

*Silvianthemum suecicum* gen. et sp. nov.,  
a new saxifragalean flower  
from the Late Cretaceous of Sweden

By ELSE MARIE FRIIS



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## *Abstract*

*Silvianthemum suecicum* is a new fossil flower from the Late Cretaceous of Scania, southern Sweden, based on extremely well preserved specimens with a wealth of details intact. In floral and reproductive characters *Silvianthemum* is closely related to flowers of modern taxa included in the Escalloniaceae, a saxifragalean family of woody plants now growing predominantly in the southern hemisphere. *Silvianthemum* is related to the Escalloniaceae mainly in its bisexual and actinomorphic flowers with epigynous and pentamerous perianth, colpate (colporoidate) pollen with perforate tectum, narrow elongate ovary with numerous ovules, thin-walled reticulate seeds and a distinct nectary disc. Calyx consists of five small sepals that do not cover the petals in the flower bud. Petals are larger and probably had a protective function in the bud. *Silvianthemum* is further united with some escalloniaceous taxa in having distinct glandular trichomes. The fossils also show considerable agreement with flowers of other woody saxifragalean plants, especially in the Iteaceae and the Hydrangeaceae and to some extent also to the Cunoniaceae. The discovery of *Silvianthemum* from the Late Cretaceous of Sweden establishes the woody saxifragalean families as an ancient group. It further provides evidence that taxa considered typical of the southern hemisphere may have been represented in the northern hemisphere in earlier periods.

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## Introduction

The saxifragalean complex is typically classified with the “lower” Rosidae and is often considered as a phylogenetically central group within the subclass, occupying a relatively basal position with respect to most “higher” rosids (e.g. Takhtajan 1969, 1980). The central position of the group coupled with its high diversity and the disjunct distribution pattern of many saxifragalean families suggests a long geological history. Despite this, early records of saxifragalean taxa are scarce. Pollen are typically small and of the general tricolpate to tricolporate type that is also common in many Hamamelididae and lower Rosidae and may be difficult to identify in the dispersed palynofloras. New discoveries of several different saxifragalean reproductive structures from the Late Cretaceous of Scania, southern Sweden, however, provides unequivocal evidence of an early differentiation of the group. This material includes two species assigned to the fossil genus *Scandianthus*, one unnamed flower described previously (Friis & Skarby 1982) and the flowers of *Silvianthemum suecicum* described in the present work. In addition a number of other saxifragalean floral structures from the same locality remain to be studied. *Silvianthemum* and the unnamed flower show close relationship to members of woody saxifragalean taxa, particularly to members of the Escalloniaceae. The flowers of *Scandianthus* also show some agreement with the woody Escalloniaceae and Hydrangeaceae, but its relationship within the group is less certain. The only other known Cretaceous fossils assigned to the Saxifragales are leaves from the Late Cretaceous of British Columbia, Canada, attributed to the hydrangeaceous genus *Philadelphus* (Bell 1957).

The Tertiary record of saxifragalean fossils is more extensive and comprises leaves as well as reproductive organs mostly from European and North American floras. Fossils from the Early Tertiary are typically related to woody saxifragalean taxa. Some of the Early Tertiary forms have been

compared to members of the Saxifragaceae, but their relationships are less certain and the earliest well documented records of this family are from the Late Tertiary (e.g. Reid 1920). The Hydrangeaceae are particularly common in the Tertiary floras, represented by leaves, flowers, stamens, fruits and seeds (e.g. Conwentz 1886, Knowlton 1902, Chaney & Axelrod 1959, Lańcucka-Środoniowa 1975, Mai 1985). The Iteaceae are represented in the fossil floras of Europe by *Adenanthemum iteoides*, a small flower described from the Early Tertiary Baltic Amber (Conwentz 1886), fruits and seeds of *Itea* (Mai 1985) and *Itea*-type pollen (e.g. Muller 1981). Although the identification was questioned by Suessenguth (1942) the presence of the Cunoniaceae in the Tertiary floras of Europe and Greenland seems to be documented by leaves related to the modern genus *Weinmannia* (Heer 1883, Kräusel 1938, Kräusel & Weyland 1942). *Weinmannia* now occurs predominantly in the southern hemisphere and is also documented for this area in the Tertiary by palynological data (e.g. Muller 1981). The Escalloniaceae is represented in the fossil record by pollen of *Quintinia*-type from New Zealand and Australia ranging in age from the Late Eocene to Present (e.g. Muller 1981). Differences in androecial structure prevents an assignment of *Silvianthemum* to the Escalloniaceae. However, the strong agreement between *Silvianthemum* and *Quintinia* in most other floral characters suggests that they had a close common ancestor and that taxa now considered as typically southern hemisphere may have played a role in the northern hemisphere floras in the past.

The presence of several different saxifragalean floral types in the Cretaceous of Sweden clearly documents that the group had a long fossil history and was already diverse by the Late Cretaceous. It further establishes the woody saxifragaleans as an ancient lineage.

## Material and Methods

The plant bearing sequence exposed in the Höganäs AB kaolin quarry at Åsen east of Axeltorp in the Kristianstad Basin, Scania (56°9'N, 14°30'E) comprises a rich flora of well-preserved angiosperm reproductive organs, mostly in the form of flowers, fruits and seeds (Friis & Skarby 1981, 1982, Friis 1983, 1985a, b, c, Friis, Crane & Pedersen, 1986, 1988, Crane, Friis & Pedersen 1986, 1989). The sediments consist of unconsolidated clays, silts and sands of presumed lacustrine and fluvial origin and are considered on paleontological and paleomagnetic evidence to be of Late Santonian to Early Campanian age (Friis & Skarby 1982, Mörner 1983, Skarby 1986). The age assignment has recently been supported by the study of megaspore assemblages from the same exposure (Koppelhus & Batten in press).

The lower portion of the exposure contains a distinct clay gyttja layer probably deposited in a lake system. The fossil assemblage recovered from this clay layer is distinct from that of the upper, predominantly sandy sequence both in preservation of the fossils and in composition. The fossils of the clay gyttja are most commonly preserved as lignitic compressions, but some charcoalfied specimens are also present. The material from the upper sequence is mostly preserved as charcoalfied fragments.

The flora of the lower clay bed is rich in taxodiaceous conifers and comprises six distinct species assigned to three new fossil genera *Quasisequoia*, *Elatidopsis* and *Paracryptomeria* (Srinivasan & Friis 1989). Angiosperms are represented by four different types of platanaceous reproductive organs (Friis et al. 1988), *Actinocalyx bohrii*, a possible ericanean flower (Friis 1985a), few hamamelidaceous flowers (Endress & Friis in prep) and several unassigned flowers and fruits. The fossil saxifragalean flowers of *Silvianthemum suecicum* described in the present work occur exclusively in the lower sequence. Two other saxifragalean species, *Scandian-*

*thus costatus* and *S. major*, previously described from the Åsen locality (Friis & Skarby 1982) are characteristic for the fossil assemblages of the upper sequence. An unnamed saxifragalean flower (Friis & Skarby 1982) is also restricted to the upper sequence.

The difference in composition of the fossil assemblages in the lower and upper part of the plant bearing sequence is also evident in the megaspore assemblages. Megaspores of isoetalean affinity (cf. *Tenellisporites aachenensis*) are common in the lower sequence while they are rare in the upper sequence that is dominated by forms of selaginellaceous affinity (Friis 1985a, Koppelhus & Batten in press).

The fossil flowers described in this paper are preserved as charcoalfied (fusainised) structures or more rarely as lignified compressions. The charcoalfied specimens in particular yield a wealth of information on morphology and anatomical details. The material was extracted from the matrix by soaking the unconsolidated sediments in water and washing the fossils over a 125 µm sieve. The fossils were cleaned further using hydrofluoric and hydrochloric acid followed by thorough rinsing in water. The specimens were then picked out and preliminary analysed under binocular microscope. Specimens selected for SEM were coated by about 1000 Å of gold and examined using Cambridge S-2 and Philips SEM 515 scanning electron microscopes. One flower bud, selected for anatomical studies, was dehydrated in an ethanol-propylene oxide series, embedded in Epon and sectioned on an LKB Ultratome III ultramicrotome. Sections were cut with glass knives and are about 3 µm thick. They were placed on microscope slides in a drop of distilled water, heated on a warm plate and studied with transmitted light without further treatment or embedding.

Herbarium material of modern Saxifragales were



studied at the Botanical Department, Swedish Museum of Natural History, Stockholm.

The specimens and preparations of fossil mate-

rial described in the present work are deposited in the palaeobotanical collections of the Swedish Museum of Natural History, Stockholm (S).

## Systematics

### Saxifragales

*Silvianthemum* Friis gen. nov.

*Derivation of generic name:* In honour of Her Majesty, the Queen Silvia of Sweden.

*Generic diagnosis:* Flower minute, perfect and actinomorphic; floral parts whorled; perianth pentamerous, epigynous. Calyx of five free sepals, much smaller than petals, completely free in bud not covering the corolla; corolla of five free petals, quincuncially imbricate in bud. Stamens apparently in a single whorl; anthers tetrasporangiate, dorsifixed. Pollen grains isopolar, spherical to prolate, triaperturate with three long colpi; pollen wall tectate and perforate. Gynoecium trimerous, carpels basally connate and adnate to hypanthium to form an inferior, unilocular ovary; styles free, stout; stigmas capitate; placentation parietal, placentae large; ovules and seeds minute, numerous, anatropous with reticulate outer surface. Nectary disc-shaped. Pedicel, hypanthium and outer surface of sepals and petals with multicellular and multiseriate glandular trichomes; inner and outer surface of petals and surface of styles with short, unicellular, eglandular trichomes.

*Type species:* *Silvianthemum suecicum* Friis sp. nov.

*Silvianthemum suecicum* Friis sp. nov.

Plates 1-7; textfigures 1-2

*Derivation of specific epithet:* From Sweden where the fossil flowers were collected.

