

Esgueiria gen. nov.,
fossil flowers with combretaceous features
from the Late Cretaceous of Portugal

By ELSE MARIE FRIIS,
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Abstract

Numerous well-preserved fossil flowers have been discovered from the Cretaceous of Portugal as a result of recent field work in Estremadura and Beira Litoral. The present work gives the first account of the new discoveries and describes combretaceous flowers from two outcrops near Aveiro (Esgueira) and Mira in the Beira Litoral region. The flowers were isolated from unconsolidated sediments of Late Cretaceous (Campanian-Maastrichtian) age and are preserved as compressed lignitized fossils or three-dimensional charcoalifications. The flowers from the two localities are minute and epigynous with a well-differentiated, pentamerous calyx and corolla, androecium in two whorls, three free styles, unilocular ovary and one-seeded fruits. Distinctive glandular trichomes as well as simple, stiff hairs occur over most of the surface of the flowers. Based on these shared characters the flowers from the two localities are assigned to the same new genus, *Esgueiria*. There are, however, a number of distinctive features that distinguish the flowers from the two localities and they are assigned to two separate species. In *E. adenocarpa* from Esgueira the glandular trichomes are restricted to the hypanthium wall while in *E. miraensis* from Mira glandular trichomes are also present at the base of the styles. The characters of *Esgueiria* indicate a close relationship with modern members of the Combretaceae although the presence of three free styles in the fossil flowers is a feature that does not occur in the extant family and may link the fossils with other rosoid families.

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Introduction

Continental sediments of Cretaceous age are common in the Estremadura and Beira Litoral regions of western Portugal from the Torres Vedras area to north of Aveiro. These sediments in the western Portuguese Basin span a considerable stratigraphic interval covering most of the Cretaceous and contain a number of megafossil floras with angiosperm leaves ranging in age from mid-Early Cretaceous to Maastrichtian. The first comprehensive account of the leaf floras was given by Saporta (1894) and revisions of Saporta's work and descriptions of new material were subsequently presented by de Lima (1900) and Teixeira (1945, 1946, 1947, 1948, 1950, 1952). Generic assignments of the fossil angiosperm leaves were based mostly on morphological comparison with modern plants and many of the determinations are in need of reevaluation incorporating also other characters such as epidermal features. Recent studies of palynological samples from the Cretaceous of Portugal have also revealed rich assemblages of angiosperm pollen and particular emphasis has been placed on studies of the very diverse Normapolles assemblages (Diniz, Kedves & Simoncsics 1974, Kedves & Pittau 1979, Kedves & Diniz 1981, 1983, Kedves & Párdutz 1981, 1982, Kedves 1989, Batten 1986, 1989).

During field work in Portugal in the summers of 1989 and 1990 a number of new Cretaceous floras yielding well-preserved angiosperm flowers have been discovered in road cuts, open quarries and coastal exposures. Samples were collected from strata ranging in age from the Valanginian to the Maastrichtian, but so far angiosperm remains have been discovered only in sediments from the mid-Early Cretaceous (Aptian or possibly slightly older)

through to the latest Late Cretaceous (Maastrichtian). The fossil angiosperm reproductive material is an important new source for studying the structure, biology and relationships of Cretaceous angiosperms and shows the same patterns of organization as have been observed for other European and North American floras of the same age. Preliminary results indicate that very few of the taxa are shared between the North American and European floras.

The very small size of the angiosperm flowers, fruits, and seeds from Portugal is characteristic for most previously described Cretaceous floras (e.g. Friis 1983, 1984, 1985a,b, 1990, Tiffney 1984, Knobloch & Mai 1986, Drinnan et al. 1990, 1991, Pedersen et al. 1991), and there is also a remarkably high proportion of epigynous forms as reported in other Cretaceous assemblages from Europe and North America (e.g. Friis 1985a, Friis & Crepet 1987, Friis & Endress 1990). The fossil flora collected near Aveiro in Esgueira at the fountain Olho de Agua comprises 15 different taxa of fossil flowers in which position of perianth and gynoecium could be established. In most of these, the gynoecium is inferior and only three kinds of hypogynous flowers have been identified so far. *Esgueiria adenocarpa* described in the present work is one of the small epigynous forms from Esgueira. It is the most abundant angiosperm fossil in the flora and is significant because of its close relationship with modern members of the Combretaceae. Flowers of *Esgueiria* have also been identified from the Mira locality about 25 km south of Aveiro. These are distinct from *E. adenocarpa* in several features and are described as a separate species, *Esgueiria miraensis*.

Material and methods

Esgueira (Olho de Agua)

The fossil flowers and fruits of *Esgueiria adenocarpa* described in the present work have been collected at a road building site at the fountain Olho de Agua in Esgueira in the vicinity of northeastern Aveiro, Portugal (40°39'6"N; 8°37'24"W; Carta Geologica de Portugal 16A Aveiro). The Aveiro area forms the northernmost part of the Western Portuguese Basin and comprises the youngest of the Cretaceous strata in the basin ("Arenitos e argilas de Aveiro" corresponding to the Série flúvio-marinha of Choffat, 1900). The sediments at the Esgueira (Olho de Agua) locality are alternating layers of light brown to grey sands, silts and clays with abundant plant fossils. The plant fossils are typically organically preserved in the darker layers and preserved as impressions in the light brown and oxidized horizons. The age of the sands and clays of Aveiro is indicated by Teixeira and Zbyszewski (1976) as being Maastrichtian, while Barbosa (1981) indicated a Coniacian-Maastrichtian age for the whole series. A brief note on the Normapolles pollen occurring at Esgueira (Olho de Agua) was given by Medus (1981). In addition to *Interporopollenites proporus* only a few species of *Vacuopollis* were recorded. This paucity of Normapolles taxa distinguishes the Esgueira (Olho de Agua) assemblage from most other Cretaceous pollen assemblages in the area. There are, however, similarities with palynofloras from the upper part of the Ilhavo sequence, and Medus (1981) suggested a latest Campanian age for the palynoflora from Esgueira. Based on palynological samples a Campanian-Maastrichtian age was also suggested by Batten (1986) for the near-by localities (Forca, Arada, Chousa do Fidalgo, Presa near Ilhavo), while Kedves and Diniz (1967) indicate a Santonian-Campanian age for material collected in a clay pit in Aveiro.

Plant megafossils were previously reported from

the Esgueira locality by de Lima (1900), Teixeira (1946), Lauverjat and Pons (1978), Pons and Broutin (1978) and Pons, Lauverjat and Broutin (1980). In certain horizons twigs of *Frenelopsis oligostoma* are extremely common. Other horizons are dominated by leaf remains of angiosperms. The leaf impressions are typically densely packed so that the morphology of the individual leaves is difficult to study. Leaf margins when preserved are entire.

The fossil specimens sieved out of the sediment samples from Esgueira are typically lignitized and slightly compressed, or more rarely charcoaled. In several samples cuticles of *Frenelopsis* are the dominant fossil remains, but some samples have abundant angiosperm flowers. More than 15 taxa of angiosperm flowers have been recognized to date. *Esgueiria adenocarpa* is represented in the flora by more than one thousand specimens and is by far the most common fossil flowers. It has been observed in all but one of the samples collected at this locality (Portugal 84-87 collected 1989 by KRP and EMF; Portugal 112-117, 119-121 collected 1990 by KRP and EMF). Small pieces of angiosperm leaves are occasionally present among the isolated plant material, but due to their fragmentary nature they usually do not yield sufficient morphological information for detailed systematic study.

One of the floral structures present in the Esgueira flora has been related to the pollen of *Interporopollenites*. It is a minute, epigynous and unisexual form with extremely reduced perianth parts. It belongs to a new genus of Normapolles-producing plants. Staminate and pistillate flowers of this genus also occur abundantly in sediments of approximately the same age from the Mira locality. The *Interporopollenites* flowers from the two localities belong to two distinct species (work in progress).

In all samples small charcoaled fragments of wood are common. They comprise gymnospermous

as well as angiospermous types and are currently under investigation by Dr. P. Herendeen and so far two major types of angiosperm wood, assigned to *Icacinoxylon* and *Paraphyllanthoxylon*, have been identified (Herendeen 1991).

Mira

The fossil flowers of *Esgueiria miraensis* described in the present work were extracted from clay samples collected in an old clay pit in the southern vicinity of Mira, Beira Litoral, Portugal (40°25'N; 8°44'15"W, Carta Geologica de Portugal 16C Vagos). Mira is situated in the northern part of the Western Portuguese Basin about 25 km south of Aveiro. Cretaceous sediments in the vicinity of Mira only reach the surface in small localized areas. They are referred to the "Argilas de Vagos" and "Conglomerado de Mira" and indicated as being of Santonian?-Maastrichtian age (Barbosa 1981). A symbol for plant fossils on the geological map and stratigraphic column indicates that the plant bearing Cretaceous sediments near Mira belong to the upper part of the sequence (Campanian-Maastrichtian). A marine deposit about 1200 m west of the church in Mira was dated based on ammonites and other faunal elements to the Late Campanian (Beauvais, Berthou and Lauerjat 1975). According to the geological map and descriptions from the area the stratigraphic position of this deposit is approximately the same as the plant bearing beds a little further south.

Angiosperm leaves have been reported previously from Portomar just north of Mira and from Preza east of Mira (Saporta 1894, de Lima 1900). Saporta (1894) noted that leaves of dicotyledonous angiosperms were dominant, but he did not provide descriptions of the material. de Lima (1900) reported leaves of *Cornus*, *Credneria*, *Echitonium*, *Laurinea*, *Myrica*, *Nelumbium*, *Prophyllum*, *Rhamnus* and *Ziziphus* from Preza and Portomar but none of these were described or figured. Kedves and Pittau (1979) reported a rich assemblage of Normapolles forms from Preza and suggested a Santonian-Campanian

age for the sequence. According to Barbosa (1981) this Preza locality is close to Mira. The Preza (Preza) locality studied by Batten (1986) is situated further north, close to Aveiro and Ilhavo (see above).

Samples Portugal 99-102 comprise dark grey clays and silts collected at the entrance of the Mira clay pit in 1989 (KRP and EMF). Samples Portugal 103-111 comprise greenish clays with abundant pyrite and some shells collected in a new excavation in the southern part of the pit in 1990 (KRP and EMF). All samples collected from the Mira clay pit are rich in angiosperm remains. They are usually well-preserved, mostly as charcoalifications in samples Portugal 99-102 or lignitized and often pyritized in samples Portugal 103-111. Several different kinds of flowers, as well as numerous different fruits, seeds and dispersed stamens, have been identified from the Mira samples. Some of the fossil taxa occur throughout the section while others are restricted to either the greenish clay or to the dark grey clays and silts. Many of the flowers, fruits and leaf fragments from Mira are characterized by the presence of a more or less dense indumentum. In contrast to the samples from Esgueira, flowers of *Esgueiria* are extremely rare in the Mira samples and only 8 specimens have been discovered to date, all from samples Portugal 99-100. The dominant angiosperm fossils in the Mira flora are remains of Normapolles flowers. Two different genera have been identified, both with unisexual flowers. They are distinct in structure and may belong to different families. One of the Normapolles flower types contains pollen similar to dispersed grains of *Interporopollenites*, while the other contains pollen similar to dispersed grains of *Pseudopapillopollis* (work in progress). Platanoid inflorescences and dispersed stamens have been identified in several samples. Other angiosperms identified from the Mira locality are small unisexual flowers of flacourtiaceous affinity, several rosoid flowers, and seeds of two monocotyledonous plants, *Spirematospermum* (extinct member of the Zingiberaceae) and *Epipremnum* (Araceae). Both *Spirematospermum* and *Epipremnum*

are characteristic elements of the *Nyssa-Taxodium* swamp communities that covered huge areas in Europe and Asia during the Tertiary. Seeds of *Spirematospermum* have been reported previously from the Campanian of North America (Friis 1988) and from the Maastrichtian of Central Europe (Knobloch and Mai 1986), while *Epipremnum* has not previously been recorded from the Cretaceous. In addition to flowers, fruits, seeds, and leaf fragments, angiosperm remains from Mira also include well-preserved wood fragments that are now under examination by Dr. P. Herendeen.

Methods

The material studied here was sieved out from the sediments in water. The fossils were then cleaned in

HF, HCl and H₂O and dried in air. The fossil reproductive organs are all very small, generally less than 2-3 mm in length. Morphological details were studied using Phillips 515 and Jeol 800 scanning microscopes. Specimens for structural and anatomical studies were dehydrated in an ethanol-propylene oxide series, embedded in Epon and sectioned on a an LKB Ultratome III ultramicrotome with a glass knife (sections 3 µm thick).

Comparative studies of modern Combretaceae and related myrtalean plants were based on a survey of the literature and herbarium material in the botanical collections at the Swedish Museum of Natural History.

All specimens and preparations studied in the present work are stored in the palaeobotanical collections of the Swedish Museum of Natural History (S).

