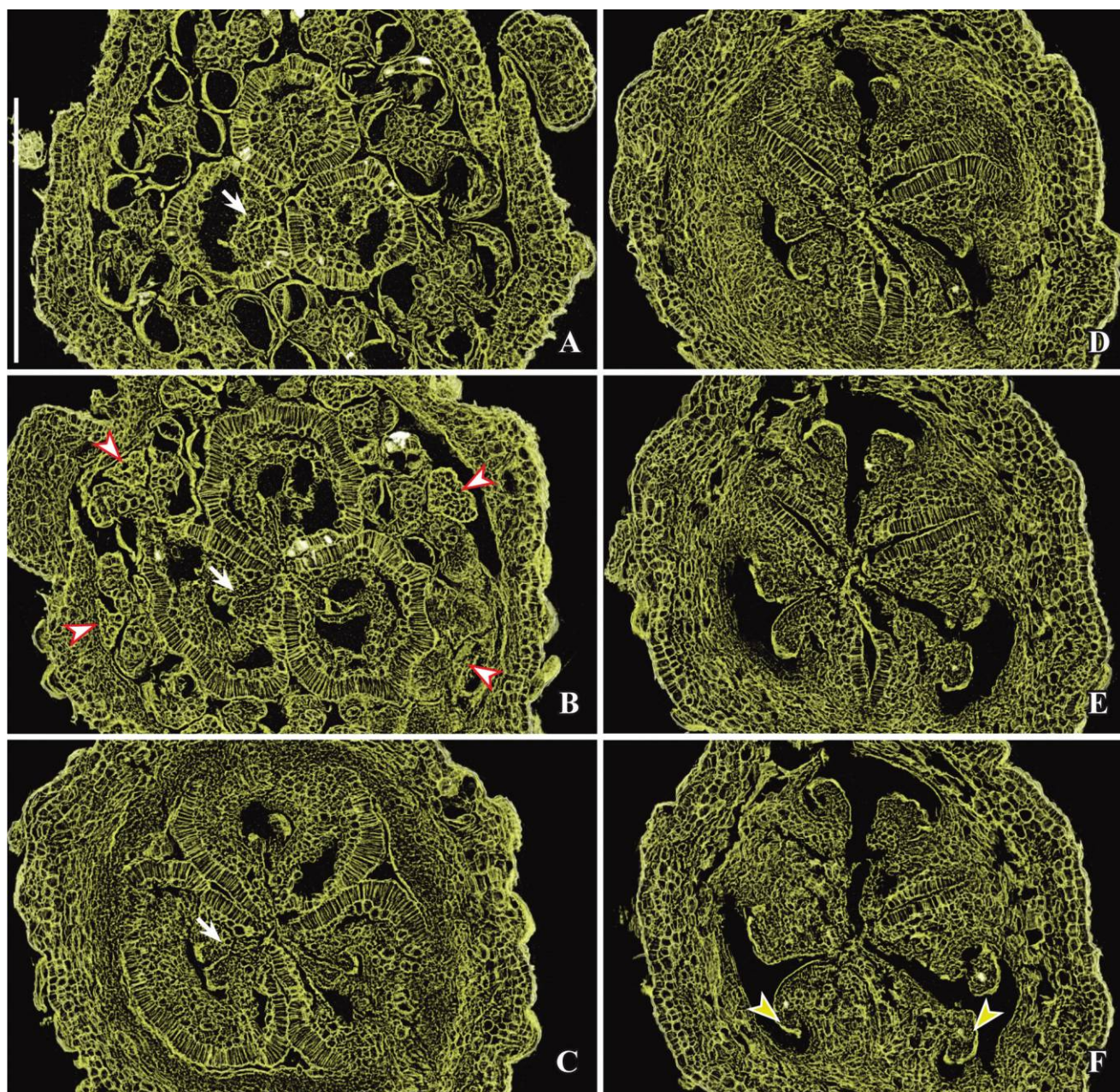


Fig. 7 *Silvianthemum suecicum*. Synchrotron-based X-ray tomographic microscopy reconstructions of holotype (S100376, sample GI32197) showing cut voltex slices in transverse view with details of internal structures from about the middle of the apocarpous styles (A) to the transitional zone between apocarpous and symplicate zone (D–F); ventral suture of apocarpous styles marked for one style with arrow; radiating palisade cells continue into the transitional zone; apocarpous styles apparently postgenitally united (A–C). A, Details of stamens with small pollen sacs and broad region between pollen sacs. B, Section below anther attachment showing triangular sections of filaments (arrowheads). C, Section immediately below insertion of stamens. D–F, Sections in transitional zone showing region of placentation (arrowheads in F). Scale bar = 500 μm .

surface of petals also bears a few multicellular peltate trichomes near the base (fig. 6B, 6C). These trichomes consist of a short stalk and a peltate head with an overall hemispherical shape. Cells of the peltate head are small and appear equiaxial. The multicellular trichomes are apparently secretory. Their surface has a thick covering, is often shiny, and sometimes bursts open (observed on the hypanthium; fig. 12C).