*Specific diagnosis:* Sepals short lanceolate bearing a

large apical multicellular gland. Petals ovate with entire margin. Pollen grains minute to small with perforate, densely pitted tectum. Nectary irregularly lobed. Glandular trichomes distributed on pedicel, hypanthium and basal portions of sepals and petals.

*Holotype:* S100376 (Sample GI32197) figured Pl. 1, fig. 1.

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

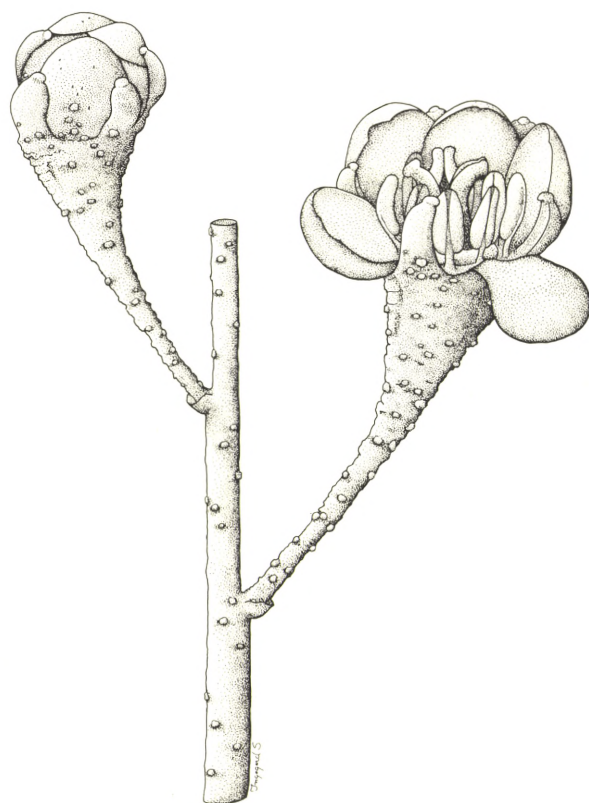
*Type stratum:* Lower unit (clay gyttja).

*Age:* Late Cretaceous (Late Santonian/Early Campanian).

*Material:* A few flower buds and several mature flowers/fruits recovered from the lower unit at Åsen, predominantly in the clay gyttja horizon (samples GI32106, GI32107, GI32108, GI32145, GI32167, GI32170, GI32189, GI32197). Most of the specimens are preserved as three dimensional charcoalifications; a few flowers are preserved as slightly compressed lignite fossils (S100376-100380, S100383-100389, S100394-100407, S100409-100411).

### Description and remarks on the species

All flowers are detached and the inflorescence structure is unknown. However, a number of small axes associated with the flowers and bearing similar glandular trichomes probably represent inflorescence fragments and indicate that the flowers were borne in a simple raceme (textfig. 1). The fragments are composed of a main axis, about 0.5



Textfigure 1. Reconstruction of *Silvianthemum suecicum* gen. et sp. nov.

mm in diameter, bearing short lateral branches that terminate in a circular abscission scar, about 0.4 mm in diameter.

*Flower:* The material mainly comprises specimens preserved in flowering or fruiting stage. In these specimens perianth and androecium are usually lost and the organization of the flower is best studied in the flower buds of which a few well preserved specimens have been discovered.

Flowers are minute and epigynous with an elongate, slender ovary. They are born on an indistinct pedicel that grades into the flower without a joint. Flower buds are up to 3.5 mm long and about 1 mm in diameter. Mature flowers with pedicel preserved are up to 6.2 mm long and about 2 mm in diameter.

Perianth is pentamerous and bicyclic. Androecial structure not fully understood. Gynoecium is trimerous.

*Perianth:* Calyx is composed of five short and lanceolate sepals, about 0.3 mm wide and 0.6 mm long. In the flower buds they are completely free and about half the length of the petals (Pl. 1, figs. 1-2). They appear fleshy or leathery and in transverse sections they are almost semicircular, composed of several layers of isodiametric parenchyma cells (Pl. 5, fig. 1). At the apex of each sepal there is a distinct, large multicellular gland, apparently distinguished from the other glandular trichomes of the flower in lacking a stalk (Pl. 4, fig. 1). Large glandular trichomes occur also near the base of the sepals. Epidermal cells are almost isodiametric. Stomata are irregularly oriented and occur in two dense bands on the outer surface of the sepals (Pl. 4, fig. 2).

Corolla is composed of five ovate petals with entire margins. Petals are quincuncially imbricate in the bud (Pl. 1, figs. 1-2; textfigs. 1-2), about 0.9 mm wide and 1 mm long. Lamina is composed of an epidermis and up to four layers of isodiametric parenchyma cells embedding several vascular traces. Both the inner and outer surface of petals are covered by densely spaced, short, unicellular



Textfigure 2. Floral diagram showing organization of *Silvianthemum*. Observe that androecial structure is uncertain.



and probably eglandular trichomes (Pl. 4, fig. 1; Pl. 6, fig. 2). Multicellular glandular trichomes occur occasionally near the base of the petals (Pl. 4, fig. 1).

*Androecium:* It has not been possible to establish number and arrangement of stamens with certainty as none of the studied specimens had the androecium preserved intact. In two specimens that have remnants of androecium preserved only eight or nine stamens appear to be present (Pl. 1, fig. 5; Pl. 2, fig. 1). Also in the flower bud that have been sectioned less than ten stamens appear to be present. There is no size difference of adjacent stamens and they all appear at the same level (Pl. 5, fig. 1). Further, the positions of the stamens are not distinctly median to the perianth parts (Pl. 5, fig. 1). These anomalies may possibly have resulted from fossilization and the most likely organization of the androecium is a bicyclic arrangement with two whorls of five stamens. However, the possibility that the fossil flowers were irregular with more than five stamens in a single whorl cannot be excluded.

Stamens are free and dorsifixed. Complete stamens have only been observed in flower buds that have been opened mechanically with needles. In this material filaments are very short, triangular in outline. Anthers are about 0.2 mm wide and 0.5 mm long, tetrasporangiate with two pairs of pollen sacs dehiscing by longitudinal slits. The dorsal pollen sacs are slightly larger than the ventral. Connective tissue is distinct with a single vascular bundle (Pl. 6, fig. 1).

*Pollen:* Clumps of pollen grains have been observed in several specimens occurring on the surface of the styles and in the stigmatic area. Pollen grains are all of the same kind. They are spherical to prolate in equatorial view and almost spherical in polar view, about 8.5-10  $\mu\text{m}$  long, triaperturate with three long colpi that almost meet at the pole (Pl. 3, figs 4-5). Some pollen grains, however, appear more irregular and grains with four colpi have also been observed (Pl. 3, fig. 6). The presence of a simple or

diffuse endoaperture is suggested by a rupture in the middle of the furrows in some grains (Pl. 3, fig. 4). Pollen wall is tectate with a perforate tectum. Perforations are densely spaced, generally with circular lumina, about 0.6  $\mu\text{m}$  in diameter; longer lumina occur occasionally near the apertures. Aperture membrane is slightly granular.

*Gynoecium:* Gynoecium is composed of three carpels, connate and fused to the hypanthium at the base to form a unilocular and inferior ovary that is elongate and narrowly conical in shape. Above the hypanthium, carpels are free with a short fertile portion and a longer stylar portion. Styles are solid and stout with a capitate stigma and with a distinct ventral slit penetrating to the center of the style (Pl. 2, fig. 2; Pl. 6, fig. 2). In the flower buds the styles are short, closely appressed (Pl. 2, fig. 2), while they are longer and slightly spreading in more mature specimens (Pl. 1, fig. 3, Pl. 2, fig. 1). The styles are five- to six-angled in transverse section with an outer layer of palisade-shaped epidermal cells and an inner layer of isodiametric parenchyma cells (Pl. 2, fig. 4; Pl. 6, fig. 2). Short unicellular trichomes are densely spaced over the surface of the styles, except near the stigmas (Pl. 2, fig. 6; Pl. 4, figs 4-5). Stigmas are almost circular in outline and with a restricted central papillate area at the top (Pl. 3, figs 1-2).

Placentation is parietal with three large, stalked placentae that project into the locule. In the flower bud they are clearly separate (Pl. 5, fig. 2), while in the more mature specimens the placentae reach almost to the center of the ovary.

The fruit is apparently a capsule that dehisced apically between the styles.

*Ovules:* Ovules and seeds are numerous and minute, about 0.1 mm long, anatropous, and borne at the margins and dorsal surface of the placentae. Seed coat is thin with only the outer epidermal layer preserved. Epidermal cells are shallow with polygonal and slightly elongate facets, 0.045 mm  $\times$  0.001 mm. Anticlinal and inner periclinal cell walls

are strongly thickened giving the seed surface a reticulate appearance (Pl. 3, fig. 3).

*Nectary:* A slightly lobed disc is inserted above the hypanthium between the androecium and gynoecium (Pl. 2, figs 1,3). The epidermal cells are polygonal and isodiametric with a papillate outer cuticle and apparently scattered stomata-like opening. In one specimen a shiny black substance occurs inside the disc and between the styles (Pl. 2, figs 3, 5) and is believed to represent nectar secreted by the disc.

*Trichomes:* Peltate glandular trichomes are scattered over the surface of the pedicel, hypanthium, basal portions of sepals and petals and at the tip of the sepals (Pl. 4, figs 1, 3). They often appear shiny and darker than the other floral tissues. They are multicellular and multiseriate composed of a short stalk, about 0.03 mm in diameter, and a disc-shaped head, about 0.1 mm in diameter, two or three cell layers thick and with a very thick outer cuticle (Pl. 7, fig. 1). In one of these glandular

trichomes seen in transverse section the outer cuticle is ruptured (Pl. 7, fig. 1), probably to release secretion accumulated in the heads.

Unicellular and probably eglandular trichomes are densely spaced on both surfaces of the petals and on the styles. They are short, about 0.002 mm long and conical in outline (Pl. 4, figs 4-5).