Systematic descriptions

Genus: *Esgueiria* Friis, Pedersen & Crane gen. nov.

Derivation of generic name: From the village of Esgueira where the flowers occur abundantly in Cretaceous sediments.

Diagnosis: Flowers crowded in dense inflorescences, small, pedicellate, epigynous and perfect. Perianth pentamerous; androecium basically pentamerous; gynoecium trimerous. Calyx with five free, imbricate sepals. Corolla of five free petals with contorted aestivation in the bud. Androecium with stamens in two whorls; anthers bithecate, tetrasporangiate, dorsifixed; pollen tricolporate or tricolpate, tectate. Ovary unilocular with several ovules pendant from the apex; styles three, free; fruit unilocular with a

single seed. Indumentum of simple stiff hairs and multicellular, peltate glands.

Type species: *Esgueiria adenocarpa* Friis, Pedersen & Crane; other species: *E. miraensis* Friis, Pedersen & Crane.

Esgueiria adenocarpa Friis, Pedersen & Crane sp. nov.
Plates 1-7; Text-figures 1-3.

Derivation of specific epithet: From aden- (gr.: gland) and carpus (gr.: fruit).

Specific diagnosis: Ovary and fruit narrowly elongate. Glandular trichomes restricted to the hypanthium, typically arranged in three longitudinal

rows near the top of the ovary. Simple trichomes on the surface of ovary, calyx, filaments and styles.

Dimensions: Flower bud with calyx completely covering corolla: total length: 0.85 mm; length of ovary: 0.35 mm; maximum breadth of the ovary: 0.3 mm. Flower buds with corolla extending beyond calyx: total length: 1.9-2.25 mm; length of ovary: 1.05-1.2 mm; maximum breadth of ovary: 0.35-0.4 mm. Larger specimens without corolla: length of ovary/fruit: 1.5(1.88)2.2 mm; breadth of ovary/fruit: 0.55(0.67)0.9 mm; length of sepals: 0.9-1.0 mm; breadth of sepals: 0.25-0.3 mm. 15 specimens were measured. Pollen: length about 13 μm ; equatorial diameter about 10 μm .

Holotype: S100639 (from sample Portugal 86, figured Pl.1, figs. 1, 10).

Type locality: Esgueira (Olho de Agua), Portugal.

Type stratum: "Arenitos e argillas de Aveiro".

Age: Late Cretaceous (Campanian-Maastrichtian).

Material: 6 complete flower buds (S100639, S100647, S100660-S100662) and more than one thousand incomplete specimens often with remains of calyx (S100640-100646, 100648-100659, S100663-S100665, S100672-S100691). Most of the fossils are slightly to strongly compressed and lignitized, but a few are preserved three-dimensionally as charcoal. From samples Portugal 84-87, 112-117 and 119-121.

Description and remarks on *Esgueiria adenocarpa*

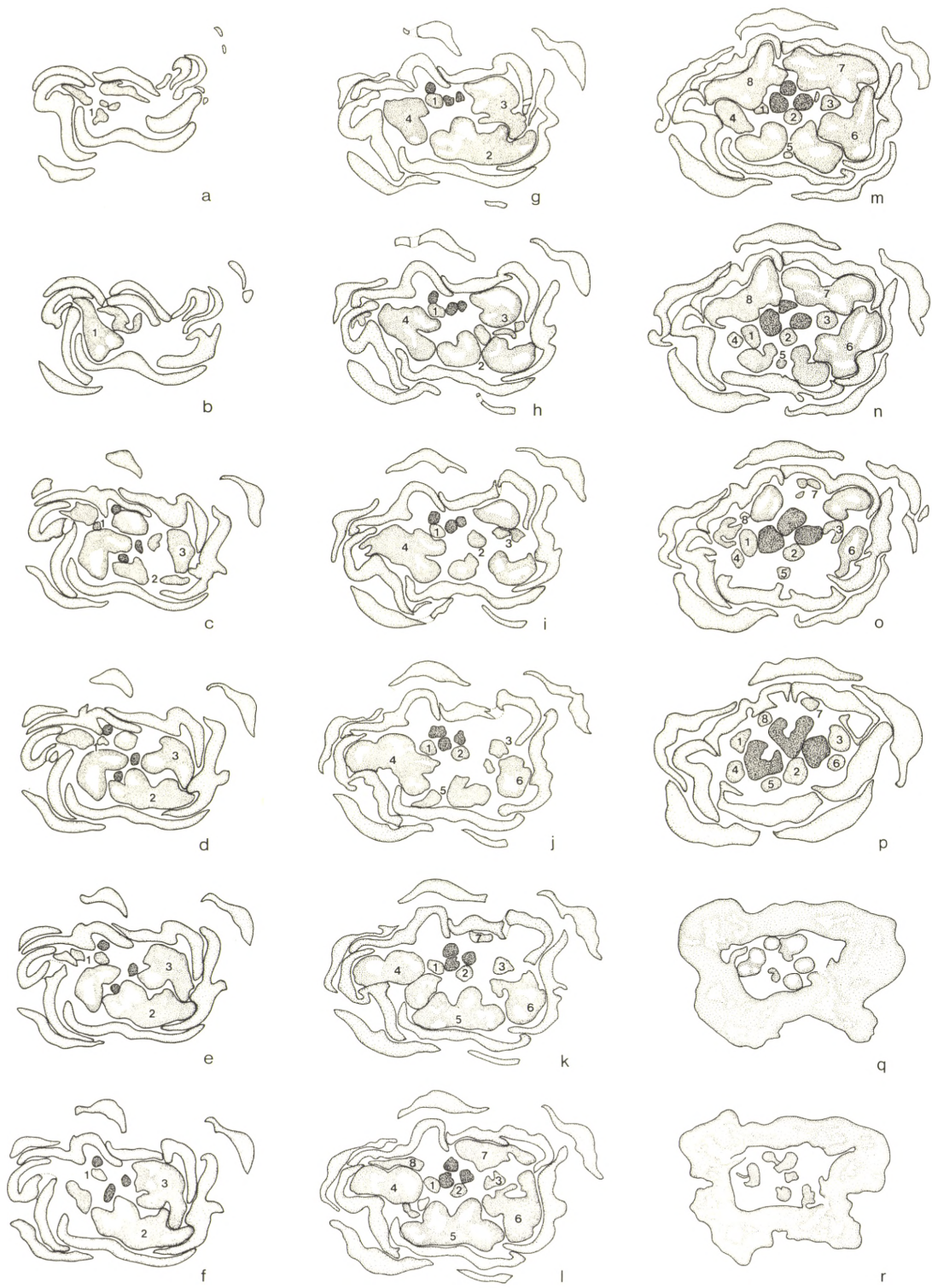
The organization of the flower has been studied mainly from serial sections of three flower buds. Flower buds are rare and only six specimens have been recovered to date. All of the buds are lignitized and somewhat compressed which complicated the interpretation of the sections. A series of sections through one flower bud is illustrated with line drawings in text-figure 1 to document our interpretation of several aspects of floral structure. The floral diagram in text-figure 2 is based extensively on these sections. The reconstructions of *E. adenocarpa* in text-figure 3 are based mainly on SEM studies.

Inflorescence structure: Most flowers and fruits are detached from the inflorescence axis, but one fragment with about 20 flowers (Pl. 1, fig. 11-12) and another with about 10 flowers documents that flowers were borne in a dense, probably racemose inflorescence. It is not possible from the fragments to infer the shape of the inflorescence, but the flowers are arranged almost parallel and all in the same direction which indicates that the inflorescence was probably not completely spherical.

Flower: The flowers are epigynous with well-developed calyx and corolla, slightly zygomorphic with the zygomorphy being expressed in the androecium (Pl. 5, fig. 1; Pl. 7, fig. 2; Text-fig. 2). Flowers are apparently pedicellate subtended by a short subulate prophyll (Pl. 1, fig. 8). The pedicel is short, about 0.025mm, with a distinct joint at the base of the flower. The flowers tend to break at this joint and pedicel and prophyll are rarely preserved.

Perianth: The calyx consists of five free, narrowly triangular sepals with imbricate aestivation (Pl. 2, figs 1-2; Pl. 6, fig. 1; Pl. 7, fig. 2; Text-fig. 1). In the smallest flower bud the calyx covers the corolla completely (Pl. 1, fig. 7). In the five other buds the calyx lobes extend for about two thirds of the length of the corolla (Pl. 1, figs 1, 10). Remains of calyx lobes have been found on most specimens although they are often broken (Pl. 2, figs 1-5) and calyx was probably persistent. The corolla has five free petals that are contorted in the flower bud (Pl. 5, figs 1-2; Pl. 7, fig 1; Text-fig. 1). Remains of petals are extremely rare in specimens other than the flower buds and the corolla was probably caducous.

Androecium: Stamens apparently abscised early after anthesis together with the corolla, and the remains of androecium have only been observed in a few smaller specimens and in serial sections of the flower buds. Two of the flower buds showed the position of stamens, although in both specimens details of the androecial arrangement were extremely difficult to study. The stamens are arranged in two





Text-figure 2. Floral diagram showing general organization of *Esgueiria*.

whorls which are free to the base and not fused to the perianth. In both specimens eight stamens are present (Pl. 6, fig. 1; Pl. 7, fig. 2; Text-fig. 1). The anthers of the two whorls are arranged at different levels in the bud, but apparently not in a consistent pattern. In flower bud S100660 stamens of the antisepalous whorl are placed above those of the antipetalous whorl. In the antisepalous whorl three stamens only were developed while in the antipetalous whorl all five stamens were present (Pl. 5, figs 1-2; Pl. 6, fig. 1; Text-fig. 1). In this specimen the antisepalous stamens seems to form the outer whorl. In the flower bud S100647 the arrangement of stamens is difficult to establish, but the uppermost anther in the bud appears to be antipetalous (Pl. 7, fig. 1). When tracing the filaments through the sections to their base the antisepalous stamens appear to form the inner whorl while the antipetalous stamens form the outer whorl indicating an obdiplostemonous arrangement although this is not completely clear. Anthers are bitecate and tetrasporangiate, sagittate, introrse and dorsifixed. The connective tissue is broad and thickened dorsally.

Anthers are large relative to the flower bud and occupy most of the space between the petals. They

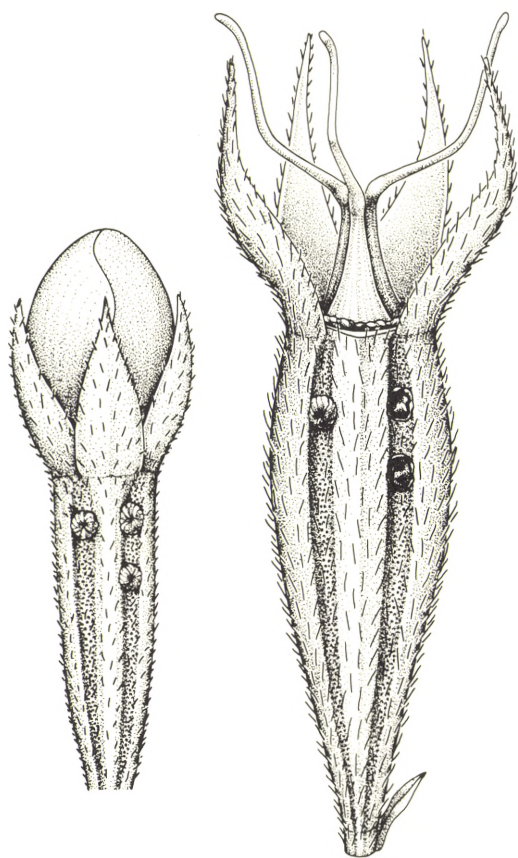
Text-figure 1. Selected sections through a flower bud of *Esgueiria adenocarpa* (S100660) from apex of flower (a) to top of ovary (r) showing imbricate calyx, contorted corolla and position of stamens (1-8) and styles (darker). Total number of sections through S100660 is 210.

are about 0.2 mm broad and about 0.15 mm long (the latter figure calculated from the sections). Filaments are circular in cross-section with a single vascular bundle. In both flower buds filaments of the antisepalous stamens have a slightly larger diameter than those of the antipetalous stamens.

Pollen: Pollen grains have not been observed *in situ* in the anthers in any of the specimens that have been studied using SEM and no pollen grains were preserved in the anthers of the specimens that were sectioned. Numerous grains, however, have been observed inside the flowers, on the stylar region and attached to the stigmas (Pl. 3, figs 1-6). Except for a single grain they are all of the same kind. Their abundance and also their occurrence on the stigmatic surface suggests that these grains were produced by the *Esgueiria* flowers. Pollen grains are minute, about 13 μm long and about 10 μm in equatorial diameter. They are triaperturate, tectate, and foveolate. They are typically infolded at the apertures and it is not possible from SEM-studies to establish whether they are tricolpate or tricolporate.