SRXTM analyses of two flower buds (the holotype, S100376, and specimen S171503) clearly show that the androecium in these specimens consists of eight stamens (figs. 6G, 6H, 8B). Serial sections of the flower bud included in the original description (S100394) also show eight stamens, although they are not as well preserved. Also, a more fragmentary specimen (S100378; plate 1, fig. 4 in Friis 1990) shows

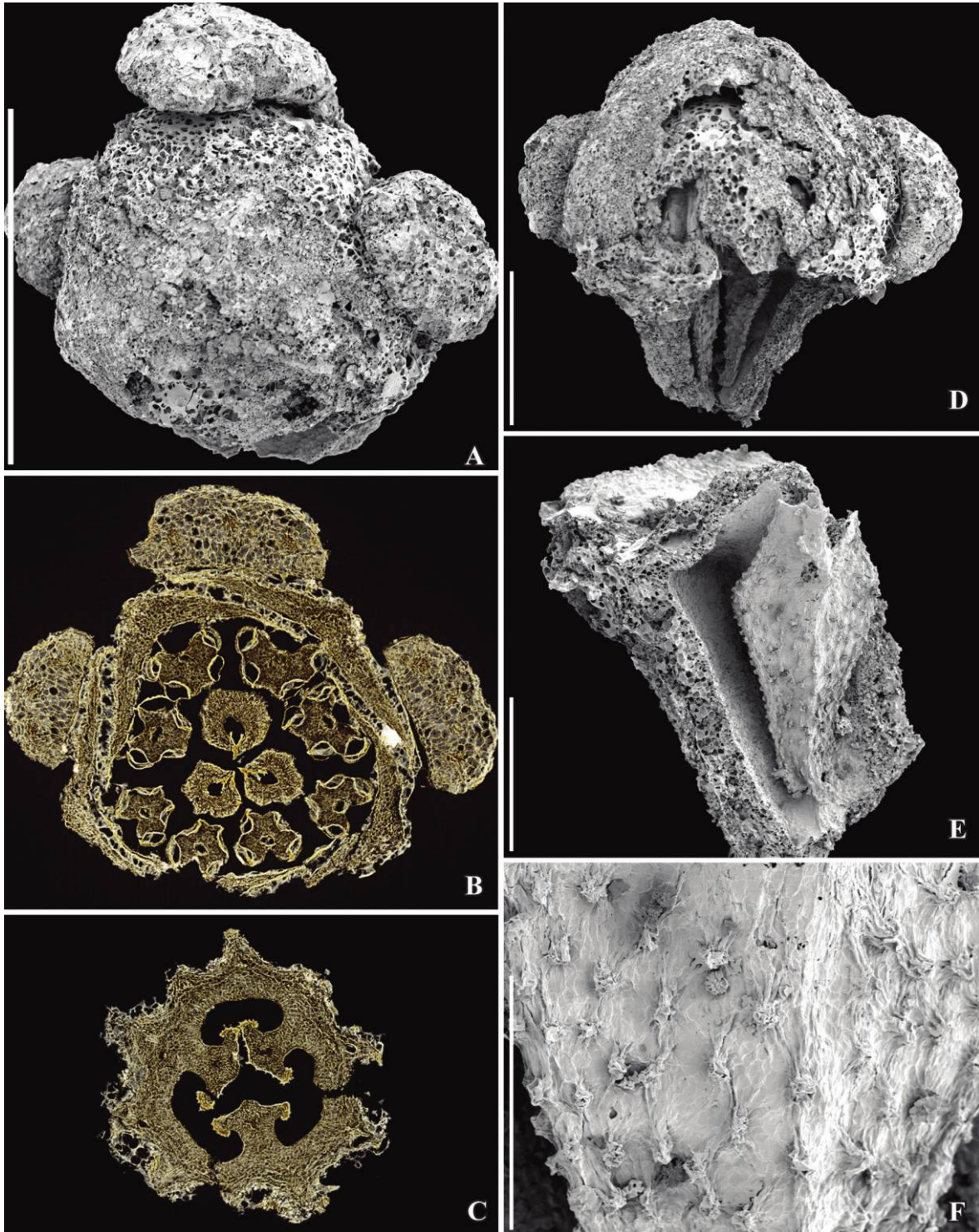


Fig. 8 *Silvianthemum suecicum*. SEM micrographs (A, D–F) and synchrotron-based X-ray tomographic microscopy reconstructions of flower bud (S171503, sample G132116) showing cut voltex slices in transverse view with details of internal structures (B, C). A, Flower bud in apical view showing three sepals and five petals; two sepals broken off; surface of petals poorly preserved. B, Section through flower bud at about the middle of the apocarpous styles showing the three sepals, remnants of the five quincuncial petals, eight stamens with broad anthers and small pollen sacs, and three apocarpous styles. C, Section through flower bud in the middle of the symplicate zone showing unilocular ovary and three incomplete septa, each with distinct placental zone (yellowish color). D, Lateral view of flower bud showing the perianth above and the ovary below; fragment of ovary wall broken off and shown in E. E, Fragment of ovary broken of flower bud showing one incomplete septum and placental zone. F, Detail of inner surface of incomplete septum shown in E; small projections on the adaxial surface are interpreted as young ovules. Scale bars = 1 mm (A; applies to A–C), 500 μm (D), 250 μm (E), 100 μm (F).