### Associated leaves

Small leaves with glandular trichomes similar to those of *Silvianthemum suecicum* occur associated with the flowers and are believed to have originated from the same plants. Small complete leaves, up to about 10 mm long, are exstipulate and linear (Pl. 4, fig. 6). They are thick and coriaceous in texture and have a distinct midvein. Larger fragments also indicate a linear leaf outline. Leaf margin is serrate and teeth distinct, apparently glandular (Pl. 4, figs 6-7). Secondary and tertiary vein pattern have not been observed and although the teeth resemble the rosoid type, their structure cannot be established with certainty.

## Discussion

### Comparison with modern Saxifragales

The characters of the fossil flowers indicate a close relationship to flowers of some modern taxa included in the Englerian suborder Saxifragineae. This group is highly heterogeneous comprising herbaceous as well as woody forms and the circumscription and taxonomic treatment of the complex vary considerably. Engler (1930) included 12 families in the Saxifragineae of which the Saxifragaceae is the largest with 80 genera in 15 subfamilies (Penthorioideae, Saxifragoideae, Lepuropetaoideae, Parnassioideae, Tetracarpaoideae, Pterostemono-

ideae, Iteoideae, Brexioideae, Kirengeshomoideae, Kanioideae, Baueroideae, Hydrangeoideae, Escallonioideae, Montinioideae and Phyllonomoideae). Most of these subfamilies were classified at the rank of families by other taxonomists (e.g. Hutchinson 1959, 1969, Takhtajan 1959, 1969, 1980, Cronquist 1968, 1981). The classification of Saxifragaceae *sensu lato* into several independent families is strongly supported by investigations of floral morphogenesis (Klopfer 1973), seed anatomical studies (Krach 1976, 1977) and palynological



evidence (Hideux 1972, Hideux and Ferguson 1976). This approach has also been adopted in the present study.

Several authors have emphasised the highly heterogeneous nature of the families included in Engler's Saxifragineae and Saxifragaceae and suggested a polyphyletic origin of the group (e.g. Klopfer 1973, Krach 1976, 1977). The woody members have often been separated into a distinct order. Hutchinson (1959, 1969) placed the Cunoniales (Pterostemonaceae, Cunoniaceae, Philadelphiacae, Hydrangeaceae, Grossulariaceae, Oliniaceae, Greyiaceae, Escalloniaceae, Bauraceae, Cryptoroniaceae) in his phylum Lignosae separate from the herbaceous taxa classified in the order Saxifragales. Takhtajan (1959) separated most of the woody families in the order Grossulariales and assigned the herbaceous forms to the Saxifragales. In later studies Takhtajan (1969, 1980) united both woody and herbaceous taxa in a single order (Saxifragales). Classification of the woody and herbaceous taxa in two orders, Cunoniales and Saxifragales, was also suggested by Klopfer (1973). Krach (1976) distinguished three woody orders (Escalloniales, Cunoniales, Grossulariales). The separation of the woody taxa in one or several orders is supported by several floral and vegetative characters. However, no unequivocal classification has been suggested so far and the broad concept of the saxifragalean complex corresponding to the Saxifragales of Takhtajan (1969) has therefore been adopted in the present discussion. This concept approximately corresponds to the Englerian Saxifragineae.

Floral characters in saxifragalean taxa are discussed below and compared to characters observed in *Silvianthemum*.

*Flower:* The flowers of the saxifragalean families exhibit a diverse morphology. They are mostly perfect, but unisexual flowers characterize the Paracryphiaceae, Brunelliaceae and Montiniaceae and also occur scattered in other families such as the Cunoniaceae. The flowers are typically actinomorphic, while zygomorphic forms are rare. Isomerous

flowers with carpel number equal to that in the other floral whorls occur in some taxa, but most saxifragalean flowers are heteromerous, typically with pentamerous perianth and androecium and bimerous gynoecium.

*Perianth:* In most saxifragalean taxa perianth is bicyclic with sepals and petals in whorls of four or five, more rarely in six or more (e.g. Engler 1930, Bense & Palser 1975a, b, c, d). As pointed out by Klopfer (1973) prominent, imbricate sepals that have protective function in the flower bud prevail, but in the woody taxa of the Hydrangeaceae, Escalloniaceae and Iteaceae sepals are less prominent and the protective function taken over by the larger petals. A similar arrangement is seen in *Silvianthemum*.

*Androecium:* Five main types of androecium organization were recorded for the saxifragalean complex (e.g. Gelius 1967, Klopfer 1973). Most members of the Saxifragaceae *sensu stricto* have a bicyclic androecium with stamens in an obdiplostemonous arrangement. In a few other taxa with dicyclic androecium (*Brunellia*, some Hydrangeaceae) the arrangement is diplostemonous. Haplostemonous androecia with a single whorl of episepalous stamens are characteristic for several families including the Escalloniaceae and the Iteaceae. Obhaplostemonous forms are less common. Polyandric androecia are recorded only in members of the Hydrangeaceae. In these taxa the stamens arise in a centripetal direction by division of stamens in a single whorl (e.g. Gelius 1967, Klopfer 1973).

The androecium in *Silvianthemum* is not fully understood and therefore difficult to compare with that of modern forms. It is, however, clearly distinguished from the haplostemonous/obhaplostemonous forms by the presence of more than five stamens.

*Pollen:* Pollen morphology and wall structure vary considerably in the Saxifragaceae *sensu lato* (e.g. Erdtman 1952, Wakabayashi 1970, Hideux 1972,



Pastre and Pons 1973, Hideux and Ferguson 1976). Pollen grains are mostly prolate to spherical and isopolar, dispersed in monads except for the pollen of *Carpodetus* (usually placed in the Escalloniaceae) which are dispersed in tetrads. The aperture arrangement varies from tricolpate to tricolporoidate, tricolporate and triporate. Exceptions are some species of *Itea* (biporate), *Ixerba* (tetracolpate), *Ribes* (periporate) and *Quintinia* (stephanocolpate). Tectum types vary from smooth tectate to perforate or reticulate forms and forms with various suprategal ornamentations. Hideux and Ferguson (1976) considered the latter to be more advanced. Based on a numerical analysis of the distribution of 25 palynological characters in 129 genera and species of Saxifragaceae *sensu lato* Hideux and Ferguson (1976) concluded that there is no clear grouping of pollen types. They found, however, a concentration of less advanced types within the woody families Cunoniaceae, Escalloniaceae, Iteaceae and Hydrangeaceae. The pollen grains observed on the styles of the fossil *Silvianthemum* may also be grouped together with the less advanced types, mainly on the basis of their perforate tectum. The aperture structure is less certain, but clearly not of highly complex type.

*Gynoecium*: The position of ovary varies within the Saxifragales from superior to semi-inferior and inferior although none have a completely superior ovary (e.g. Klopfer 1973). An inferior ovary characterizes most of the woody taxa. The number of carpels is commonly two, but taxa with three or four carpels occur in several families e.g. the Hydrangeaceae and the Escalloniaceae. Forms with pentamerous gynoecia are more rare. In most saxifragalean taxa two different carpellary zones may be distinguished, a peltate zone in which the with carpel margins are congenitally fused and an impeltate zone with free or postgenitally fused margins (Morf 1950). Morf (1950) reported the peltate zone to be lacking in the woody saxifragalean taxa studied as well as in the Francoaceae and the *Heuchera*-group. Klopfer (1973), on the other hand, stated that lack

of peltate carpel portion occurred only in *Francoa*.

Ovaries are typically syncarpous or rarely paracarpous. They are usually bi- or trilocular with central placentation or in some taxa unilocular with parietal placentation. The Escalloniaceae typically have a locular ovary, but in *Quintinia* the fusion is not complete and in *Q. sieberi* the ovary is trilocular only at the base (Bensel & Palser 1975c, Endress personal communication 1989). In *Quintinia* and other unilocular forms placentae may penetrate almost to the center of the ovary to form a pseudolocular ovary similar to that of the fossil *Silvianthemum*.

Styles are mostly free. In the Escalloniaceae, however, they are completely fused, except in *Quintinia* that also may have free styles. Four stigma types were recognized, all with a relatively small stigmatic area (Morf 1950). Three types (löffelförmige, köpfchenförmige, kommissural) have a decurrent papillate zone, while the papillae are restricted to the top of the stigma in the forth type (narbenförmige). This type is characteristic for *Escallonia* and *Itea* and members of the *Heuchera*-group (Morf 1950) and also characterizes the fossil *Silvianthemum* which shares most other gynoecium characters with the woody saxifragalean taxa, especially with species of *Quintinia* (Escalloniaceae).

Like in *Silvianthemum* fruits of most saxifragalean taxa are capsules and typically dehisce at the apex between the styles.

*Ovules*: All saxifragalean taxa have anatropous ovules. Bitegmic ovules characterize most families, but the Escalloniaceae, Hydrangeaceae and Tetracarpaeaceae are distinguished by their unitegmic ovules (e.g. Corner 1976, Krach 1976, 1977). Ovules are mostly numerous and seeds small. A lower number of seeds occur in some taxa especially in the Grossulariaceae and in some Escalloniaceae. The seeds are often distinctly sculptured, the ornamentation being formed from variously shaped cuticular papillae or from thickenings of the anticlinal walls (e.g. Krach 1976, 1977, Hart & Berendsen 1980, Kaplan 1981). Seeds of the Escalloniaceae,



Hydrangeaceae and Iteaceae are usually reticulate, similar to those of the fossil *Silvianthemum*, or smooth (e.g. Krach 1976).

*Nectary*: Nectariferous tissue is present in most saxifragalen families. It is often restricted to the carpel wall at the base of the styles (e.g. in most Saxifragaceae). A prominent disc-shaped nectary inserted at the top of the ovary similar to that of *Silvianthemum* characterizes the Escalloniaceae and also occurs in some members of the Hydrangeaceae and Iteaceae (e.g. Bensel & Palser 1975 a, b, c, d) as well as in the Cunoniaceae (e.g. Dickison 1975).