Gynoecium: The ovary is inferior, unilocular and formed from three carpels. It is narrowly elongated in younger specimens while larger specimens tend to be slightly broader (Pl. 1, figs 1-9). In some specimens, typically smaller, the ovary is slightly curved (Pl. 1, figs 5, 7). There are three free styles, which are relatively slender at the base and with long, filiform stigmatic branches (Pl. 1, fig. 12, Pl. 3, figs 1-4). The stigmatic surface is non-papillate.

There are no fragments of large fruits at the Esgueira locality and the material of *Esgueiria adenocarpa* may also include mature fruits. The ovary/fruit wall appears leathery; it is about 0.05 mm thick and composed of small equiaxial sclerenchyma cells. The inner epidermis has larger, cuboidal cells (Pl. 7, fig. 3). Ten vascular bundles pass up through the sclerenchymatic tissue. The ovary/fruit is ribbed and has longitudinal glandular bands alternating with non-glandular bands (Pl. 2, figs 4, 6-



Text-figure 3. Reconstructions of *Esgueiria adenocarpa* showing flowers in bud stage (a) and after anthesis with corolla and androecium abscised (b).

7). The epidermal cells over the non-glandular parts are longitudinally elongated (Pl. 4, fig. 4). Those of the glandular bands are equiaxial and verrucate (Pl. 4, figs 3, 6). The glandular bands may be sunken to form shallow grooves that extend for the full length of the ovary. There are typically three glandular bands which correspond to the junction between carpels, but occasionally an additional band may also be present.

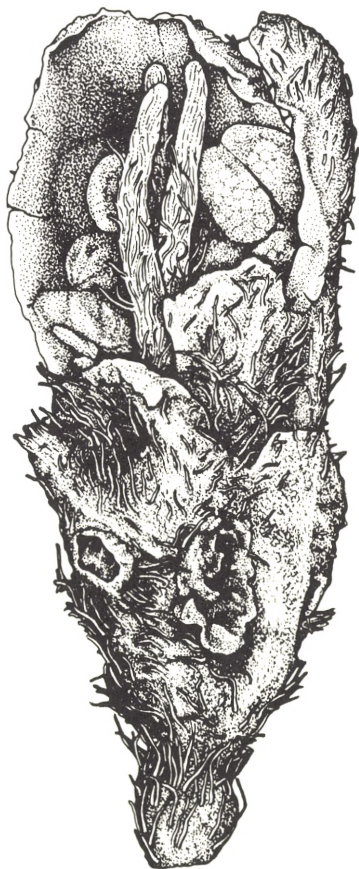
Ovules and seeds: Placentation is apical and there are up to six pendant ovules apparently in three groups (Pl. 6, fig. 2). Only a single ovule in each ovary

develops to a mature seed. The seed is anatropous, narrowly obovate. Seed coat is thin with small equiaxial outer epidermal cells.

Nectary: A low ring-shaped disk has been observed in some specimens. It is slightly irregular in shape and composed of small, isodiametric cells (Pl. 2, fig. 5). It may represent a nectary, but the possibility that it represents remnants of the androecium cannot be excluded.

Trichomes: Two different types of trichomes have been observed on the flowers. Simple, apparently unicellular, stiff hairs, are scattered over the surface of the ovary and styles and on the outer and inner surfaces of sepals. The sections indicate that these kinds of trichomes also occur on the filaments, at least in their basal part. The simple hairs are about 0.1 mm long, slightly pointed apically, and of almost equal width from base to apex. (Pl. 4, figs 1-6). Typically there is no evidence of differentiation from base to apex, but in some specimens a basal swelling has been observed (Pl. 4, fig. 6). In SEM, broken trichomes show thick cell walls and the lumen extends for at least part of the length of the trichome. The basal part appears to have a thinner wall which may have collapsed in most specimens.

Peltate, glandular trichomes occur on the ovary surface, mostly on the upper half of the ovary. These trichomes are 0.2-0.3 mm in diameter, circular or slightly elliptical in outline and partly sunken into the ovary wall (Pl. 7, fig. 3). They have a short stalk apparently of several cells and a multicellular peltate shield with cells radiating from the center (Pl. 2, fig. 7; Pl. 4, figs 1-2). The glandular trichomes are typically arranged in three rows. Specimens with four or five rows of glands have also been observed while some specimens have only one or two rows. Specimens with no glands at all are very rare. The number of glandular trichomes in each row varies from one to five or six. Within a single row the glands never occur side by side. The ovary wall of the glandular bands is often depressed either to form circular depressions for each gland or



Text-figure 4. *Esgueiria miraensis* Friis, Pedersen & Crane. Drawing of holotype (S100715, x80).

continuous longitudinal grooves. The glandular trichomes are rarely preserved intact but usually they have burst leaving a black, shining substance that sometimes fills the longitudinal grooves (Pl. 1, figs 1-2; Pl. 2 figs 4, 6).

Stomata: Stomata have been observed on the outer surface of the sepals. They are scattered, irregularly oriented and appear anomocytic (Pl. 4, fig. 5). Since relatively few specimens with intact sepals have been discovered cuticular preparations have not been attempted and stomata have been studied using SEM only.

Esgueiria miraensis Friis, Pedersen & Crane sp. nov. Pl. 8-9; Text-figures 4-5.

Derivation of specific epithet: From the town of Mira in the vicinity of which the fossil flowers were collected.

Specific diagnosis: Ovary and fruit campanulate. Glandular trichomes on the hypanthium and base of styles. Simple trichomes densely spaced on the surface of ovary, calyx, corolla, filaments and styles.

Dimensions: Flower bud: length of petals: 0.75 mm; length of ovary: 0.75 mm; maximum breadth of ovary: 0.5 mm. Flowers: length of sepals: 0.5 mm; breadth of sepals: length of ovary: 0.8-0.95 mm; breadth of ovary: 0.5-0.65 mm. Pollen: Not unequivocally identified.

Holotype: S100715 (From sample Portugal 99; figured Pl. 7, fig.4; Text-fig. 4).

Type locality: Clay pit south of Mira, Portugal.

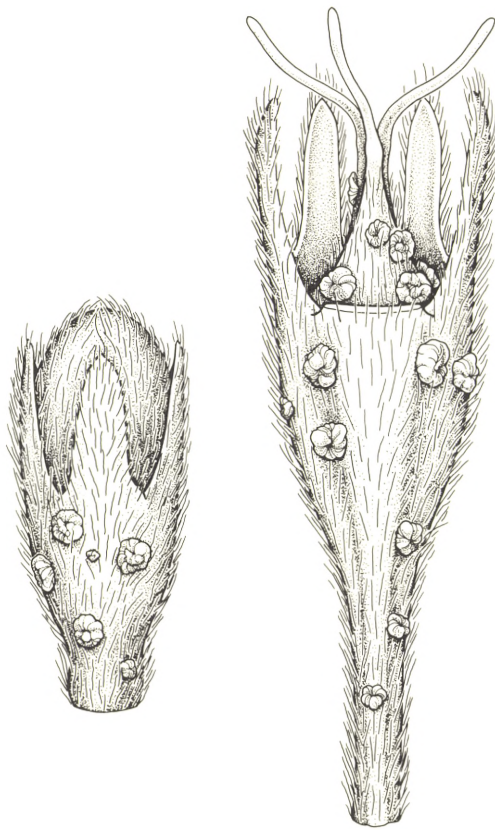
Type stratum: "Argilas de Vargas".

Age: Late Cretaceous (Campanian-Maastrichtian).

Material: 8 specimens (S100715-S100718, S100742-S100743) from samples Portugal 99-100. All specimens preserved as charcoal.

Description and remarks on *Esgueiria miraensis*

All the flowers have been recovered dispersed from the inflorescence axis and there is no indication of inflorescence structure. Although the specimens are scarce, flowers are well-preserved and yield sufficient information for unequivocal assignment to the genus *Esgueiria*. There are also sufficient details to establish that these flowers are distinct from *Esgueiria adenocarpha* at the specific level. The main features distinguishing the flowers from Mira from those of the Esgueira locality are the campanulate shape of the ovary (Pl. 8, figs 1-2; Text-fig. 4), the lack of a nectary disk and presence of glandular trichomes at the base of the styles (Pl. 8, figs 4-7). The Mira flowers also have a more dense indumentum. The fragmentary nature of the fossils caused charging in SEM. None of the material was sec-



Text-figure 5. Reconstructions of *E. miraensis* showing flowers in bud stage (a) and after anthesis with corolla and androecium abscised (b).

tioned and the reconstructions of *E. miraensis* in Text-figure 5 are based mainly on SEM-observations.

Flower: The flowers are epigynous with differentiated calyx and corolla. No pedicel has been observed.

Perianth: The calyx is incompletely preserved in all specimens. It consists of five free, narrowly triangular, sepals with imbricate aestivation. The corolla is typically abscised except in a small fragmentary flower bud (S100715) in which the corolla is partly preserved and shows three petals

(Pl. 8, fig. 3; Text-fig. 4). The petal arrangement is apparently contorted, but since the corolla is incomplete preserved the aestivation cannot be established with certainty.

Androecium: The structure of the androecium is not fully understood, since no complete flower was discovered. The fragmentary flower bud (S100715) shows part of androecium with stamens at two levels (Pl. 8, fig. 3; Text-fig. 4) indicating the presence of two whorls of stamens as demonstrated for *E. adenocarpha*. However, whether each whorl has a full set of stamens cannot be established. Pollen have not been observed *in situ* in the anthers, but numerous dispersed pollen grains have been observed on the surface of the flowers adhering to the trichomes of the ovary and the styler area. Five different pollen types have been identified so far. Most of them are represented by a single or few grains. One pollen type, however, occurs abundantly and is the only type observed in the styler region. These grains are tricolporate, minute, about 15 μm in length and about 7 μm in equatorial diameter. They are tectate with a smooth to finely punctate tectum.

Gynoecium: The ovary is campanulate in outline with an elongated slender base. It is unilocular and has three slender styles, that are free to the base (Pl. 8, figs 1-3). Ovules or seeds have not been observed in any of the specimens.

Nectary: A nectary disk has not been observed in the flowers of *E. miraensis*. The presence of glandular trichomes at the base of the styles (Pl. 8, figs 4-7) may indicate that these functioned as a nectary.

Trichomes: As in *E. adenocarpha*, the indumentum of *E. miraensis* is composed of two different types of trichomes. Simple, apparently unicellular, stiff hairs, are densely spaced over the surface of the ovary and styles, outer and inner surfaces of sepals and petals and on the filaments. The simple trichomes are about 0.1-0.2 mm long, sharply

pointed, and often twisted (Pl. 9, figs 3-4). A basal swelling is observed in some specimens (Pl. 9, fig. 6). Similar twisting is frequent in charcoalfied flowers and is probably a result of the fossilization process. Small verrucate protrusions are observed on the ovary surface between the trichomes (Pl. 9, fig. 5).

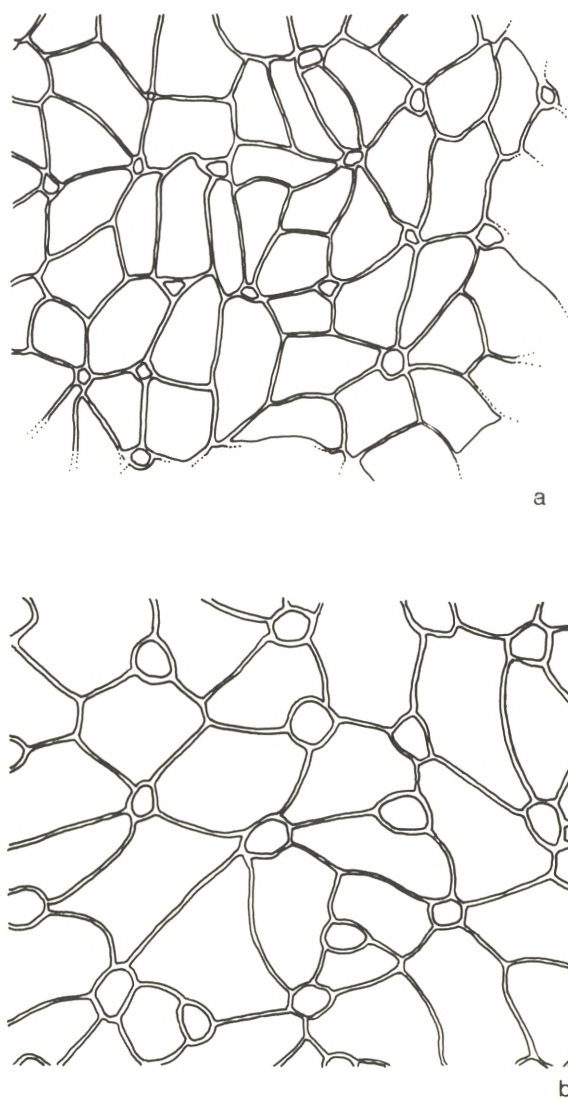
Glandular trichomes have a short stalk and circular, peltate head, about 0.1-1.5 mm in diameter. Cells of the glandular head are radially arranged and the trichomes are morphological very similar to those of *E. adenocarpa*, probably with the same internal structure. They are black and shiny, and occur both on the surface of the hypanthium and at the base of the styles (Pl. 8, figs 3-7; Pl. 9, figs 1-2). On the hypanthium they appear to be arranged in longitudinal rows, but they are not restricted to the upper part of the hypanthium as in *E. adenocarpa*. They appear to be somewhat variable in size with the larger glands occurring near the top of the ovary and the smaller glands near the base.