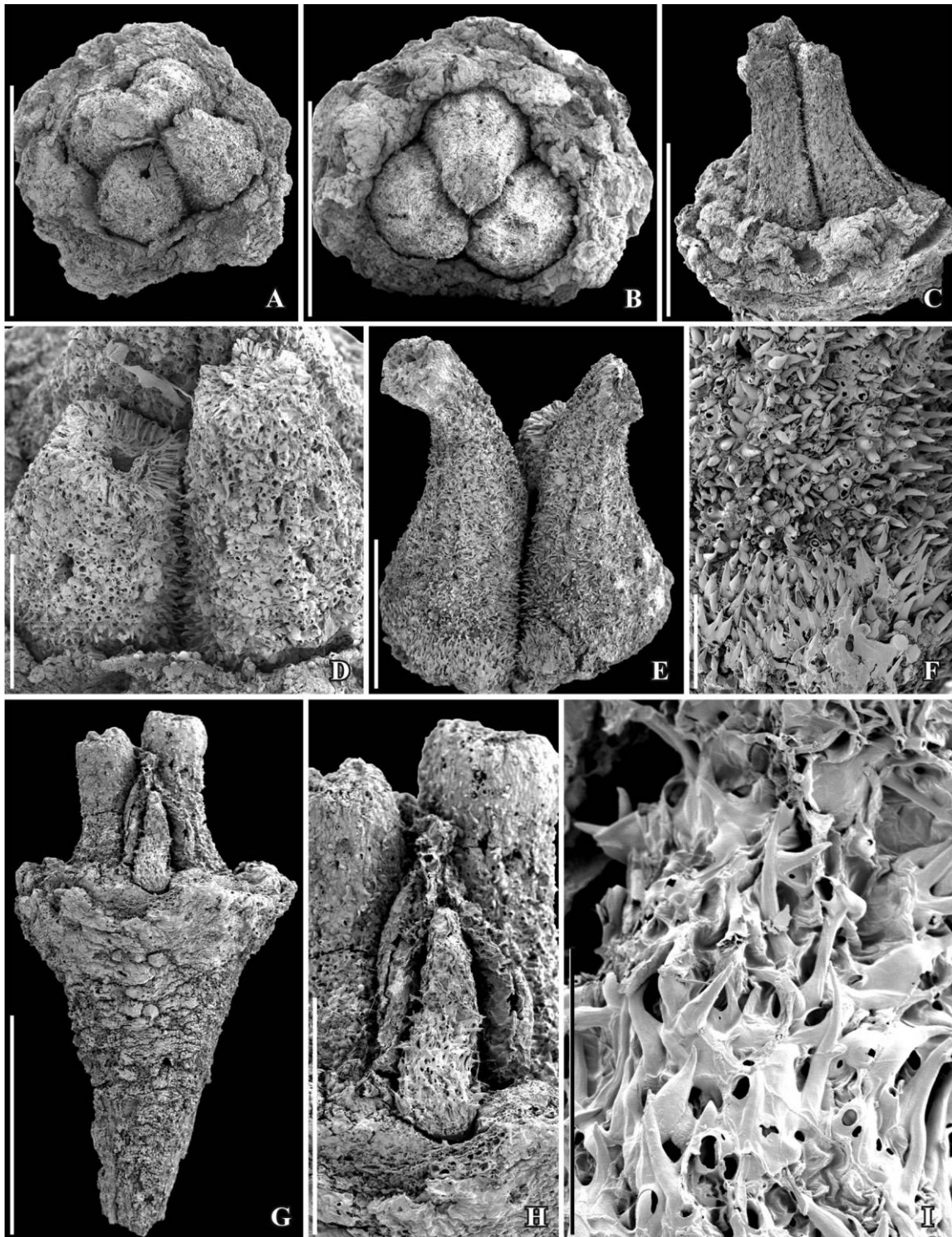


Fig. 9 *Silvianthemum suecicum*. SEM micrographs of anthetic to postanthetic flowers; perianth is lost in all specimens. A, Flower in apical view showing four apocarpous styles and nectary disk (S172541, sample Åsen 2). B, C, Flower in apical (B) and lateral (C) view showing three apocarpous styles and nectary disk (S172537, sample Åsen 7). D, Detail of A showing radiating palisade cells of styles and papillate surface. E, Three apocarpous styles isolated from flower showing densely spaced papillae (S172543, sample Åsen 2). F, Detail of E showing papillate surface. G, Flower with a single stamen preserved showing basifixed attachment of anther and surface of ovary with peltate secretory hairs (S172538, sample Åsen 3). H, I, Details of stamen shown in G showing hairy surface of filament. Scale bars = 1 mm (A–C, G), 250 μm (D), 500 μm (E, H), 100 μm (F, I).