*Trichomes*: The presence of trichomes characterizes most saxifragalean taxa. Trichomes vary considerably and comprise eglandular as well as glandular types. Eglandular trichomes are commonly uniseriate, unicellular or multicellular. Glandular trichomes are multicellular, usually multiseriate, but may also be uniseriate (e.g. Engler 1930, Bensel & Palser 1975a, b, c, d, Gornall & Bohm 1985, Gornall 1986, 1989). Glandular cells are usually clustered at the top of the trichome and may form multicellular, globular heads. Unicellular and acutely pointed trichomes similar to those of *Silvianthemum* were reported by Bensel & Palser (1975c) to be characteristic for the Escalloniaceae. This type is also characteristic for the Iteaceae, although they are typically longer than those of Escalloniaceae (Bensel & Palser 1975b). Stalked glandular trichomes with a disc-shaped head very similar to those of the fossil flower are characteristic of *Quintinia* of the Escalloniaceae (Bensel & Palser 1975c).

In most floral and reproductive characters considered the fossil flowers of *Silvianthemum suecicum* show close correlation with modern members of the Escalloniaceae, especially with species of *Quintinia*. They are united by the insignificant, unprotective calyx, the more prominent corolla, pollen grains with perforate tectum, narrow elongate, inferior ovaries, seeds with reticulate ornamentation, a distinct nectary disc at the top of the ovary and acutely

pointed unicellular trichomes as well as the characteristic stalked multicellular glandular trichomes with disc-shaped heads. In most Escalloniaceae the ovary is bi- or trilocular with a single style, but in *Quintinia* fusion is not complete. It has free styles and the ovary is partly unilocular, resembling the fossil in having large placentae that protrude almost to the center of the ovary (Bensel & Palser 1975c, Endress personal communication 1989). The only distinct difference between the fossil flowers and those of the Escalloniaceae is the structure of the androecium which is clearly haplostemonous in all modern forms. *Silvianthemum* is further distinguished from *Quintinia* in having pollen grains with three colpi like most Escalloniaceae, while *Quintinia* has pollen grains with five colpi. The presence of individual grains in *Silvianthemum* with irregular colpi configuration (four colpi), however, indicate that this difference may not be systematically significant.

Ovules of the Escalloniaceae are unitegmic, but although the seed coat in *Silvianthemum suecicum* is thin, apparently with a single cell layer only, it has not been possible to establish whether the seeds developed from uni- or bitegmic ovules.

The inflorescence in *Quintinia* is a simple raceme. Although only detached *Silvianthemum* flowers have been discovered small fragments of inflorescences indicate that they may have been born in similar inflorescences. Leaves of *Quintinia* may be coriaceous and narrowly elliptic or almost linear and bear glandular trichomes, similar to leaves associated with *Silvianthemum*.

The Escalloniaceae is a predominantly southern hemisphere family with most of its taxa occurring in Australasia. In the New World the family extends to Central America (Good 1964). *Quintinia* comprises shrubs and small trees ranging from the Philippines and New Guinea to Australia, New Caledonia and New Zealand (Engler 1930).

### Comparison with fossil Saxifragales

Three species of saxifragalean affinity have previ-



ously been described from the Upper Cretaceous strata of Scania viz *Scandianthus costatus*, *S. major* and one unnamed flower (Friis & Skarby 1982). The latter shows considerable morphological and organizational similarity to the flowers of *Silvianthemum*, first of all in its very narrow, conical ovary, the epigynous and pentamerous perianth with small fleshy sepals that are completely free, also in the flower bud, and larger imbricate petals. It also has a unilocular ovary with parietal placentation and stalked placentae that protrudes almost to the center of the ovary bearing numerous ovules/seeds with a reticulate surface and have free, stout styles with a distinct outer palisade layer. At the top of the ovary the flower has a distinct intrastaminal nectary disc. The unnamed flower differs mainly from *Silvianthemum* in its bimerous gynoecium, an obhaplostemonous arrangement of the androecium and lack of glandular trichomes.

The two species of *Scandianthus* share many characters with modern flowers of the Escalloniaceae and Hydrangeaceae, but they also show considerable agreement with members of the Saxifragaceae, particularly with members of the *Heuchera*-group, and with Vahliaceae (Friis & Skarby 1982). They are similar to *Silvianthemum* in the epigynous and pentamerous arrangement of the perianth, the unilocular ovary with parietal placentae bearing minute, reticulate seeds, the presence of a distinct nectary disc at the top of the ovary, the free, stout styles and in having pollen grains with perforate tectum. They are, however, distinguished from the flowers of *Silvianthemum* in several respects. Sepals are larger, imbricate and completely covering the petals in the bud, while petals are smaller arranged in a free aestivation. The androecium is clearly bicyclic with the stamens in a diplostemonous arrangement. Gynoecium is bimerous with pendulous placentae. These differences indicate that *Scandianthus* and *Silvianthemum* represent two distinct evolutionary lines. While *Silvianthemum* and the unnamed flower may be attributed confidently to the woody saxifragalean complex, the position of *Scandianthus* is less certain.

*Actinocalyx bohrii* is another small flower from the Late Cretaceous of southern Sweden. Its systematic position is unresolved. Although it shows considerable agreement with members of the Diapensiaceae (Friis 1985a) it also shares some characters with members of the saxifragalean complex. Interestingly, Hall (in press) indicated a strong alliance between *Actinocalyx* and members of the Bruniaceae, a saxifragalean family now endemic to South Africa. *Actinocalyx* is distinguished from the other saxifragalean flowers from southern Sweden mainly in its sympetalous corolla, hypogynous arrangement of perianth and androecium and in the lack of a distinct nectary disc.

Three different fossil flowers of saxifragalean affinity were described from the Baltic Amber (Caspary 1881, Conwentz 1886), believed to be Early Tertiary in age, not younger than the Early Oligocene (e.g. Larsson 1978). *Adenanthemum iteoides* Conwentz shows strong similarity with some of the woody saxifragalean taxa and was compared with flowers of modern *Itea* (Conwentz 1886). It resembles the flowers of *Silvianthemum* in several respects, e.g. in the small size of the flower and in the pentamerous perianth with relatively short sepals and longer petals. It is, however, distinguished in the hypogynous arrangement of perianth and androecium, the haplostemonous arrangement of the stamens and the dimerous gynoecium. The glandular trichomes of *Adenanthemum iteoides* are also distinguished from those of *Silvianthemum* in being smaller and uniseriate.

The two other saxifragalean species from the Baltic Amber, *Stephanostemon brachyandra* (Caspary 1881) and *S. helmii* (Conwentz 1886), also possess small, pentamerous flowers. According to Conwentz (1886) they are most closely related to the herbaceous *Tellima*, *Mitella*, *Oresitrope* and related taxa. Their organization, however, is not well documented. In *S. helmii* petals and stamens are apparently abscised. Organs interpreted as paired stamens may represent a ten-lobed nectary disc similar to that of *Scandianthus*. The flowers of *Stephanostemon* are similar to *Silvianthemum* mainly in



the epigynous arrangement of floral parts, but they differ in having more prominent sepals, a bimerous

gynoecium structure and in their glabrous surface.

## Conclusions

The unique preservation of *Silvianthemum suecicum* provides the basis for detailed comparison between the fossil flowers and those of modern taxa. The close relationship to members of the Escalloniaceae, particularly to species of *Quintinia*, is documented not only by morphological and organizational similarities, but also by anatomical features including cellular details of the trichomes.

Together with other fossil flowers previously described from the same locality (Friis & Skarby 1982) *Silvianthemum* clearly documents that several distinct saxifragalean lineages had evolved by the Late Cretaceous. The various saxifragalean taxa now recorded in the Late Cretaceous flora of Swe-

den are all epigynous and have a unilocular ovary with parietal placentation, suggesting that these conditions may be ancestral within the Saxifragales. The great similarity between *Silvianthemum* and modern Escalloniaceae further suggests that the woody taxa of the saxifragalean complex constitute an ancient stock. The Escalloniaceae predominantly occur in the southern hemisphere, in Australasia, Africa and south America, but the presence of *Silvianthemum* in the fossil flora of Sweden indicates that closely related forms were already established in Europe in the Cretaceous and that the present distribution pattern in part may be explained by extinctions.