Associated leaves from Esgueira and Mira

Plate 10, Text-fig. 6a

Angiosperm leaves from the Esgueira locality are difficult to study and in those horizons with larger fragments or complete leaves they are typically densely packed, overlapping, and usually preserved as impressions with no cuticular remains while fragments of leaves and axes with cellular details preserved do occur among the material that has been sieved out of the sediment samples. They are usually very small and provide little information on leaf morphology. Several leaf fragments have trichomes identical to those observed on the fossil flowers and these fragments are believed to belong to the *Esgueiria* plant. Similar leaf fragments have also been identified from the Mira flora.

Leaf fragments from Mira indicate that the leaves were simple, entire margined and with pinnate venation. On the presumed lower surface the midrib is raised and the primary veins are dis-



Text-figure 6. Schematic drawings of epidermal cells and trichome bases of upper surface of fossil leaf (6a – same specimens as shown in Pl. 10, figure 7, S100722) and of extant *Guiera senegalensis* (6b – redrawn from photo in Stace 1965b) (x700).

tinct (Pl. 10, fig. 1). Leaf margins have distinct small drop-shaped depressions, about 0.4 mm long and 0.2 mm wide (Pl. 10, fig. 3) that may represent glandular teeth. The indumentum of the lower surface is dense with simple stiff hairs and peltate glan-

dular trichomes (Pl.10, figs 2,4-6). On the upper surface trichomes consists of simple hairs only and the indumentum is less dense. Epidermal cells of upper and lower leaf surface have straight anticlinal wall. Those of the upper epidermis could be studied in more detail in area with abraded cuticle. The

epidermis cells have three, four or rarely more anticlinal walls that often meet at acute angles (Pl. 10, fig. 6; Text-fig. 6a). The trichomes are surrounded by 5-6 radiating cells, and are so closely spaced that typically the trichome base cells are shared (Pl. 10, figs 5-6).

Discussion

Systematic position of *Esgueiria*

The pentamerous structure of the flowers as well as the triaperturate pollen clearly place *Esgueiria* in the higher (non-magnoliid) dicotyledons. Epigynous flowers characterize several dicotyledonous families and are especially common in members of the subclasses Rosidae and Asteridae. Asterid taxa with inferior ovaries are distinguished from *Esgueiria* primarily by their sympetalous corolla. Within the Rosidae flowers with an inferior ovary and choripetalous corolla occur in the Saxifragales, Myrtales, Cornales, and Araliales. Comparisons with extant taxa included in these orders indicate that the closest modern relatives to *Esgueiria* should be sought among members of the Myrtales, but there is also some agreement with members of the Saxifragales. The main difference between the fossil flowers and members of the Myrtales is the presence of three free styles in the fossil. Free styles are common in members of the Saxifragales, but the fossils differ from these in the low number of ovules and in the single-seeded, indehiscent fruit. Shield-like glandular hairs and simple trichomes occur in both Saxifragales and Myrtales, but the glandular trichomes of the fossils are particularly comparable to those Combretaceae of the Myrtales.

Among the myrtalean families the character combination of small, epigynous flowers with con-

torted corolla, androecium in two whorls, few ovules, apical placentation, and a unilocular, single-seeded fruit occurs only in the family Combretaceae. Morphological and anatomical details of the flowers, particularly features of the indumentum, also support a close relationship between *Esgueiria* and modern Combretaceae. Some members of the Melastomataceae (e.g. *Memecylon* L.) also have a similar combination of features to that seen in the fossil flowers, but they differ in their larger floral size and their distinctive anther morphology and dehiscence. Most other Melastomataceae also have multilocular ovaries and numerous ovules. Multiovulate ovaries also characterize most other myrtalean families, and together with multi-staminate androecia further distinguish many myrtalean taxa from the *Esgueiria* flowers (e.g. Ronse Decraene and Smets 1991).

The Combretaceae is a pantropical family of trees and shrubs, which are particularly diverse in tropical and subtropical regions of Africa. The family includes about 550-600 species in 19 genera (Stace 1965a, Exell and Stace 1966) classified into two subfamilies. The Strephonematoideae includes the single genus, *Strephonema*, with semi-superior ovary while the Combretoideae includes the remaining genera that all have inferior ovaries (Engler and Diels 1899, Exell 1931, Stace 1965a). The

separation of *Strephonema* from the other genera of the Combretaceae is also supported by wood data (Vliet 1979), pollen structure (Patel, Skvarla and Raven 1984) and epidermal characters (Stace 1965a). The genera of the Combretoideae are separated into three tribes: Combreteae (*Calopyxis*, *Calycopteris*, *Combretum*, *Guiera*, *Meiostemon*, *Quisqualis*, *Thiloa*), Terminalieae (*Anogeissus*, *Buchenavia*, *Bucida*, *Conocarpus*, *Finetia*, *Pteleopsis*, *Terminalia*) and Laguncularieae (*Dansiea*, *Laguncularia*, *Lumnitzera*, *Macropteranthes*) (Engler and Diels 1899, Exell 1931, Stace 1965a, Exell and Stace 1966, Vollesen 1981). Floral and leaf characters of modern Combretaceae are briefly summarized below and compared to those of the fossil material.

Inflorescence structure: Flowers are typically borne in elongated spikes or racemes, or in dense globular heads. In the fossil material only fragments of inflorescences are preserved and a detailed comparison with modern inflorescences is therefore not possible. However, the fossil inflorescences were clearly densely packed and perhaps similar to the subcapitate inflorescences seen in genera such as *Guiera*.

Flower: Flowers are small, bisexual or more rarely unisexual, actinomorphic or slightly zygomorphic. Except for *Strephonema* they are all epigynous as in the fossil flowers.

Perianth: Perianth is pentamerous, rarely tetramerous or with a larger number of parts. The calyx is borne directly on top of the ovary in some taxa or it is borne on an extension of the hypanthium that forms a basal tube (Kelchröhre of Brandis, 1893). Calyx lobes are free or fused at the base. Aestivation of the calyx is valvate or imbricate. Tube and calyx lobes are deciduous in many taxa, but persistent calyx as occur in the fossil flowers is present in Laguncularieae and some Combreteae (*Bucida*, *Calycopteris*, *Guiera*). The corolla is present in *Strephonema* and members of the Laguncularieae,

some Combreteae (*Combretum*, *Guiera*, *Meiostemon*, *Quisqualis*) and one member of Terminalieae (*Pteleopsis*) but is otherwise lacking. Aestivation of corolla is valvate, imbricate or contorted.

Androecium: Stamens are usually twice as many as sepals, arranged in two whorls in an obdiplostemonous arrangement (Brandis 1893). Stamens of the outer whorl may be reduced in number. Stamen filaments are typically inflexed in the bud, but at anthesis they become exerted. Anthers are small, dorsifixed and versatile. They are tetrasporangiate and dithecal, opening by longitudinal slits. Pollen grains are tricolporate or heterocolpate and sometimes syncolpate. They are tectate and surface sculpture varies from finely punctate to rugulate, striate and echinate. Pollen of *Strephonema* differs from those of other Combretaceae in their reticulate exine surface (Patel, Skvarla and Raven 1984).

Gynoecium: The gynoecium is composed of three, more rarely two, four or five, fused carpels (e.g. Cronquist 1981). All taxa have a single style in contrast to the three free styles that characterize the fossil flowers. In all other gynoecium characters, however, there is good agreement between the fossil material and modern Combretaceae. The ovary is unilocular typically with 2-6 anatropous ovules that are pendant from the apex. Fruits are one-seeded, usually indehiscent with a leathery or woody pericarp. They typically enlarge considerably after fertilization and become distinctly winged in many taxa. In taxa with enlarged winged fruits the infructescence axis usually elongates. Wings are not developed in all taxa and the fruits of *Guiera* remain densely packed in the infructescence (Exell 1962) as is observed in the fossil material.

Nectary: Nectaries occur in many combretaceous flowers and show a great variety in both form and position. They may be inserted between androecium and gynoecium or connected with the hypanthium cup.

Trichomes: Distinctive trichomes occur in all members of the Combretaceae and are of considerable taxonomic importance (Stace 1965a, 1969a, b, 1973, 1980a, b). Stace (1965a) distinguished three main trichome types: 1) Non-glandular trichomes are typically unicellular stiff hairs with very thick cell walls and a swollen base with a conical internal compartment. This trichome type (“combretaceous hairs”) is, with a few exceptions, known in all Combretaceae (Stace 1965a). Non-compartment hairs with thinner cell wall do also occur in some species, but are rare. Both species of *Esgueiria* have simple, stiff hairs with thick cell walls. Swollen trichome bases have also been observed in the fossil material indicating that they are comparted. 2) Stalked glands have a multicellular head born on a multicellular stalk. The head is typically only slightly broader than the stalk. This type of trichomes has not been observed in the fossil specimens. 3) Scale glands have a peltate and scale-like, multicellular head that is much broader than the stalk. The stalk is unicellular or multicellular and may be very short. These scale glands occur only in *Combretum*, *Guiera*, *Thiloa*, and *Calycopteris* and are very similar in general structure to those of the *Esgueiria* flowers. In particular scales of *Guiera* and some *Combretum* species show great similarity with those of the fossils in having rather few, larger cells comprising the peltate head which are arranged in a radiating pattern. In *Guiera* the scales may be sunken and “filled with a dark glutinous substance secreted between cell-plate and the raised cuticular membrane” (Stace 1965a, p. 239). This glutinous substance may be equivalent to the black, shiny substance observed in the fossil flowers.

Leaves: The leaves of all Combretaceae are entire-margined with pinnate venation. Several epidermal characters, such as the shape of epidermal cells, degree of undulation of anticlinal walls and stomatal configuration are of great systematic value (e.g. Stace 1965a, 1981). Stomata are basically anomocytic, except for *Strephonema* that has paracytic stomata (Stace 1965a). Anticlinal walls of epi-

dermal cells are undulate or straight, and their number per cell varies. The epidermal characters observed for the fossil leaf fragments are very similar to those described for *Guiera*. Stace (1965a) emphasized that in this genus the upper epidermal cells are distinct with straight anticlinal walls, that are low in number and often meet at acute angles (Stace 1965a). An illustration of *Guiera* (Pl.4D in Stace 1965b) shows three- to four-sided cells and hair bases very similar to those of the fossils (Text-fig 6b).

The characters of the fossil flowers indicate close relationship to modern members of the Combretaceae. Within the Combretaceae the fossils are most similar to the genus *Guiera* of the tribe Combretae. This is also supported by the characters of associated leaf fragments. A significant difference between the fossil flowers and the modern forms is the presence of three free styles in *Esgueiria* in contrast to the single style of all modern Combretaceae. Carpel number in Combretaceae is, however, typically three as in *Esgueiria*, although other numbers also occur. The position of free styles may place *Esgueiria* close to the base of the Combretaceae, and perhaps more specifically close to the base of the tribe Combretae. The presence of both calyx and corolla and the absence of a hypanthium cup also support a relatively basal position with respect to extant Combretaceae.

If our interpretation of relationship between the fossil flowers and the Combretaceae is correct and if the systematic position of the Combretaceae in the Myrtales is also correct then the single style must have developed independently in the Myrtales several times. A more detailed evaluation of this problem would require information from other organs of the fossil plants such as fossil wood, complete leaves and phyllotaxy of leaves.

Fossil history of the Combretaceae

Fossil wood and leaves assigned to the Combretaceae occur abundantly in the fossil record

while reproductive organs (flowers, fruits, infructescences, dispersed pollen) are more rare. The earliest record of the family is leaves of *Terminaliphyllum rectinerve* Velenovský from the Cenomanian of Czechoslovakia (Velenovský 1889) and leaves of *Conocarpites formosus* Berry from the Cenomanian-Turonian Tuscaloosa formation, Alabama, USA (Berry 1919a). None of this Cretaceous leaf material has been reinvestigated and the accuracy of these determinations, based solely on major morphological features, is uncertain. Another Cretaceous report of Combretaceae is wood described as *Terminalioxylon intermedium* (Kräusel) Mädél-Angeliwewa & Müller-Stoll from Upper Cretaceous sediments of Sudan (Mädél-Angeliwewa and Müller-Stoll 1973). All other reports of Combretaceae are from Tertiary and Quaternary strata. Fossil wood is common from Tertiary deposits in tropical regions in Asia, Africa and South America while numerous fossil leaves assigned to the Combretaceae have been recorded from the Tertiary floras of Europe and North and South America. Fossil taxa assigned to the Combretaceae are briefly reviewed below.