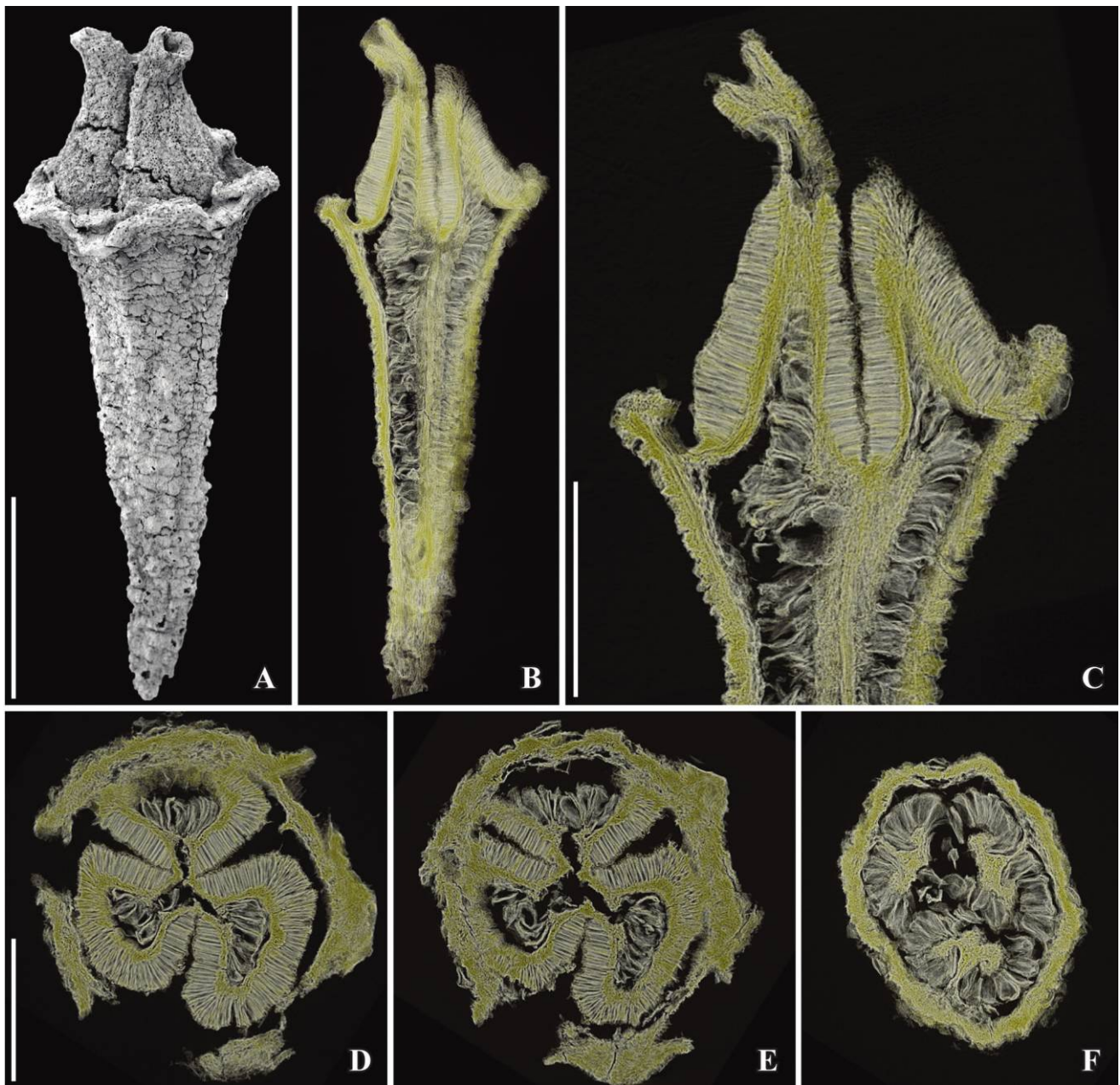


Fig. 10 *Silvianthemum suecicum* (S171578, sample Åsen 7). SEM micrograph (A) and synchrotron-based X-ray tomographic microscopy reconstructions showing internal structures in cut voltex slices (B–F). A, Lateral view of flower with long tapering ovary and three apocarpous styles. B, Longitudinal section through central part of flower showing placentation and distinct radiating palisade cells of styles. C, Detail of apical part of flower in longitudinal section showing radiating palisade cells of styles and placentation in the apocarpous, transitional, and symplicate zone. D, Transverse section in stylar zone. E, Transverse section in transitional zone between the apocarpous styles and the symplicate zone. F, Transverse section approximately in the middle of the ovary showing the three placenta extending toward the center of the locule. Scale bars = 1 mm (A; applies to A, B), 500 μm (C, D; scale in D applies to D–F).

6 filaments and 2 scars of filaments. Therefore, the suggestion that *Silvianthemum* might have had two whorls, each with five stamens, and that one or two stamens were lost or obscured during fossilization (Friis 1990) can be ruled out. Adjacent stamens are apparently of equal size, and all eight stamens may belong to the same whorl.

Complete stamens have been observed only in preanthetic specimens (S100376, S100383, S100394, S171503) and one probably more mature specimen (S172538). The stamens are more or less upright with distinct filament and anther. Filaments are short and stout (figs. 6D, 9G, 9H), triangular to circular in cross section (fig. 6H). Anthers are sagittate and