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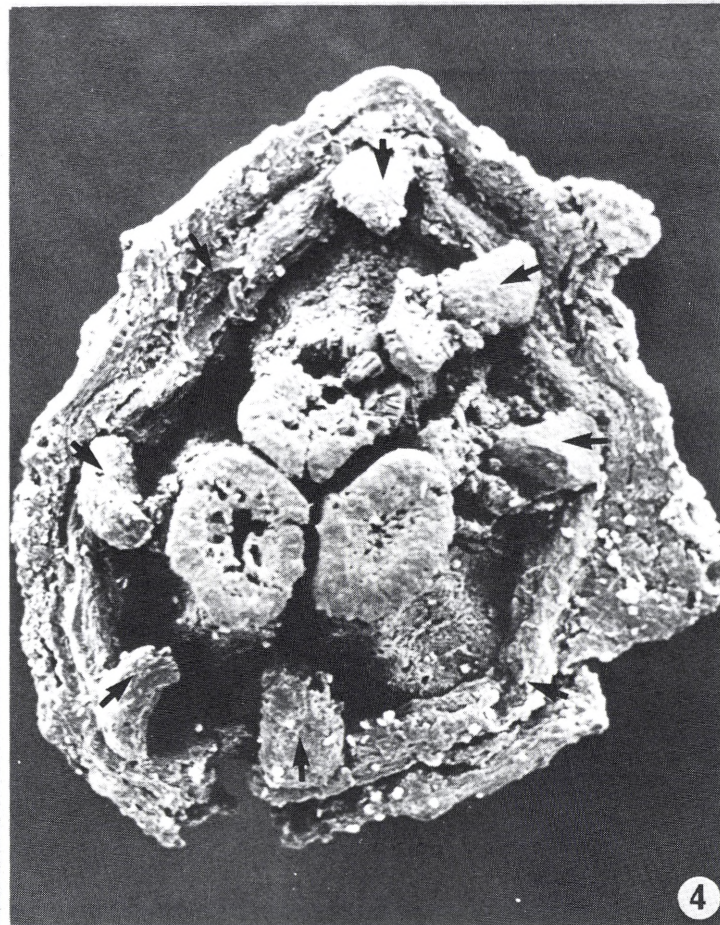
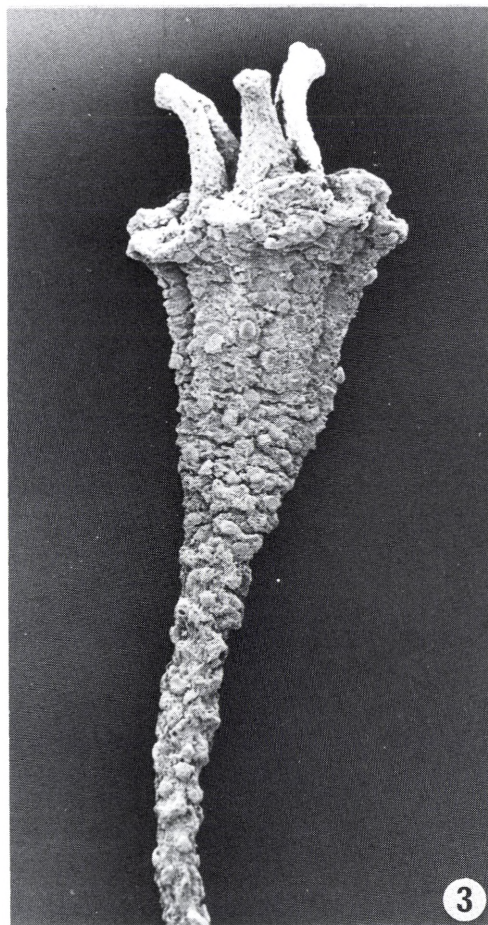
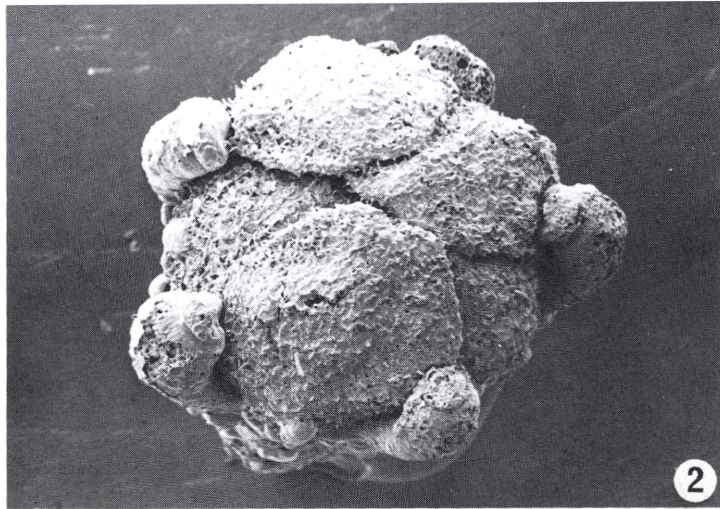
Plates 1-7

## PLATE 1

*Silvianthemum suecicum* Friis gen. et sp. nov. from the Late Cretaceous of Sweden. SEM-micrographs.

1. Holotype. Flower bud showing epigynous position of perianth and small size of sepals (S100376,  $\times 30$ ).
2. Apical view of holotype showing quincuncial imbrication of corolla (S100376,  $\times 50$ ).
3. Mature specimen in which perianth parts have abscised showing the three diverging styles (S100377,  $\times 20$ ).
4. Apical view of specimen with part of androecium preserved; position of stamens indicated with arrows (S100378,  $\times 95$ ).





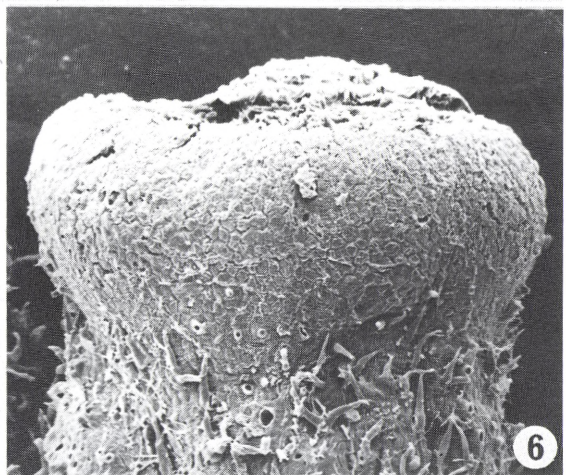
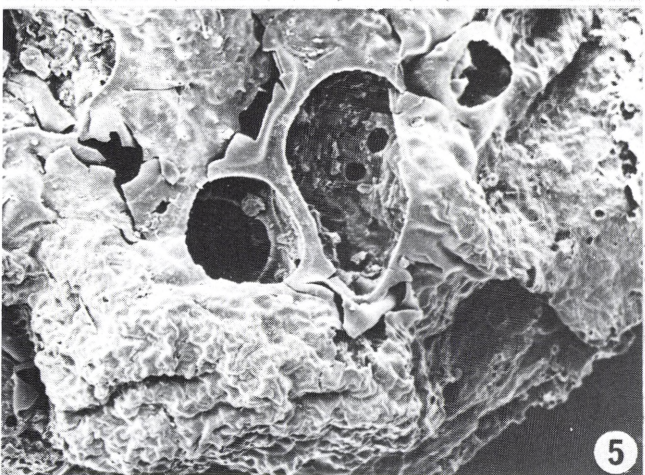
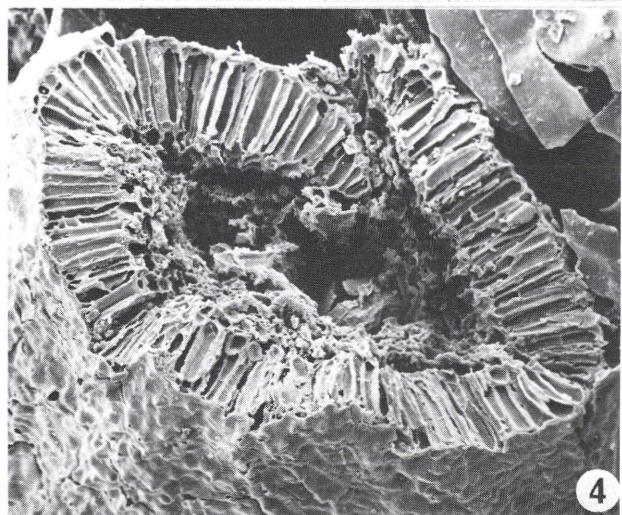
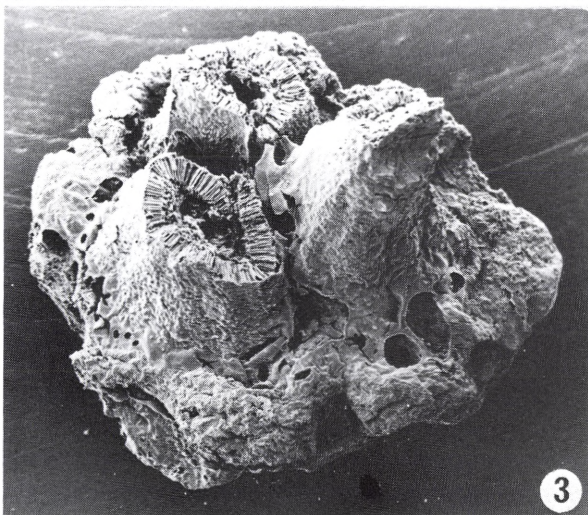
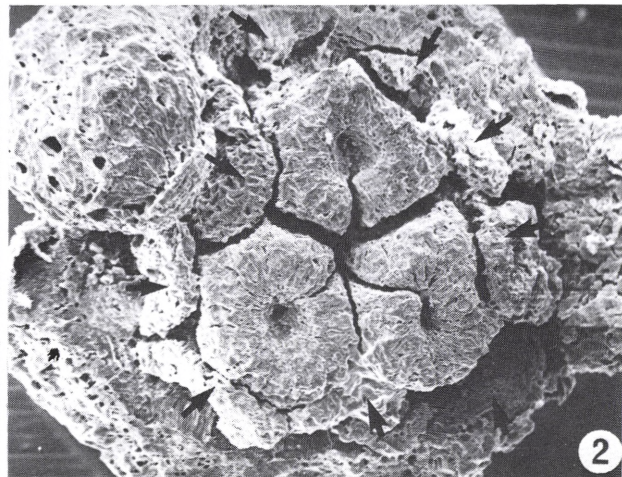
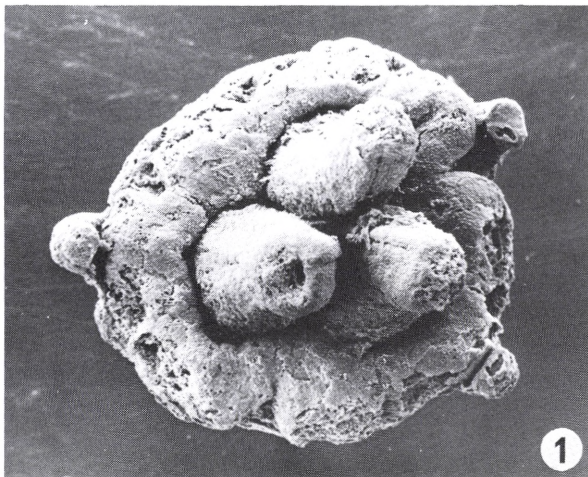


## PLATE 2

*Silvianthemum suecicum* Friis gen. et sp. nov. from the Late Cretaceous of Sweden. SEM-micrographs.

1. Apical view of specimen with three spreading styles surrounded by a distinct disc (S100379,  $\times 35$ ).
2. Apical view of small specimen with appressed styles and remnants of androecium; position of stamens indicated by arrows (S100383,  $\times 200$ ).
3. Apical view of specimen with lobed disc and possible remnants of nectary (S100384,  $\times 40$ ).
4. Detail of figure 3 showing broken style with distinct palisade cells (S100384,  $\times 150$ ).
5. Detail of figure 3 showing disc and base of style embedded in a shiny substance possibly representing remnants of nectar (S100384,  $\times 125$ ).
6. Apex of styles (S100386,  $\times 175$ ).