Flowers: *Combretanthites eocenica* Berry (1913) was based on a single flower discovered from Eocene sediments in Tennessee, USA. It is preserved as an impression fossil, but several morphological details are clear. The flower was described as pedunculate, tetramerous or pentamerous with a single style and 12 stamens. The number of stamens is difficult to establish from the figures and may have been misinterpreted. There are several characters that do not agree with the assignment of the flower to Combretaceae. The flower appears to be hypogynous in contrast to the epigynous flowers of modern Combretaceae, and further differs in its long pedicel and in the shape of the anthers. Pedicellate and hypogynous flowers with long exerted stamens characterize legume flowers of the tribe Mimosoideae and *Combretanthites eocenica* shows strong similarities with the fossil flowers of *Protomimosoidea buchananensis* Crepet and Taylor (1986) also described from

Eocene deposits of Tennessee. The mimosoid affinity of *Protomimosoidea buchananensis* is well documented and according to W.L. Crepet (pers. comm. 1991) it is most probable that *Combretanthites eocenica* also belongs to the Mimosoideae.

Fruits: Several fruits have been assigned to modern genera of the Combretaceae. The systematic assignment of an infructescence fragment and dispersed fruits from the Miocene flora of Herzogenrath, Lower Rhine basin, Germany, described as *Conocarpus tertiaria* Menzel (1913) is not fully documented according to Kirchheimer (1957). The fossil species, *Terminalia vera* Berry (1926) is based on two-winged fruits recorded from several Eocene localities in Tennessee and Kentucky. These fruits were associated by Berry (1926) with fossil leaves known from the same strata and described as *Terminalia lesleyana* (Lesquereux) Berry. Winged fruits assigned to *Terminalia* have also been reported from the late Tertiary of Bolivia (Berry 1919b). The fossil material described by Berry has not been reinvestigated. Winged fruits ascribed to the Combretaceae have also been reported from the Late Cretaceous-Early Tertiary Deccan Intertrappean beds of Mohgaonkalan, India by Mistri & Kapgate (1990). The systematic position of this material, however, is not fully documented. Mistra and Kapgate (1990) stated that the fossil fruits “show more similarity to the tropical family Combretaceae (*Anogeisus* and *Gyrocarpus*)” and stressed the similarity with the latter by establishing a new genus, *Gyrocarpusocarpon*, for the fossil fruits. *Gyrocarpus*, however, is usually assigned to the magnoliid family Hernandiaceae.

Pollen: According to Muller (1981) the earliest well-documented pollen of the Combretaceae is *Terminalia*-type pollen described by Salard-Cheboldaeff (1978) from the Upper Eocene to Lower Miocene of Cameroon as *Heterocolpites laevigatus* Salard Cheboldaeff. Leopold (1969) reported three different types of Combretaceae pollen from the

Miocene of the Marshall Islands that she assigned to *Terminalia*, *Lumnitzera* and cf. *Combretum*.

Leaves: A large number of fossil leaves have been assigned to the Combretaceae. Most of them were assigned to modern genera, but several extinct genera have also been established to accommodate fossil leaves with combretaceous-like morphology. Modern genera identified in the fossil record include *Bucida* L. (Berry 1921), *Combretum* L. (Berry 1916, 1924a, b, 1935, 1936), *Conocarpus* L. (Berry 1924a, 1925), *Laguncularia* Gaertner (Berry 1916, 1924a), and *Terminalia* L. (Unger 1847, Ettingshausen 1853, Berry 1924a, 1935, Weyland 1943, Kirchheimer 1957). *Combretiphyllum* Menzel (Menzel 1909), *Terminaliophyllum* Geyler (1887), and *Terminaliphyllum* Velenovský (1889) were established to accommodate combretaceous-like leaves that could not be included in any modern genus.

All fossil leaves assigned to the Combretaceae have been determined solely on the basis of morphological similarities, and epidermal characters have not been described for any of this fossil material. Leaves of modern Combretaceae are entire-margined, but share gross morphological characters with a number of other tropical and subtropical angiosperm groups and many of the determinations may be incorrect. All modern members of the family have distinctive epidermal features, including the presence of so called combretaceous hairs (Stace 1965a), and reinvestigation of the leaf fossils using

cuticular analysis will therefore be crucial for testing the validity of the current systematic determinations.

Wood: Fossil wood assigned to the Combretaceae is very common and typically referred to form genera. *Terminalioxylon* Schönfeld (1947) was established on the basis of fossil wood from the Tertiary of Columbia, South America. A detailed study of *Terminalioxylon* wood was later undertaken by Mädél-Angeliewa and Müller-Stoll (1973). They indicated that the wood of *Terminalioxylon* shared features known not only in modern *Terminalia*, but also in *Combretum* and *Anogeissus* Wall. ex Guillem. & Perr. They gave a survey of *Terminalioxylon* species with diagnostic characters, distribution and references to original descriptions. An updated list of *Terminalioxylon* species was later given by Prasad (1988). A total of about 40 species have been described from Africa (Algeria, Egypt, Ethiopia, Libya, Mali, Somalia, Sudan, Tunisia), South America (Brazil, Columbia) and Asia (Java, Sumatra, Vietnam, Indonesia, Burma, India). The earliest record is *T. intermedium* (Kräusel) Mädél-Angeliewa and Müller-Stoll (1973) from the Late Cretaceous of Sudan. *Combretacinium* Felix (1894) is a fossil wood from Caucasus, USSR, and includes a single species, *Combretacinium quisqualoides* Felix. According to the reevaluation of fossil combretaceous wood by Mädél-Angeliewa and Müller-Stoll (1973) this species should be excluded from the family.

Conclusion

The discovery of fossil flowers from the Late Cretaceous of Portugal with combretaceous characters indicates a long geological history for the family. The close similarity of the fossil flowers to members of the tribe Combreteae, and to the genus *Gueira* in particular, may have importance for understanding present biogeographic patterns. The tribe Combreteae has many species in Africa today and *Gueira*

is now restricted to West Africa. Close relationship between a European Cretaceous taxon and modern plants with predominantly gondwanan distribution has previously been demonstrated for *Silvianthemum suecicum* from the Santonian/Campanian of Scania which show close similarity to southern hemisphere members of the Escalloniaceae (Friis 1990).

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Plates 1-10

PLATE 1

Esgueiria adenocarpa Friis, Pedersen & Crane gen et sp. nov., from the Late Cretaceous of Esgueira, Portugal. Sample Portugal 85. Figures 1, 4-12 SEM-micrographs; figures 2-3 reflected lightmicrographs.

1. Flower bud; holotype (S100639, x30).
- 2-4. Flower with several glandular grooves. Same specimens shown in reflected light and in SEM (S100650, x30).
5. Small fragmented flower bud with slightly curved ovary (S100673, x30).
6. Small flower with parts of perianth and styles preserved (S100689, x30).
7. Flower bud with sepals completely covering petals (S100687, x75).
8. Larger flower with short pedicel showing prophyll (S100643, x30).
9. Flower with sepals preserved (S100676, x30).
10. Detail of holotype showing calyx and corolla (S100639, x75).
11. Fragment of inflorescence with many compressed flowers (S100674, x20).
12. Detail of inflorescence showing apical part of a flower with sepals and long stylar branches (S100674, x110).

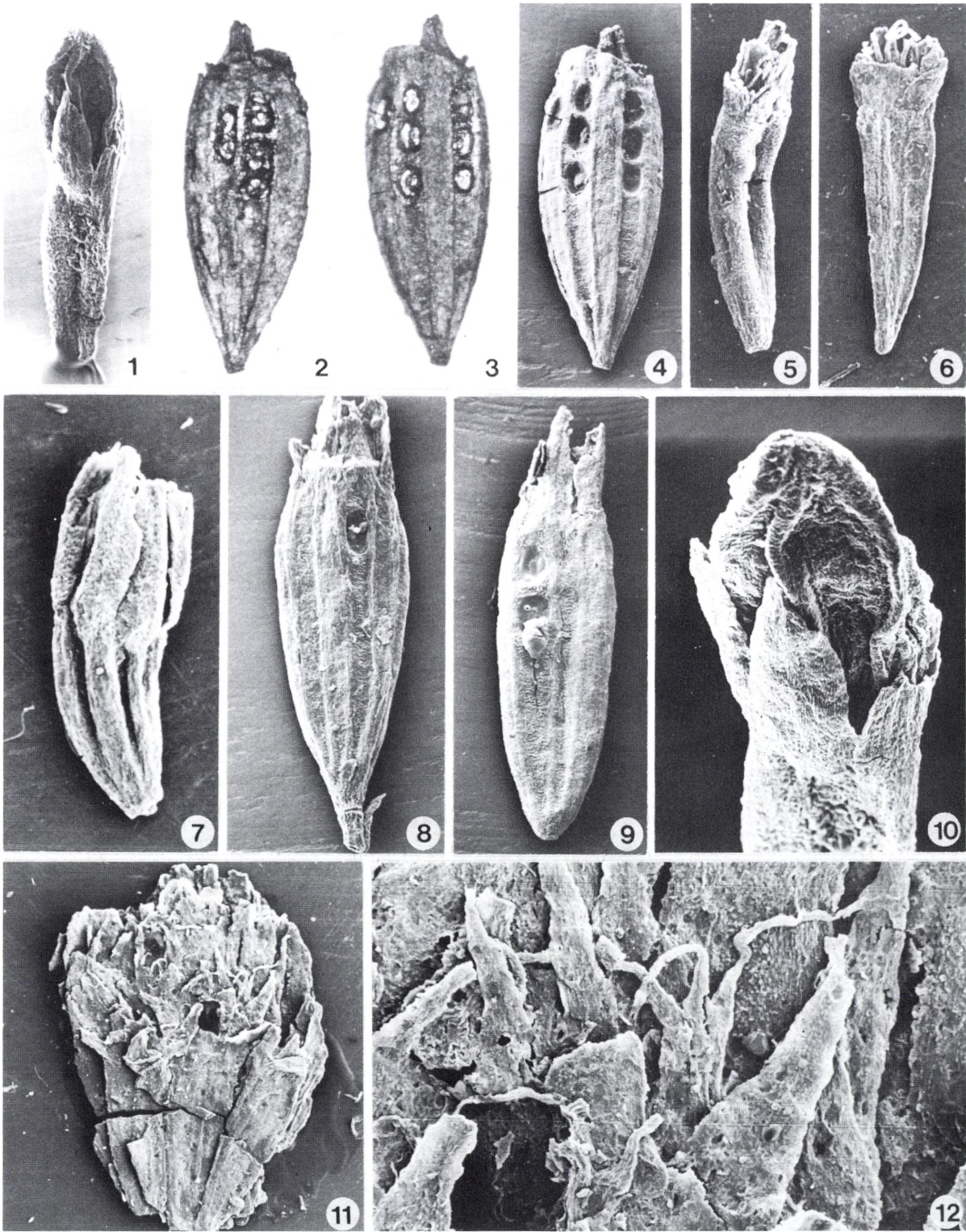


PLATE 2

Esgueiria adenocarpha Friis, Pedersen & Crane gen. et sp. nov., from the Late Cretaceous of Esgueira, Portugal. SEM-micrographs.

1. Apical part of flower with calyx partly preserved (S100644, x45).
2. Apical part of flower with remains of calyx (S100676, x77).
3. Apical part of flower showing compressed scale-like glandular trichomes and base of styles (S100651, x50).
4. Apical part of flower showing position of glandular trichomes and base of the three styles (S100649, x50).
5. Detail of flower showing basal part of styles surrounded by nectary-like ring (arrow) (S100682, x150).
6. Surface of ovary showing a shiny substance remaining after glandular trichomes have burst (S100650, x85).
7. Surface of ovary with intact glandular trichomes (S100646, x110).