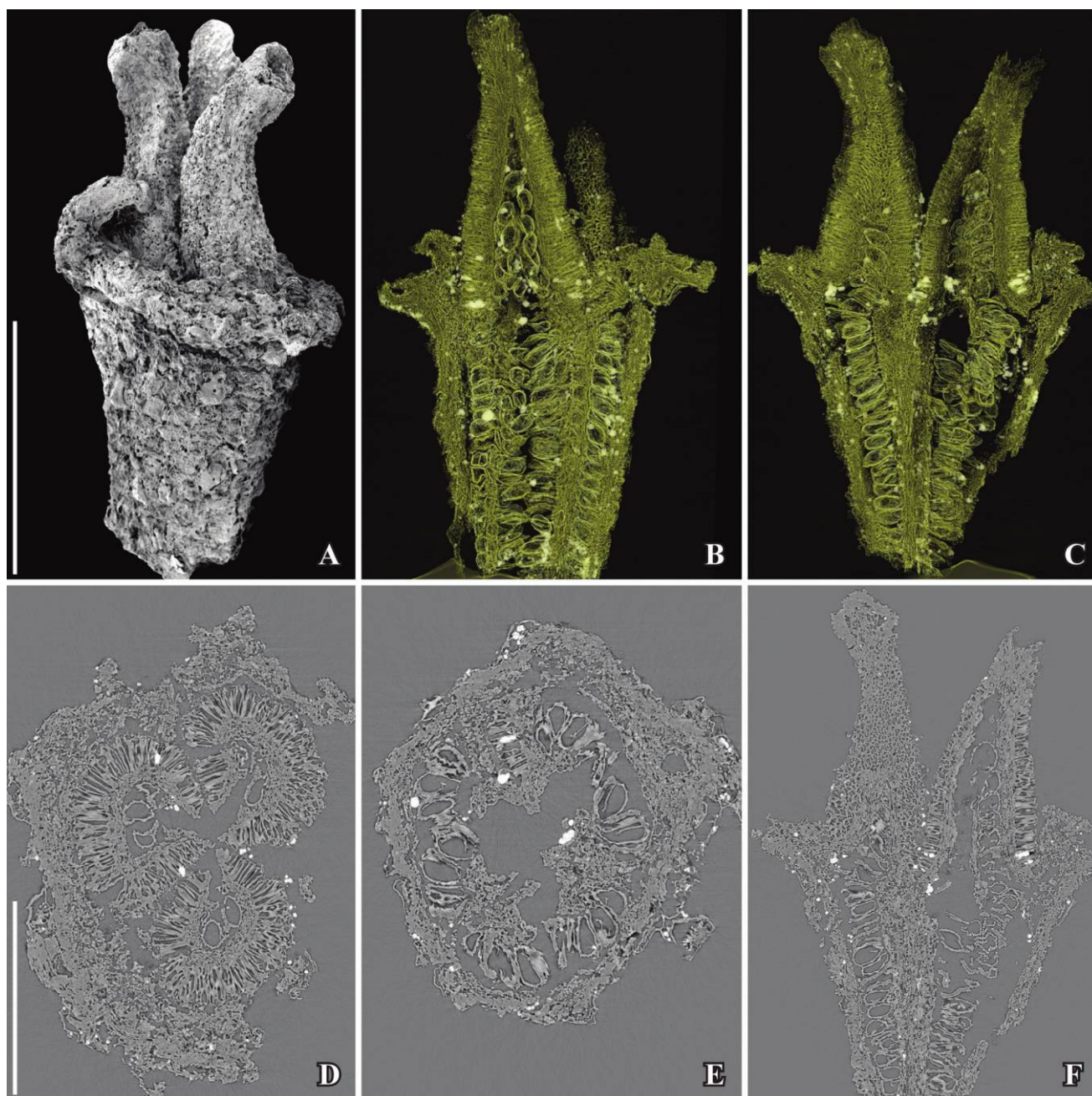


Fig. 11 *Silvianthemum suecicum* (S171544, sample GI32197). SEM micrograph (A) and synchrotron-based X-ray tomographic microscopy reconstructions showing internal structures in cut voltex slices (B, C) and orthoslices (D–F). A, Lateral view of flower with one sepal and three apocarpous styles preserved. B, C, Longitudinal section through central part of flower showing placentation and distinct radiating palisade cells of styles; sections perpendicular to each other. D, Transverse section in stylar region showing ovules borne at the margins of the carpels. E, Transverse section just below the transitional zone between the apocarpous and symplicate zone showing the three incomplete septa extending toward the center of the locule and ovules borne on the margins in several rows. F, Longitudinal section, same region as in C, showing the extent of the placentation in the stylar region. Scale bars = 1 mm (A; applies to A–C, F), 500 μm (D; applies to D, E).

dorsifixed in the lower half, with introrse dehiscence (fig. 6D). They are bithecate and tetrasporangiate (figs. 6G, 6H, 8B). The connective is extensive, and pollen sacs are small compared with the total width of the anther (fig. 8B).

Filaments concealed in floral buds appear glabrous in

SRXTM. In one probably more mature specimen, where petals were lost, the single stamen preserved shows short stiff hairs on the filament (fig. 9G, 9H). No hairs have been observed on the anther of this specimen or in the flower buds that have been studied using SRXTM.