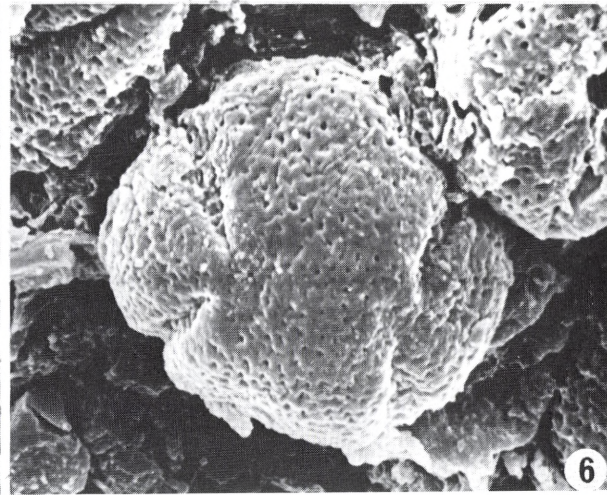
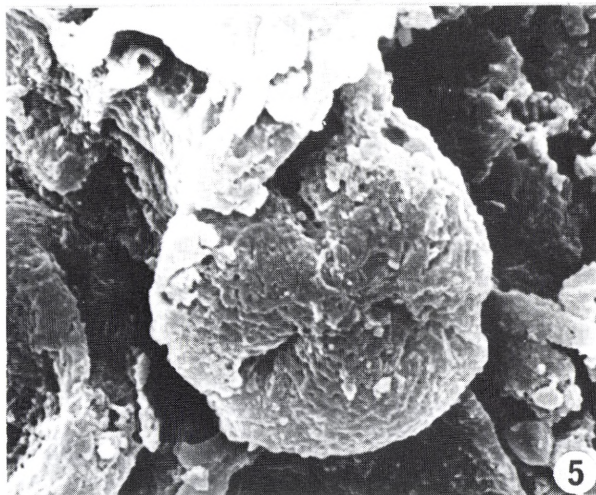
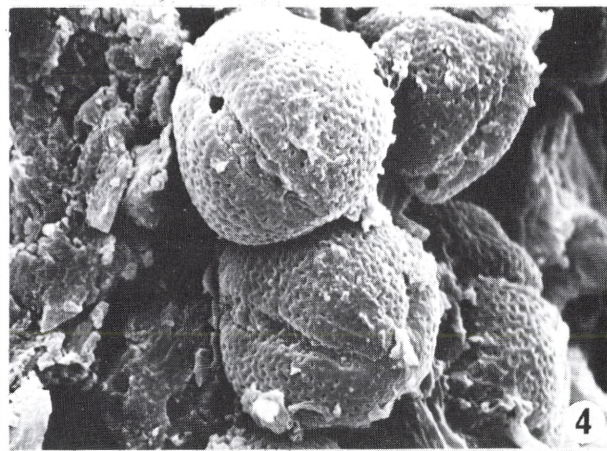
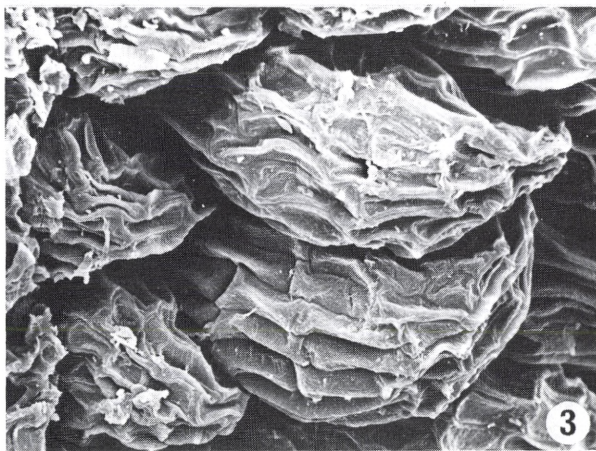
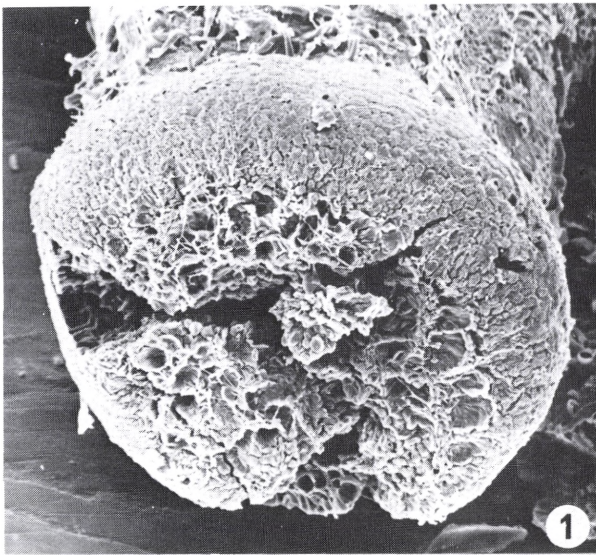


**PLATE 3**

*Silvianthemum suecicum* Friis gen. et sp. nov. from the Late Cretaceous of Sweden. SEM-micrographs.

1. Apical view of stigma showing central papillate area (S100386,  $\times 175$ ).
2. Details of papillate area shown in figure 1 (S100386,  $\times 1500$ ).
3. Ovules/seeds with reticulate surface ornamentation (S100388,  $\times 500$ ).
4. Group of pollen grains attached to the style surface (S100377,  $\times 2500$ ).
5. Polar view of pollen grain with three colpi (S100377,  $\times 4000$ ).
6. Polar view of pollen grain with four colpi (S100377,  $\times 4000$ ).







## PLATE 4

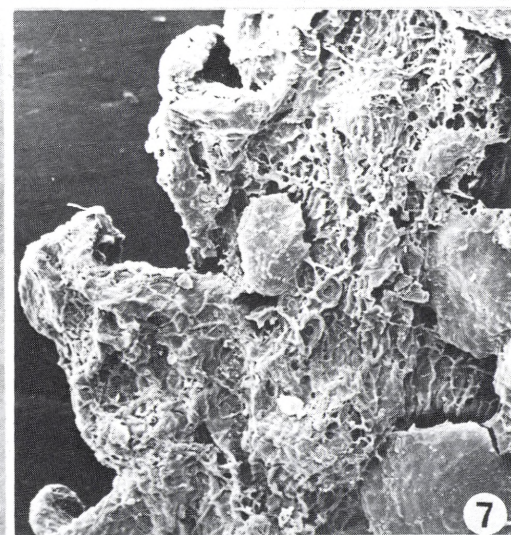
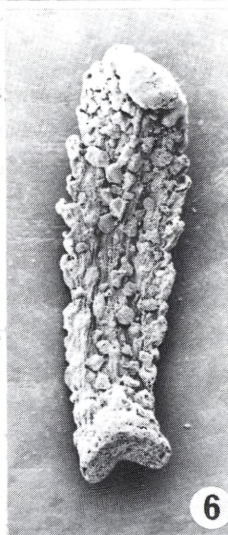
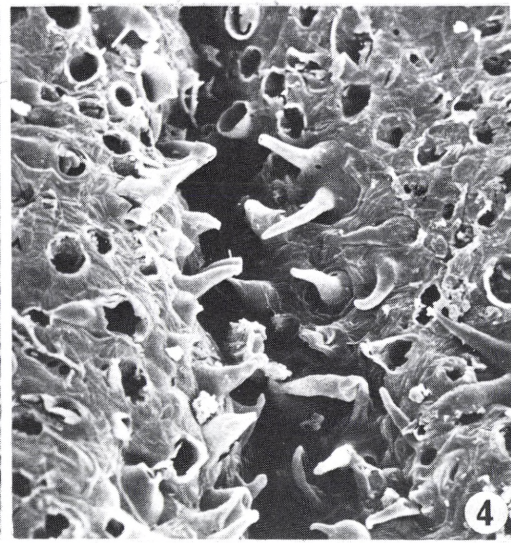
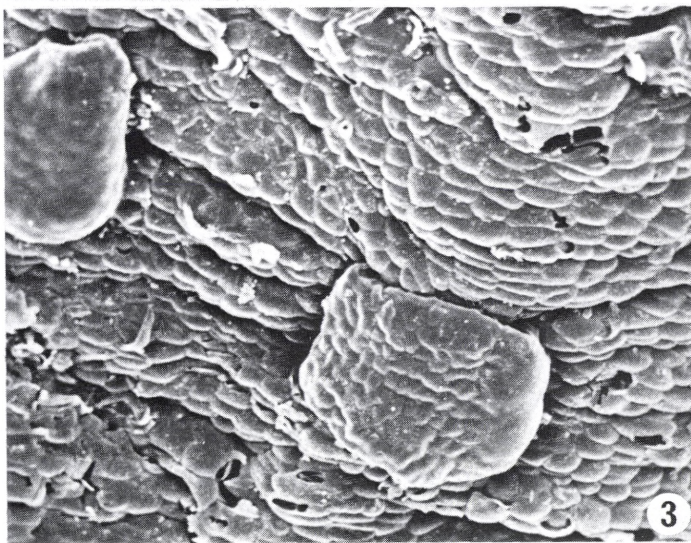
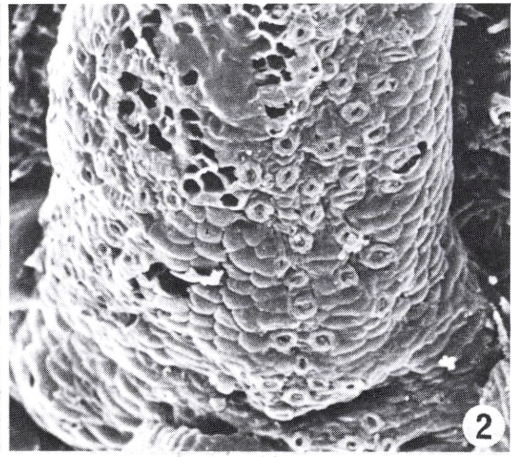
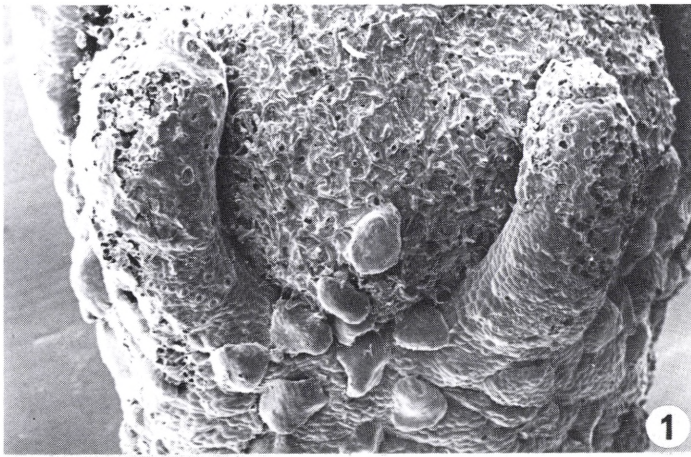
*Silvianthemum suecicum* Friis gen. et sp. nov. from the the Late Cretaceous of Sweden. SEM-micrographs.