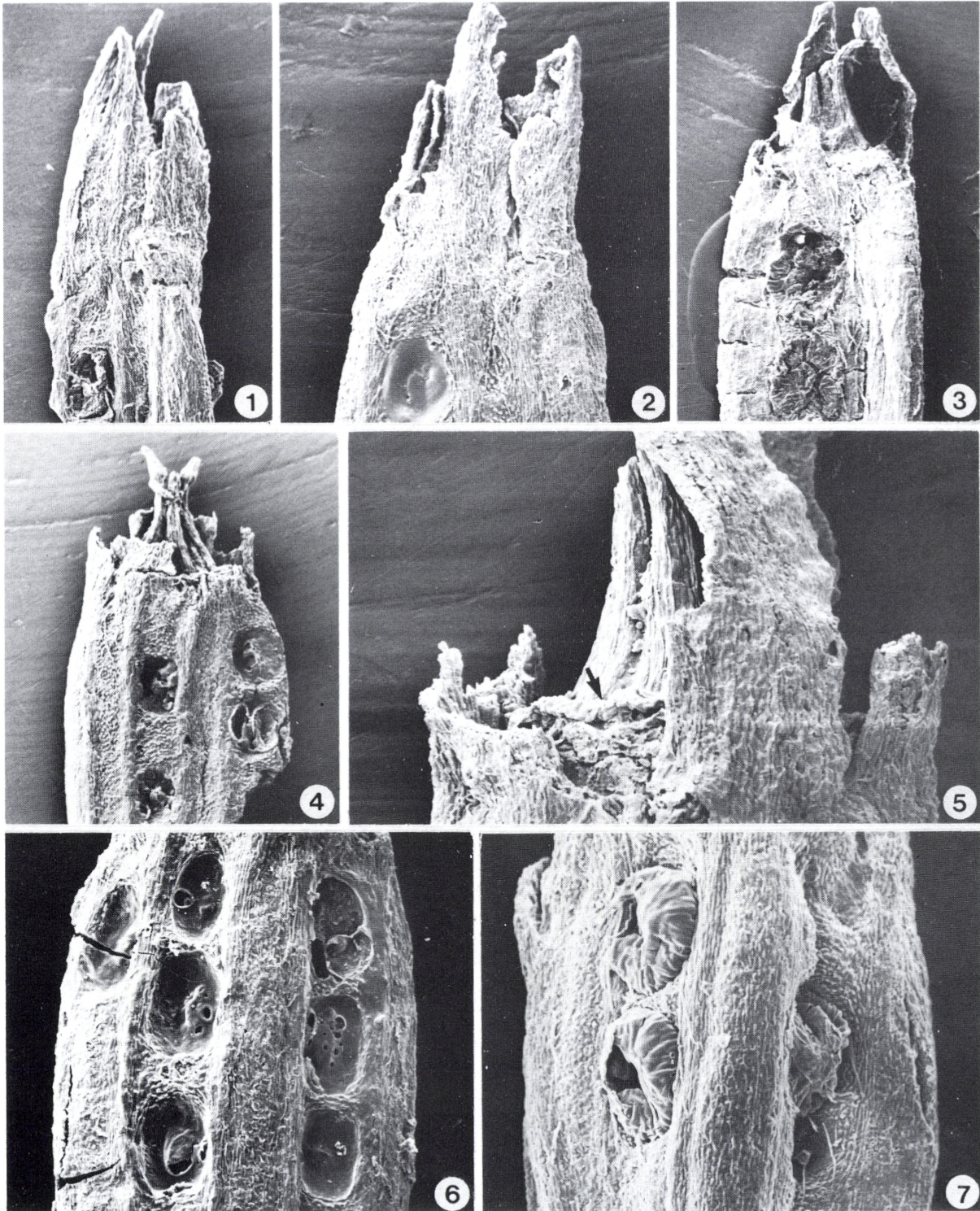


PLATE 3

Esgueiria adenocarpa Friis, Pedersen & Crane gen. et sp. nov., from the Late Cretaceous of Esgueira, Portugal. SEM-micrographs.

1. Apical part of flower with three intact sepals and styles (S100690, x100).
2. Apical part of flower showing styles and filaments (S100689, x125).
3. Detail of figure 1 showing style with cluster of pollen attached (S100690, x750).
4. Detail of figure 1 with single grain on style (S100690, x750).
5. Details of pollen grains from figure 3 (S100690, x2300).
6. Pollen grain from inflorescence showing infolded colpi and foveolate tectum (S100674, x4000).

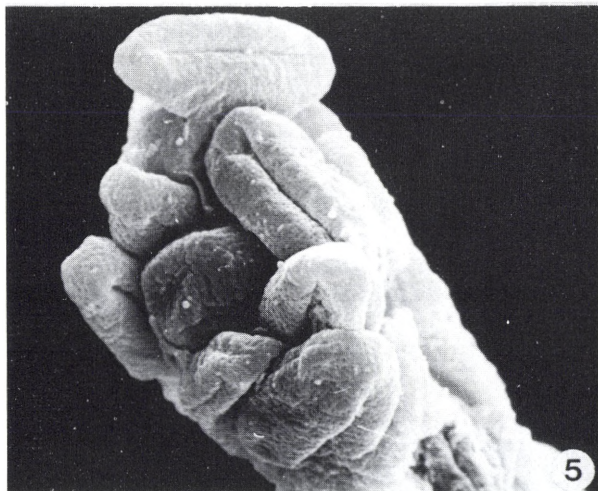
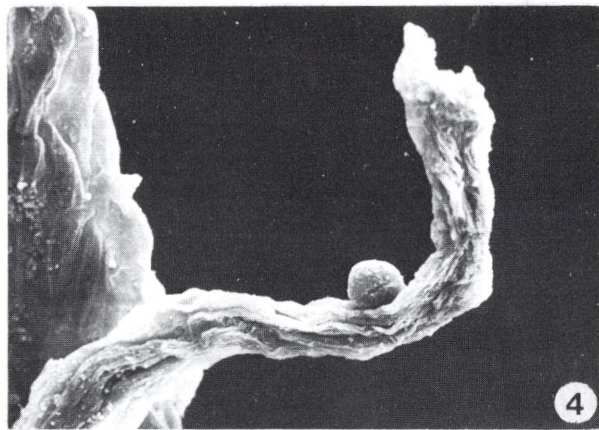
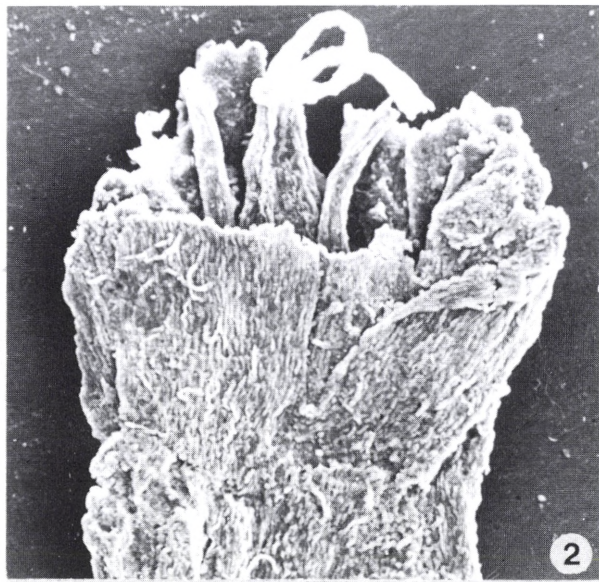
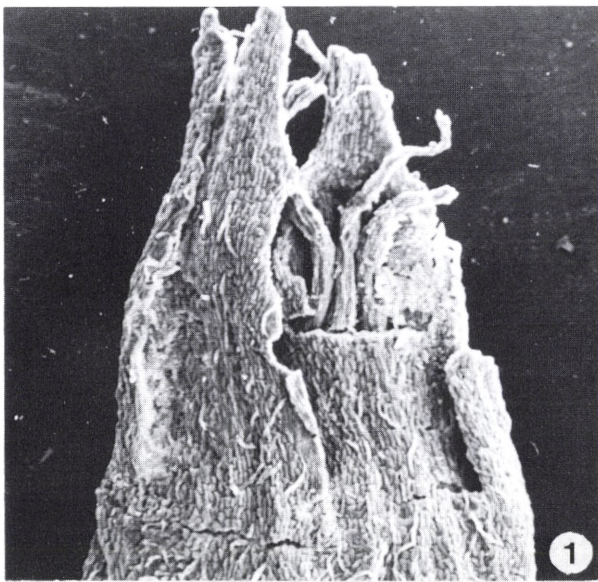


PLATE 4

Esgueiria adenocarpa Friis, Pedersen & Crane gen. et sp. nov., from the Late Cretaceous of Esgueira, Portugal. SEM-micrographs.

1. Detail of compressed glandular trichome showing scale-like shape (S100651, x160).
2. Detail of glandular trichome in depression in ovary wall (S100681, x210).
3. Detail of simple trichomes and verrucate ovary surface within a glandular groove (S100644, x400).
4. Non-glandular band of ovary with elongated cells and simple trichomes (S100644, x500).
5. Outer surface of sepal showing stomata and simple trichomes (S100690, x600).
6. Detail of simple trichomes on ovary showing basal swellings (S100676, x1400).

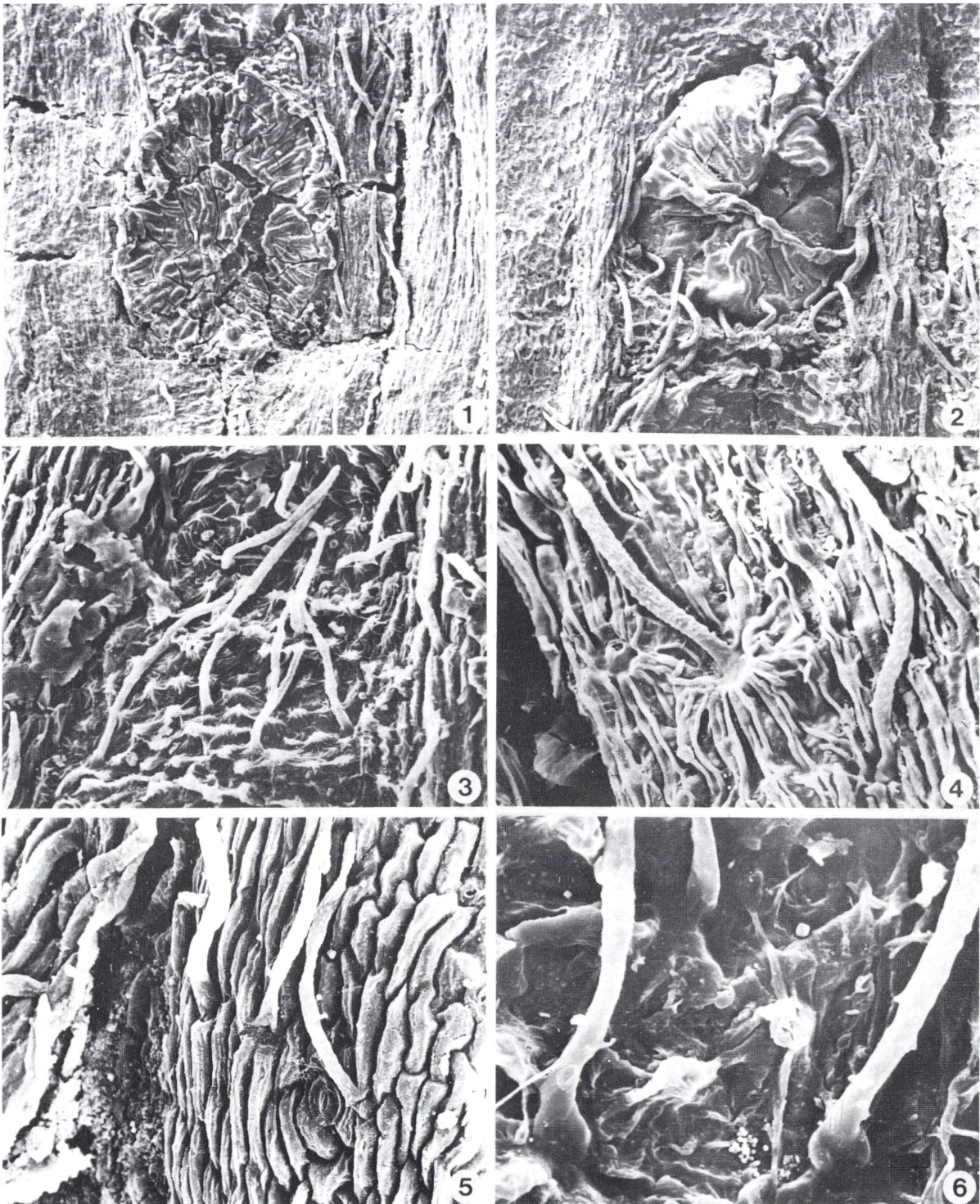


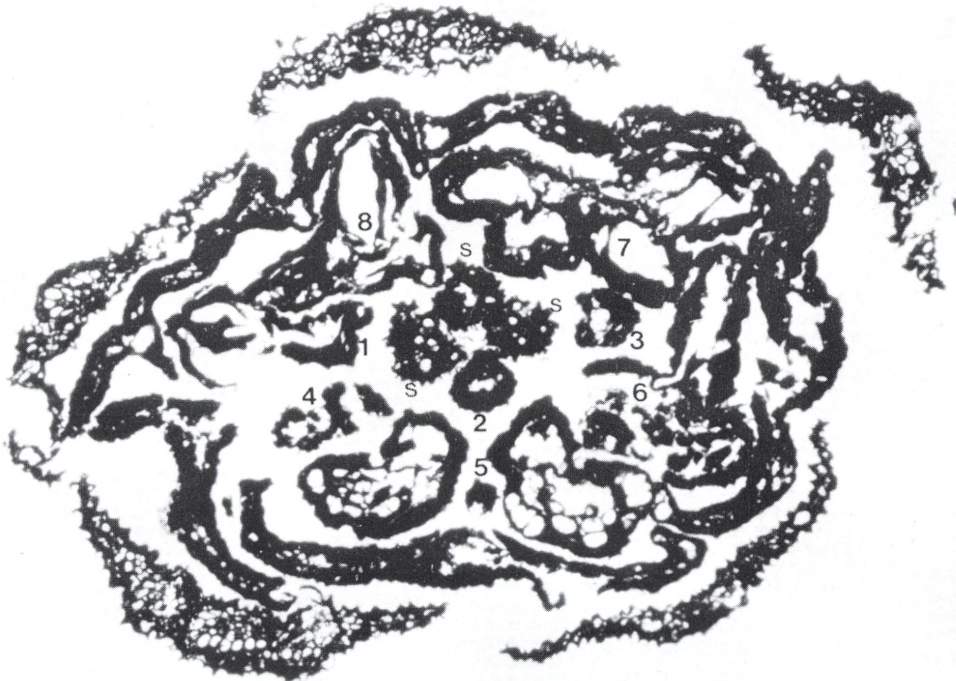
PLATE 5

Esgueiria adenocarpa Friis, Pedersen & Crane gen. et sp. nov., from the Late Cretaceous of Esgueira, Portugal. Transverse sections of flower bud. Transmitted light micrographs (S100660, x250).