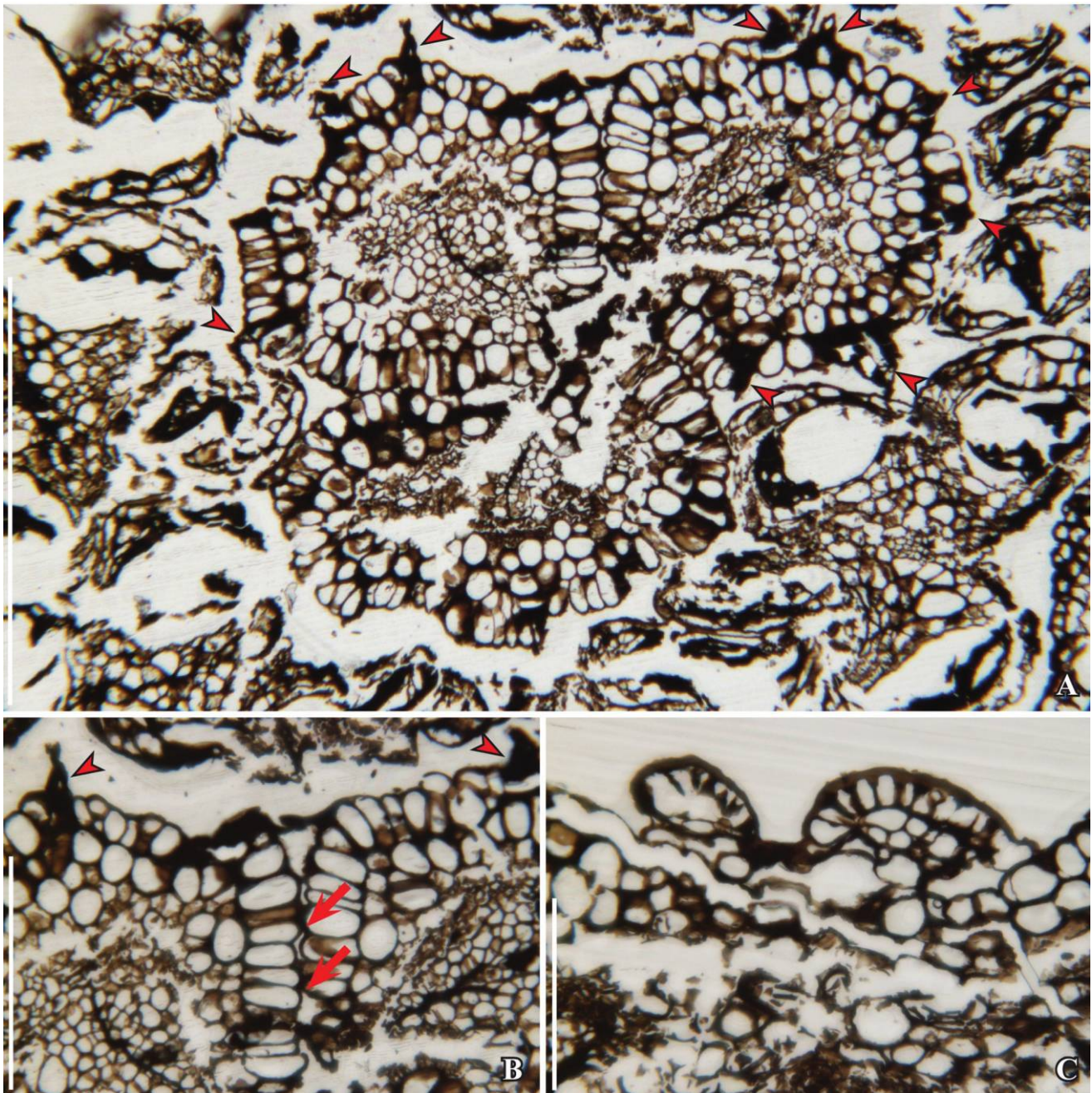


Fig. 12 *Silvianthemum suecicum* (S100394, sample GI32197). LM micrographs of microtome sections of flower bud; transverse sections. A, Section showing the three apocarpous styles with ventral slit distinct in two of the styles; radiating palisade cells distinct in all styles; darker-colored (probably tanniferous) papillate cells (red arrowheads) are interspaced between the palisade cells (S100394-16-08). B, Detail of A showing probably postgenitally united area between two styles (red arrows) and papillate cells enlarged (red arrowheads). C, Details of secretory hairs (S100394-23-07). Scale bars = 300 μm (A), 150 μm (B), 100 μm (C).

Pollen grains are rarely preserved on the flowers and have been studied only by SEM. They are 3- to 4-colpate or perhaps colpate (Friis 1990, plate 3, figs. 2, 4–6).

The gynoecium is trimerous (in one specimen, S172541, tetramerous) with a semi-inferior ovary (figs. 9A–9C, 10, 11A–11C, 11F). The carpels are united (symplicate) in the region below the insertion of the perianth and androecium (figs. 7F,

8C, 10E, 10F, 11E). Above the insertion of perianth and androecium, the carpels are free (asyplicate; figs. 7A–7C, 8B, 10D, 11D), but the adjoining faces of the styles appear to be postgenitally united (fig. 12A, 12B). Fusion of the carpels with the floral base (floral cup) begins higher up than fusion between the carpels (fig. 6D, 6F). The styles are more or less conical and robust, upright and straight in preanthetic flowers (figs.

6D–6F, 9C, 9G) while slightly outwardly bending in postanthetic specimens (fig. 10A, 10B). The styles have an indistinct ventral suture that extends for the full length of the styles (fig. 7A–7C, 7E). The apex is truncate in young specimens (figs. 6D–6F, 9G, 9H).

The epidermis in the stylar region and on the ovary roof is distinctive, consisting of high palisade cells with equiaxial facets (figs. 10B–10E, 11B–11D, 12A, 12B). They are of more or less equal size on both the dorsal and the ventral side of the styles except toward the ventral suture and the periphery of the ovary roof, where they gradually become shorter (fig. 10C–10E). The palisade cells extend for almost the full length of the styles. Below the palisade cells, there are many small, thin-walled cells that almost completely fill the inner space of the styles (figs. 6G, 12A). The outermost of these cells adjoining the palisade cells are larger than the inner cells. All cells appear to be equiaxial. The outer surface of the styles are characterized by the equiaxial facets of the epidermal cells. Toward the base of the styles or in some specimens over the full length of the styles, there are numerous short papillate to spiny hairy extensions (fig. 9C–9F). Cells with papillae/spines appear to be narrower than the other palisade cells and dark, apparently tanniferous (fig. 12A, 12B). The papillae/spines are sometimes broken, leaving small holes in the epidermis surface.

The ovary is unilocular for the full length of the symplicate zone (figs. 8C, 10F, 11E). One specimen (S171578) shows indications of an extremely short synasciadiate zone. The placental area is in the symplicate region as well as the lower half to two-thirds of the apocarpous zone (figs. 10B–10F, 11B, 11C, 11F). In the syncarpous zone, the placentation is parietal with protruding placentae (figs. 8C, 10F, 11E). In the transitional zone between the apocarpous and the symplicate region, the placentae reach almost the center of the locule (fig. 7F). Further down, they are more separated. In the upper part of the ovary, the placentae are enlarged and involute and borne at the end of the narrow intruding carpel margins (fig. 7E, 7F). In the apocarpous zone and upper zone of the symplicate region, ovules are borne on the margins of the placentae, but further down, ovules are also borne on the adaxial surface. This is clear from more mature specimens (S171578; fig. 10F), and small projections observed on the placental plate of a flower bud (S171503; fig. 8E, 8F) are interpreted as young ovules.

There are numerous densely packed ovules. Estimates from SXRTM indicate that there are ~200 ovules per carpel in 2–4 rows on each carpel margin. Ovules are anatropous, with the micropyle directed toward the placenta (figs. 10C, 11C). The ovule position is perpendicular to the surface of the placenta, with the upper ovule slightly upright and the middle and lower ovules horizontal to slightly pendant (figs. 10B, 11C). The ovules are small and do not fill the total volume of the locule (figs. 10B–10F, 11B–11F). The preservation of the material does not allow detailed observation of ovule/seed wall. Outer epidermal cells are narrow, longitudinally elongate, and the ovule surface has a reticulate appearance. In SXRTM, the ovule wall is relatively thick and homogenous, without any indication of cell structure resembling the situation in extant *Quintinia* with a tanniferous ovule surface. Sometimes the ovule surface at the micropyle is split into two parts, indicating that the ovules might have been bitegmic.

The outer surface of the hypanthium bears numerous peltate hairs of the same kind as observed on the petals (figs. 6B, 6C, 9G, 10A, 12C).

Fruit. Probably none of the specimens are preserved in the fruiting stage. In larger specimens, the styles tend to bend outward and split along the ventral suture, resulting in a central opening to the ovary (fig. 9E), indicating that the fruit dehiscence was apical between the styles.