1. Detail of holotype showing short unicellular trichomes on the corolla and larger multicellular glandular trichomes at the base of perianth and on the hypanthium (S100376,  $\times 75$ ).
2. Detail of holotype showing distribution of stomata on sepal (S100376,  $\times 110$ ).
3. Detail of holotype showing surface of hypanthium and cellular structure of the glandular trichomes (S100376,  $\times 220$ ).
4. Surface of style showing short unicellular trichomes (S100389,  $\times 385$ ).
5. Unicellular trichomes of style enlarged (S100389,  $\times 1550$ ).

Small fossil leaf from the Late Cretaceous of Sweden associated with *Silvianthemum suecicum*. SEM-micrographs.

6. Entire leaf (S100393,  $\times 15$ ).
7. Detail of leaf showing tooth margin and glandular trichomes (S100393,  $\times 150$ ).



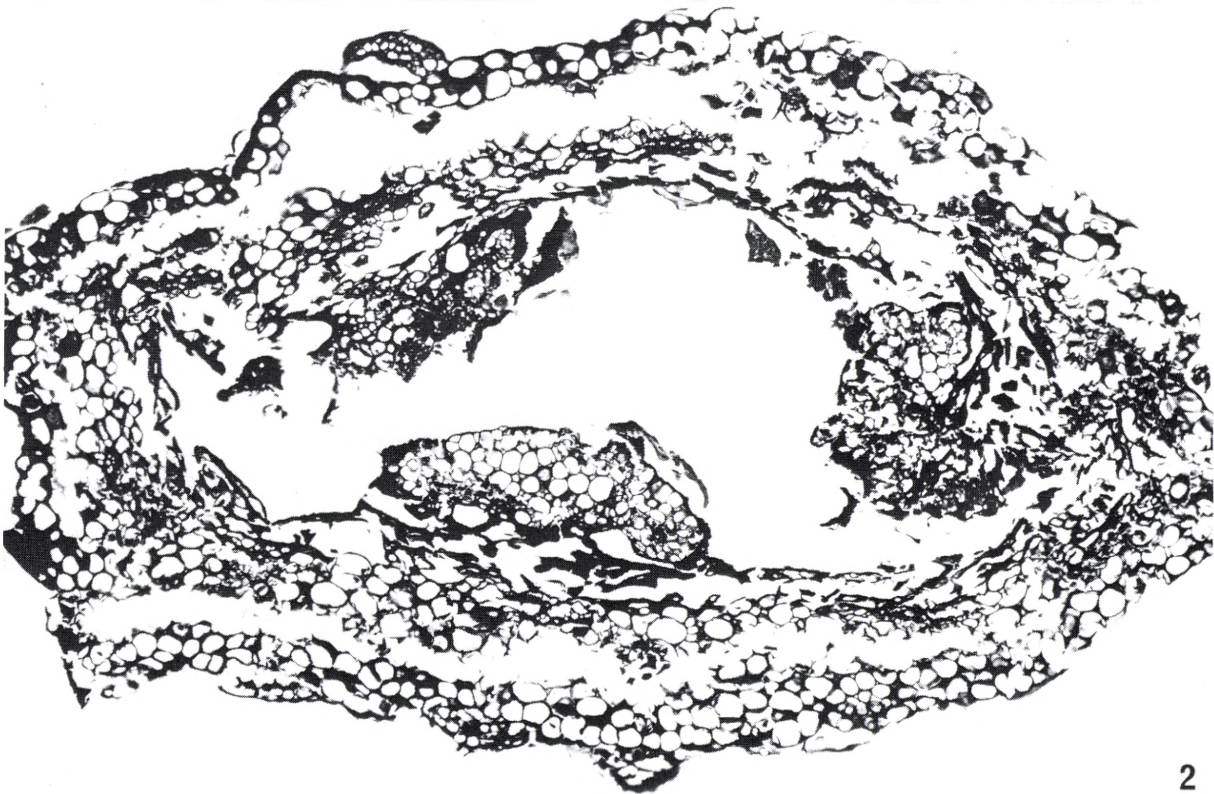
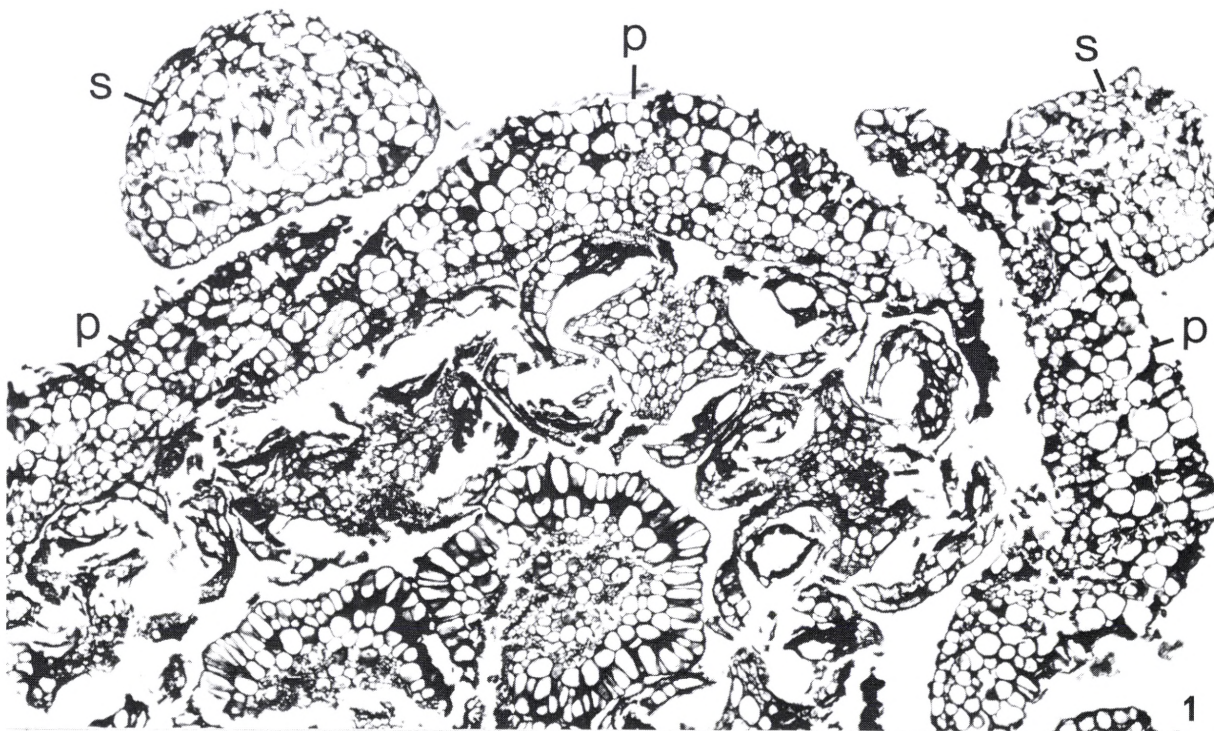




## PLATE 5

*Silvianthemum suecicum* Friis gen. et sp. nov. from the Late Cretaceous of Sweden; transverse sections of flower bud. Transmitted light micrographs.

1. Section through apical part of bud showing shape of sepals (s) and petals (p). (S100394,  $\times 150$ ).
2. Section through ovary showing the three parietal placentae (S100394,  $\times 150$ ).