1. Section in upper part of flower bud (about 0.285 mm from apex) showing three styles (s), three filaments from first whorls of stamens (1-3) and remnants of four out of the five anthers of the second whorl of stamens (S100660-96; corresponds to text-figure 1 k).
2. Section further down in the flower bud (about 0.360 mm from apex) showing remains of all 8 stamens (1-8). The sagittate shape of the anthers is illustrated in stamen no 5 (S100660-121; corresponds to text-figure 1 m).



1

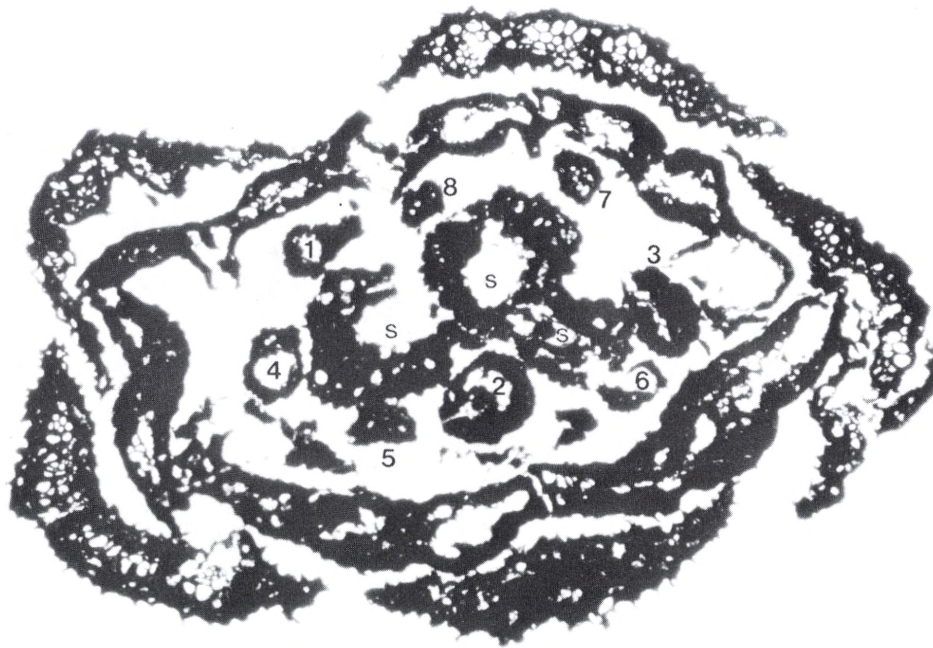


2

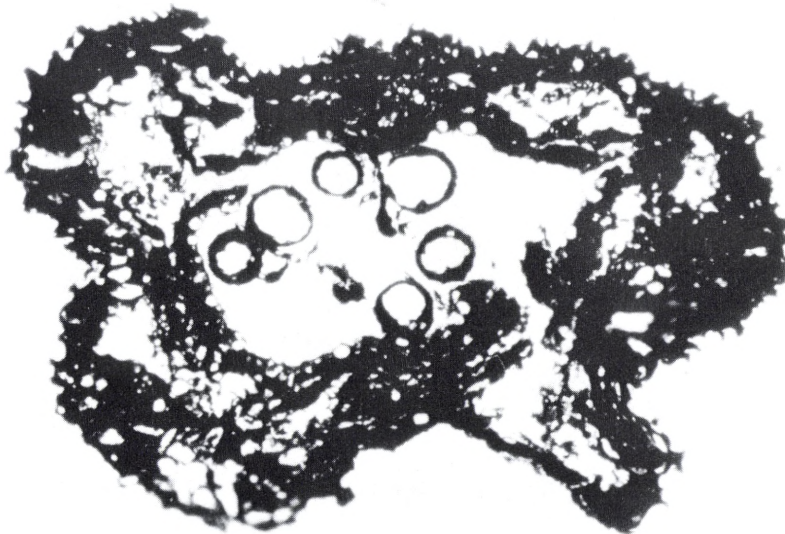
PLATE 6

Esgueiria adenocarpa Friis, Pedersen & Crane gen. et sp. nov., from the Late Cretaceous of Esgueira, Portugal. Transverse sections of flower bud. Transmitted light micrographs (S100660, x250).

1. Section of flower bud near floral base (about 0.465 mm from apex) showing base of the three styles and filaments of the eight stamens (1-8) (S100660-156; corresponds approximately to Text-figure 1 p).
2. Section through upper part of ovary (about 0.580 mm from apex) showing one locule and 6 ovules (?) (S100660-194; corresponds to Text-figure 1 q).



1

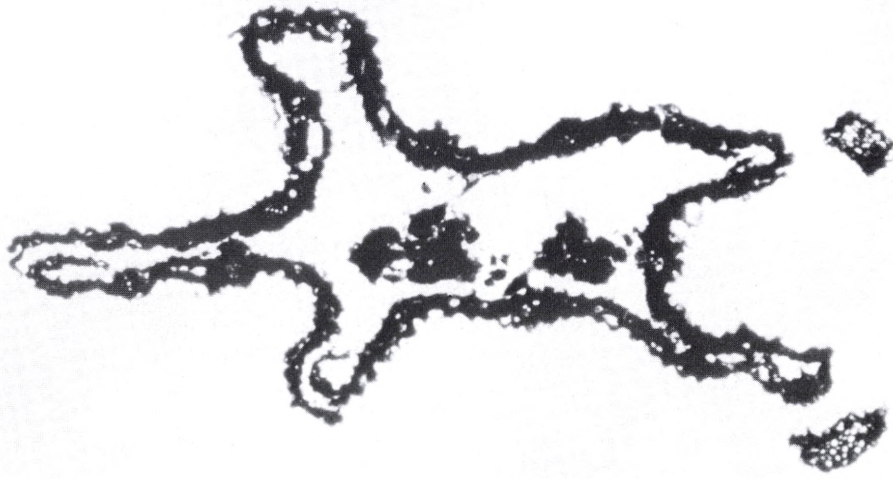


2

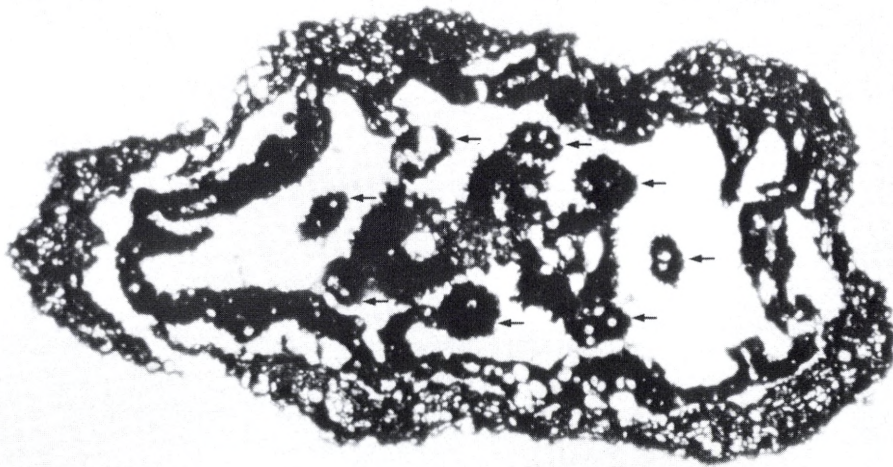
PLATE 7

Esgueiria adenocarpa Friis, Pedersen & Crane gen. et sp. nov., from the Late Cretaceous of Esgueira, Portugal. Transverse sections of flower bud. Transmitted light micrographs. (S100647, x250).

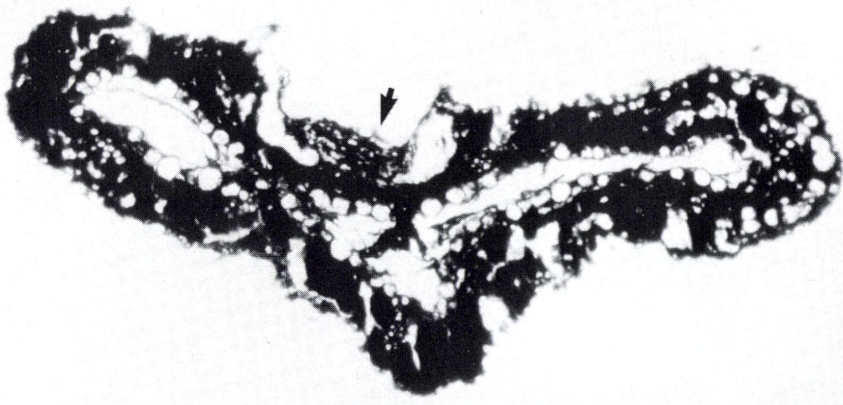
1. Section through upper part of flower (about 0.165 mm from apex) showing the contorted aestivation of corolla and remains of uppermost stamen (S100647-56).
2. Section through flower near base of styles (about 0.640 mm from apex) showing filaments of eight stamens (arrows) surrounding the three styles (S100647-213).
3. Section through upper part of ovary (about 0.875 mm from apex) showing ovary wall with cuboidal cells of inner epidermis and glandular trichome in depression in ovary wall (arrow) (S100647-292).



1



2



3

PLATE 8

Esgueiria miraensis Friis, Pedersen & Crane sp. nov., from the Late Cretaceous of Mira, Portugal. SEM-micrographs.

1. Flower with remnants of narrow calyx lobes preserved (S100717, x30).
2. Fragment of flower without remnants of perianth (S100718, x30).
3. Holotype. Apical part showing three free styles, remnants of androecium and remnants of corolla (S100715, x80).
- 4-5. Apical part of flower showing styles with simple and glandular trichomes (4: S100716, x80; 5: S100617, x80)
- 6-7. Details of trichomes at basal part of styles (6: S100718, x400; 7: S100717, x360).