Bertilanthus scanicus

Short description. The flowers are small (less than 1.4 mm in diameter) and bisexual. They have 5 sepals, 5 petals, 5 stamens (alternating with the sepals), and 2 carpels. Sepals and petals are free; carpels are united in the inferior ovary. Numerous ovules are borne on parietal placentae. A distinct 5-lobed nectary is situated at the top of the ovary.

Comments. No further material has been added since the publication of the species (Friis and Pedersen 2012), but a few additional observations are noted here. Fusion of the carpels with the floral base (floral cup) begins higher up than fusion between the carpels. Estimates from SXRTM indicate that there are ~150 ovules per carpel in 2–3 rows on each carpel margin. The ovule position is more or less perpendicular to the surface of the placenta so that the upper ovules are upright and the middle and lower ovules horizontal to slightly pendant.

Discussion

Comparative Floral Structure in Quintinia and Silvianthemum/Bertilanthus

The flowers of *Quintinia*, *Silvianthemum*, and *Bertilanthus* are comparable in general organization. All three genera also have small flowers. The fossil flowers are slightly smaller than those of *Quintinia*, but this can largely be explained by the fossilization, since coalification including charcoalfication typically causes some shrinkage (Lupia 1995), and none of the fossils have been observed as anthetic flowers with petals preserved.

Large, multicellular secretory hairs of an almost hemispherical overall shape on the outer floral surface—including the sepals, floral base, and pedicel—occur in *Quintinia* and *Silvianthemum* (on both sides of the sepals in *Quintinia*) and are only scarce in *Bertilanthus*; in *Silvianthemum*, some such hairs are also in the basal region of the outer surface of the petals (for *Quintinia* and *Silvianthemum*, see also figs. 18, 19 in Bense and Palser 1975; plate 1, fig. 1, plate 4, figs. 1, 3 in Friis 1990; fig. 6 in Friis and Endress 1990; figs. 39, 40 in Al-Shammary and Gornall 1994). In both *Quintinia* and *Silvianthemum*, such a secretory hair is also on the tip of the short sepals (see Friis 1990, plate 1, fig. 2, for *Silvianthemum* and observations of this study in *Silvianthemum* and *Quintinia quatrefagesii*). However, only in *Silvianthemum*—but not in *Quintinia*—do the hairs appear to have a thick cuticle. The pedicel has a conspicuously uneven surface in *Quintinia* and *Silvianthemum* (for *Silvianthemum*, see Friis 1990, text-fig. 1, plate 1, fig. 3). In *Quintinia*, the surface is characterized by depressions, each containing such a secretory hair. In *Silvianthemum*, the uneven surface is formed by the raised secretory

hairs. This could be a fossilization artifact caused by shrinkage of the surrounding tissue.

Unicellular hairs are present on the upper side of the petals in *Silvianthemum* and in *Quintinia* (for *Quintinia*, see also Al-Shammmary and Gornall 1994). Unicellular hairs also occur on stamen filaments and anthers in *Q. quatrefagesii* (in other *Quintinia* species, only on filaments; Al-Shammmary and Gornall 1994); in *Silvianthemum* there are also hairs on the filaments, but they are not as prominent and long as in *Q. quatrefagesii*. In *Bertilanthus*, the stamens appear glabrous.

Sepals are short and narrow in *Quintinia*, *Silvianthemum*, and *Bertilanthus*. Stomata are conspicuous on the sepals in *Silvianthemum* but in *Q. quatrefagesii* are not found as yet. Stomata were also not observed on the sepals of *Bertilanthus*. Sepals of *Quintinia* have a single vascular trace. In *Silvianthemum*, there are three traces per sepal. Vascular traces were not clear in *Bertilanthus*.

Petal aestivation is quincuncial in *Q. quatrefagesii* and *Silvianthemum* (but cochlear in other *Quintinia* species; cf. Friis and Endress 1990). Petal aestivation in *Bertilanthus* is uncertain, since no complete floral bud was observed. Petals are free in *Quintinia*, *Bertilanthus*, and *Silvianthemum* (this study; Friis 1990; Friis and Pedersen 2012).

The flowers have 5 free stamens in *Quintinia* and *Bertilanthus* (this study; Friis and Pedersen 2012). However, the stamens are antepetalous in *Bertilanthus* but antesepalous in *Quintinia*. Antepetalous stamens as in *Bertilanthus* are unusual in asterids. *Silvianthemum* is unusual in having 8 free stamens in combination with the pentamerous perianth. Stamen arrangement in *Silvianthemum* is known only for specimens with 3 carpels. In the single 4-carpellate specimen, the androecium is not preserved, and there are no distinct scars from the filaments. Thus, it is unknown how the stamens are arranged in relation to the radii of the carpels. Stamens have short, stout filaments in *Quintinia*, *Silvianthemum*, and *Bertilanthus*. The pollen sacs are relatively small in *Quintinia* and *Silvianthemum*. The connective and the connective-adjacent part of the thecae are broad. Anthers are basally dorsifixed (almost basifixed) in *Quintinia* (Endress and Stumpf 1991) and dorsifixed in the lower half of the anther in *Silvianthemum* and *Bertilanthus*.

Pollen is mainly 4-colporate in *Quintinia* (this study; Hideux and Ferguson 1976; Kodela 2006; APSA Members 2007) and 3–4-colporate (or 3–4 colpate) in *Silvianthemum* (Friis 1990) and has perhaps 3 apertures in *Bertilanthus* (Friis and Pedersen 2012).