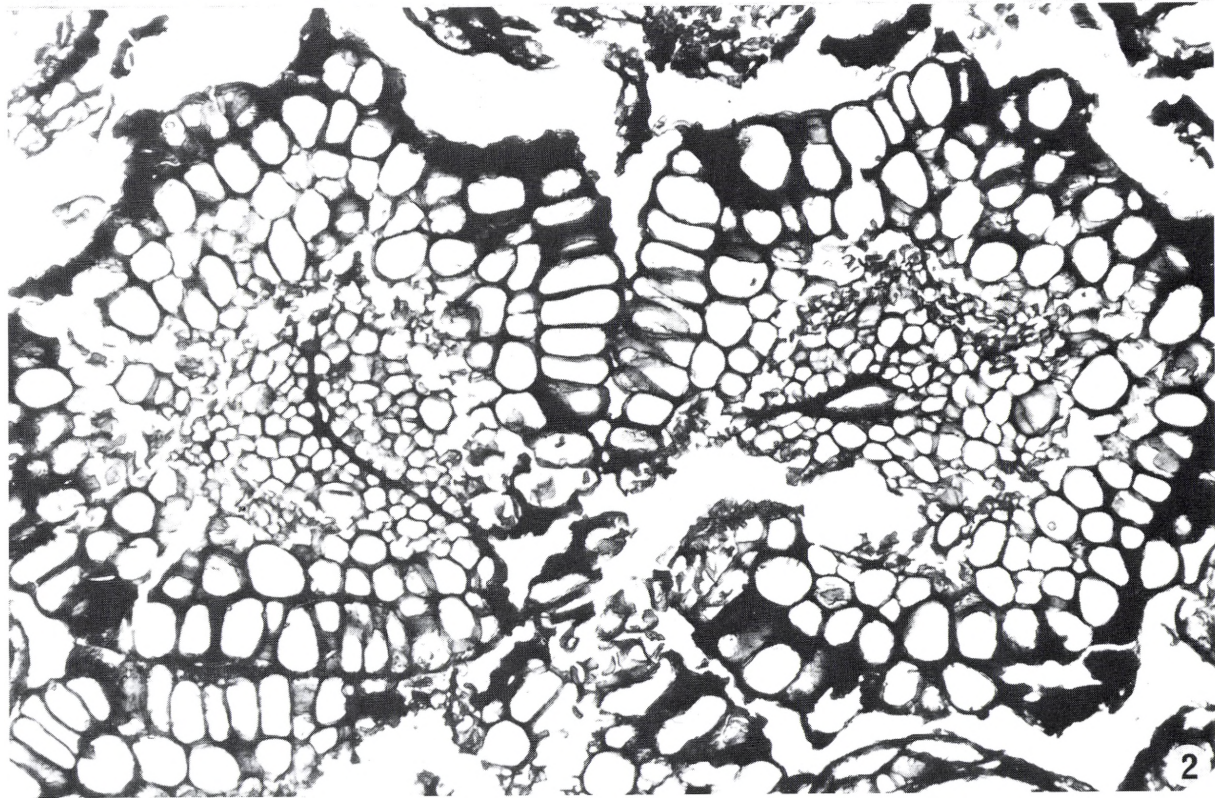
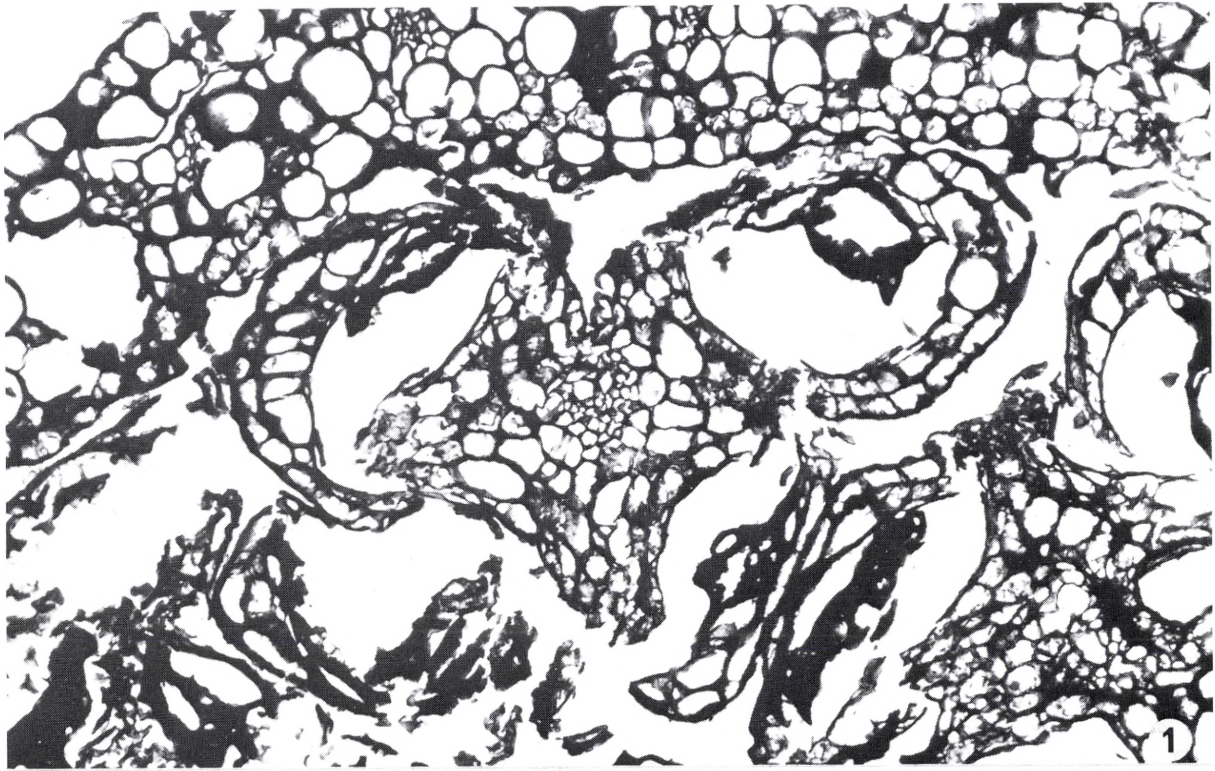




## PLATE 6

*Silvianthemum suecicum* Friis gen. et sp. nov. from the Late Cretaceous of Sweden; transverse sections of floral bud. Transmitted light micrographs.

1. Details of anther showing four pollen sacs and thick connective with a single strand (S100394,  $\times 370$ ).
2. Details of styles showing angular outline, ventral slit and stylar tissue (S100394,  $\times 370$ ).

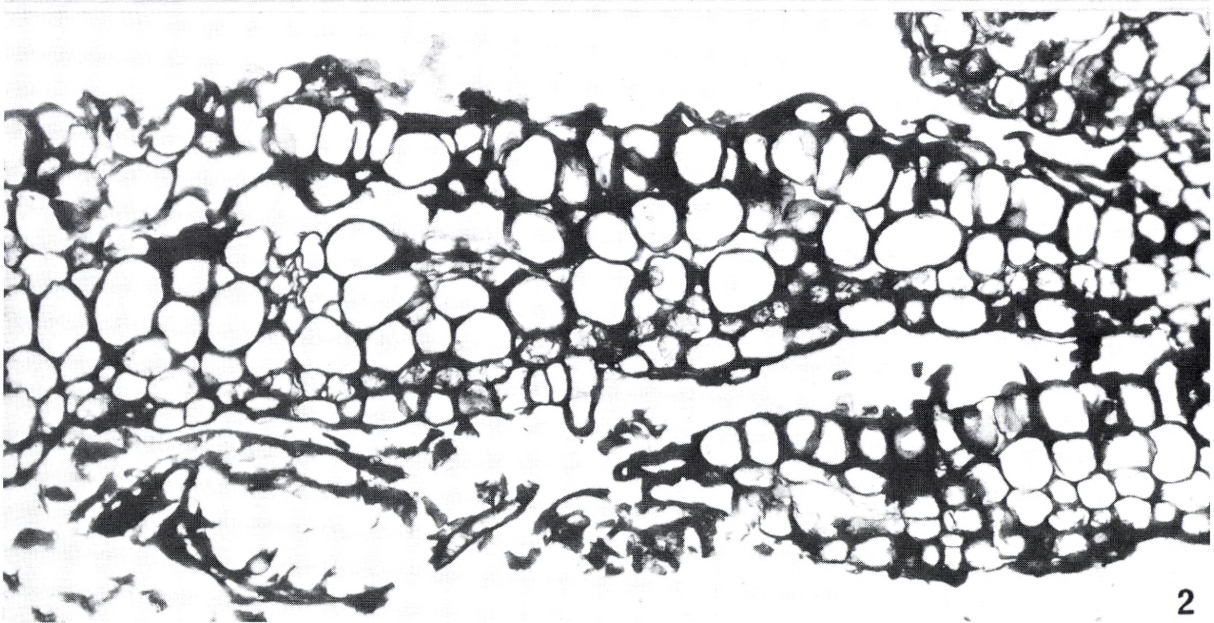
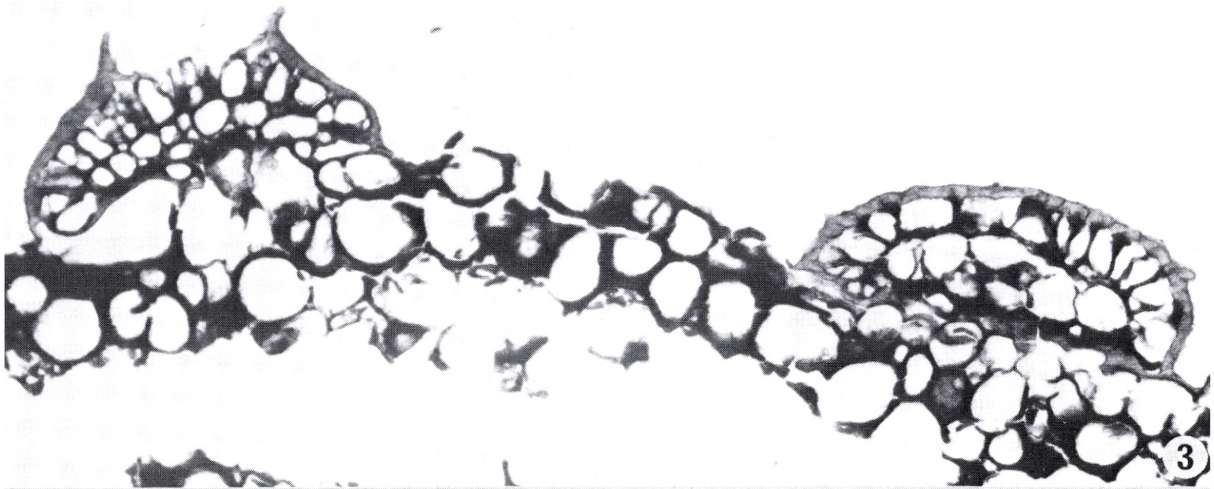




## PLATE 7

*Silvianthemum suecicum* Friis gen. et sp. nov. from the Late Cretaceous of Sweden; transverse sections of flower bud. Transmitted light micrographs.

1. Section through hypanthium wall showing multicellular glandular trichomes with thick outer cuticle; cuticle of left trichome ruptured (S100394,  $\times 370$ ).
2. Section through petal showing vascular trace and unicellular hair (S100394,  $\times 370$ ).







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