Both *Quintinia* and *Silvianthemum* have 3–4 carpels per gynoecium, whereas *Bertilanthus* has 2. In the styler zone, the gynoecium is apocarpous—but the carpels are postgenitally connected in *Quintinia* and *Silvianthemum* (in *Bertilanthus*, this feature is not clear)—and is syncarpous below. In *Quintinia* and *Bertilanthus*, the ovary encompasses only the inferior zone of the gynoecium. In *Silvianthemum*, the ovary also encompasses the lower apocarpous zone of the gynoecium, and the ovary is semi-inferior. However, in *Quintinia*, there is some variation in the extension of the locules in the upper part (fig. 3A, 3B), so that in *Quintinia fawkneri*, the ovary is less pronouncedly inferior than in *Q. quatrefagesii*. Fusion of the carpels with the floral cup begins higher up than fusion among the carpels in *Quintinia*, *Silvianthemum*, and *Bertilanthus*.

This causes the presence of long intercarpellary slits in all three genera; this feature is not so common in gynoecia with a similar architecture, as seen across the eudicots (it occurs otherwise, e.g., in Rosaceae; Kania 1973).

The ovary tapers in basal direction in *Quintinia*, *Silvianthemum*, and *Bertilanthus*. The synascidiate zone is short (in *Silvianthemum* and *Bertilanthus*, very short or lacking). The placentae are in the symplicate zone on partial septa in *Quintinia* and *Bertilanthus*. In *Silvianthemum*, ovules are also present in the lower part of the apocarpous region. In *Quintinia*, the partial septa may be almost contiguous in the center of the locule and thus almost subdividing the one locule into three locules. *Silvianthemum* and *Bertilanthus* have partial septa of a similar shape as *Quintinia*; they are somewhat smaller, but this may be an artifact as a result of stronger shrinkage of the inner parts in the fossils.

In *Quintinia*, the stigmatic surface is short or long, descending on the dorsal side of the carpels, and has conspicuous radially elongate epidermal cells. The carpel surface below this zone including the ovary roof has short flask-shaped epidermal cells with a thin and long papilla. In *Silvianthemum* and *Bertilanthus*, the extent of the stigma is unclear but may be short (Friis 1990, plate 3, fig. 1; Friis and Pedersen 2012, fig. 3B, 3C). However, the epidermis of the entire outer morphological surface of the carpels in *Bertilanthus* and to some extent in *Silvianthemum* has conspicuous radially elongate cells, and many of these cells seem to have a thin and long papilla similar to *Quintinia*, at least in *Silvianthemum* (Friis 1990, plate 4, figs. 4, 5). In *Silvianthemum*, where these cells are relatively well preserved, they appear to be filled with a black substance, probably tannin. The cell structure is unclear for *Bertilanthus*.

The vascular pattern in the gynoecium is simple in *Quintinia*, with a dorsal and two lateral bundles (for *Quintinia*, see also Philipson 1967). The same pattern is apparently also present in *Silvianthemum* and *Bertilanthus*, but the bundles are not very clear in the fossil material.

The ovules are small, not filling their locule (in all three genera). They are positioned in more than one series on each carpel flank (in all three genera). The number of ovules per carpel is high in *Silvianthemum* (more than 200) and *Bertilanthus* (more than 150) and diverse in *Quintinia* (6–20 in the species studied here; 3–4 in *Q. serrata*; Bensch and Palsler 1975).

Nectaries are on the ovary roof; they form a ring-shaped disc around the gynoecium in the *Quintinia* species of this study and *Silvianthemum* (Friis 1990; disc shallow in *Quintinia* and perhaps thicker in *Silvianthemum*). In contrast, a five-lobed disc occurs in *Bertilanthus* (Friis and Pedersen 2012) and is also figured for *Quintinia ledermannii* (Schlechter 1914).

Conclusions

Quintinia and *Silvianthemum*/*Bertilanthus* have more features in common than previously known, which strongly reinforces their earlier assumed close relationships. Similarities are especially pronounced between *Quintinia* and *Silvianthemum*, which have the same kind of secretory hairs on the floral surface and pedicel; the short, narrow sepals; the free, quincuncial petals; the broad anthers with small pollen sacs; the 4-colporate (or perhaps 4-colpate) pollen; the postgenital

union of the 3–4 apocarpous styles; the specific connection of the apocarpous carpel part with the floral base; the downward tapering ovary; the placentation on incomplete septa; and the flask-shaped epidermal cells with a thin and long papilla on the carpels.

The close similarity between *Quintinia* and *Silvianthemum/Bertilanthus* suggests that the clade including extant *Quintinia* was present in the Northern Hemisphere during the Late Cretaceous. In the Southern Hemisphere, *Quintinia* is reported from the Eocene and onward on the basis of several occurrences of dispersed pollen and a single leaf fossil and has also been found in areas outside its present distribution (Hill and Macphail 1983, 1985).

Quintinia clearly has bitegmic ovules. Among asterids, bitegmic ovules are otherwise known from only some Ericales and a few scattered isolated groups of lamiids (*Vahlia*, rudimentarily in *Phytocrene* of Icacinaceae) but not from other Paracryphiales or other campanulids (see review in Endress 2010). The mention of two integuments for *Cardiopteris* (Aquifoliales) by Takhtajan (2009) is based on observations on seeds by Doweld (2000). This statement is questionable as long as there is no published evidence on the ovules. Mauritzon (1933) mentioned the presence of two integuments in *Quintinia*, but his figures are inconclusive. This study gives the first

clear evidence for this highly unusual feature in campanulids, provided that this phylogenetic position is correct. Also the presence of free petals, as in *Quintinia*, is unusual in campanulids. In the other two genera of Paracryphiales, *Paracryphia* and *Sphenostemon*, clear petals are absent (Dickison and Baas 1977; Endress 2008). One wonders whether the systematic position of *Quintinia* in campanulids is correct, especially as the feature of bitegmic versus unitegmic ovules is otherwise macrosystematically very stable (Endress 2011a, 2011b; Endress and Matthews 2012).

Acknowledgments

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