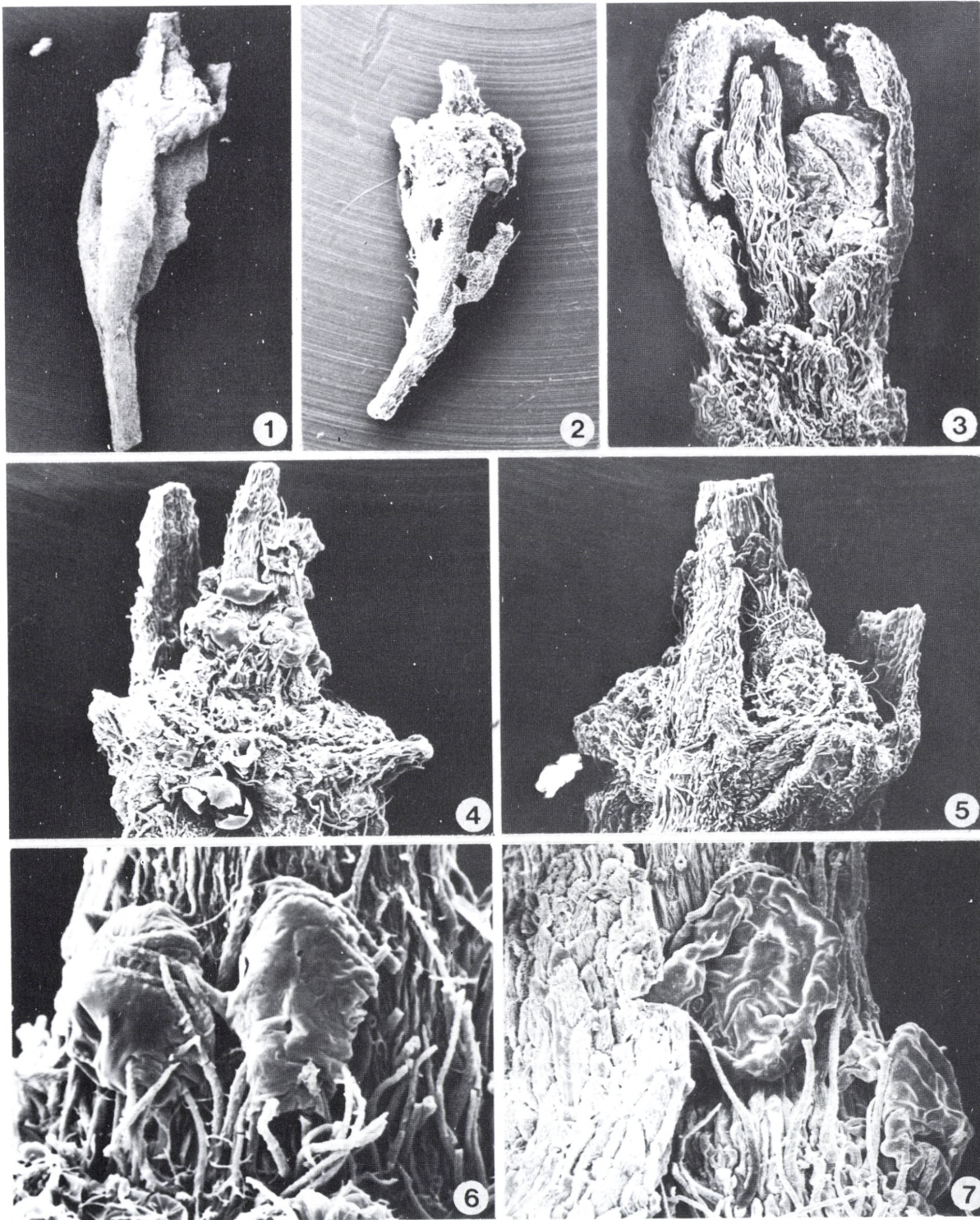


PLATE 9

Esgueiria miraensis Friis, Pedersen & Crane sp. nov., from the Late Cretaceous of Mira, Portugal. SEM-micrographs.

- 1-2. Surface of ovary with simple and glandular trichomes (1: S100716, x180; 2: S100718, x170).
3. Detail of ovary showing simple trichomes (S100718, x780).
4. Basal part of ovary showing stiff simple trichomes (S1007718, x250).
5. Abraded surface of ovary showing hair bases and verrucae (S100716, x100).
6. Detail of ovary surface showing one swollen trichome base (S100717, x100).

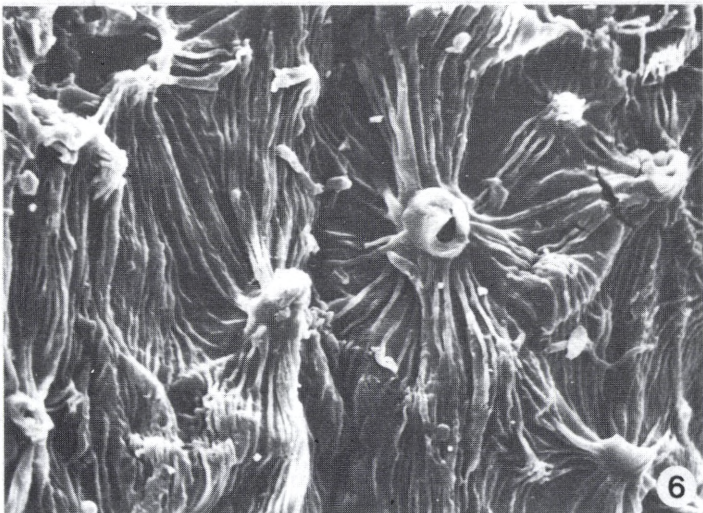
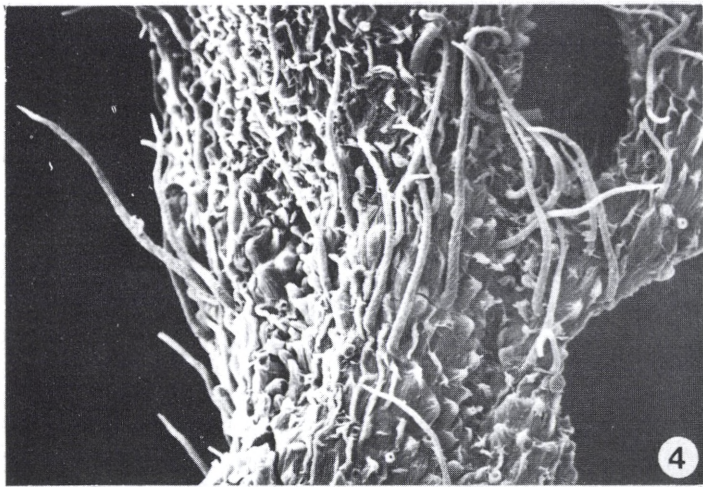
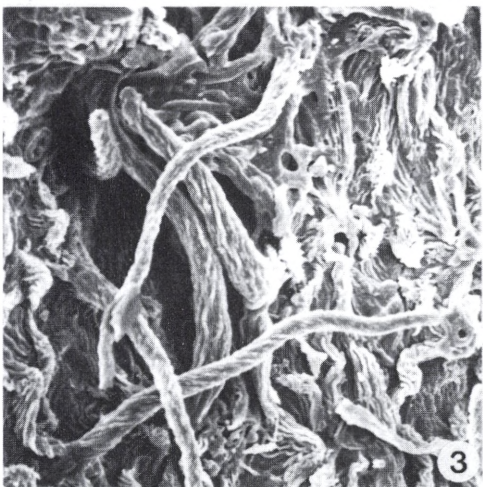
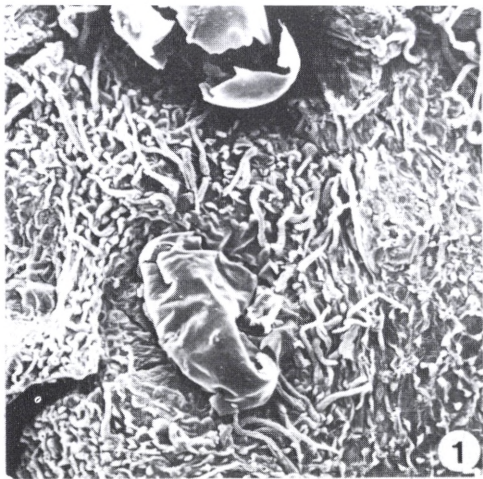
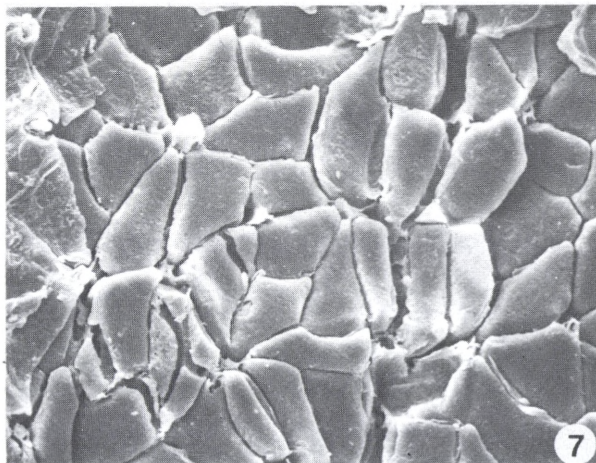
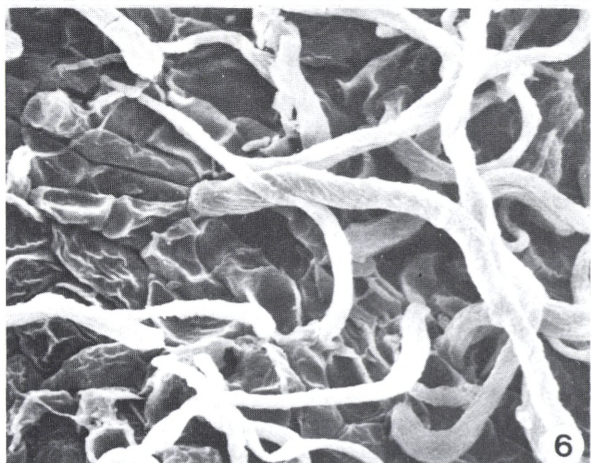
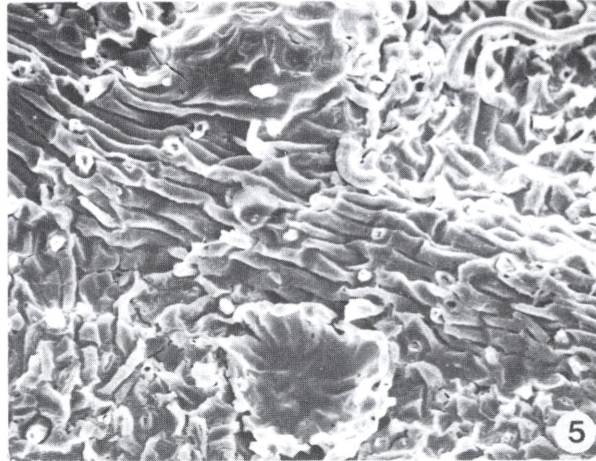
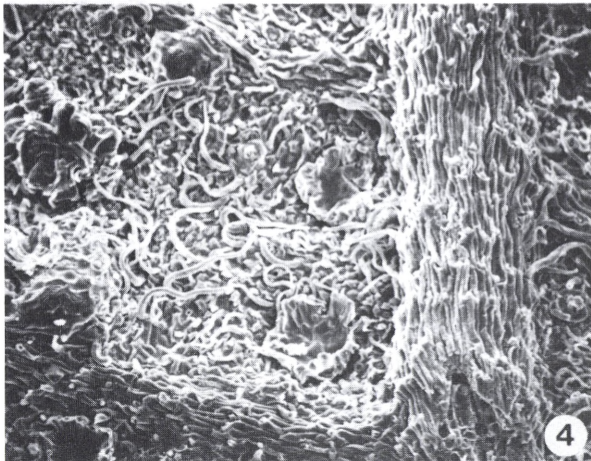
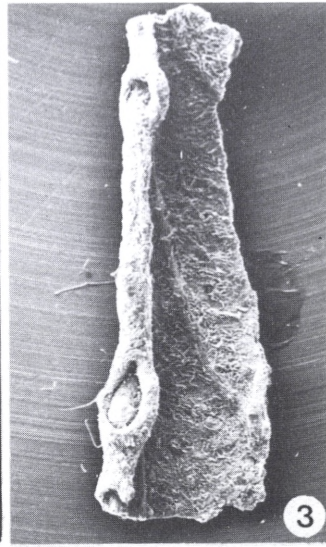
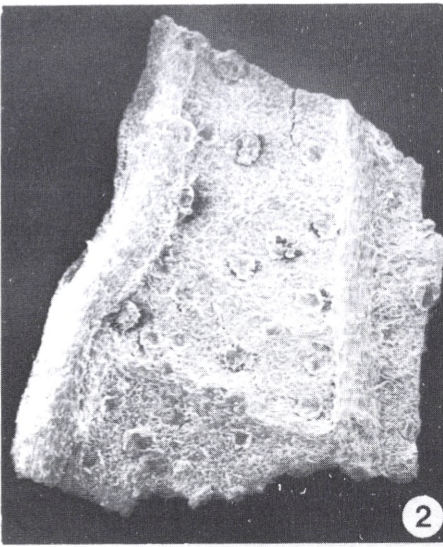
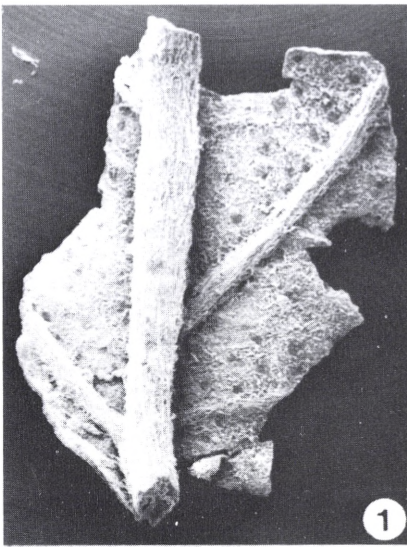


PLATE 10

Fossil leaves associated with *Esgueiria miraensis* Friis, Pedersen & Crane sp. nov. from Mira, Portugal. SEM micrographs.

1. Lower surface of leaf fragment showing strongly raised mid-rib and dense indumentum (S100720, x25).
2. Lower surface of leaf fragment showing distribution of trichomes and to the left entire leaf margin (S100719, x50).
3. Lower surface of leaf fragment showing inroled margin with marginal depressions (S100723, x25).
4. Detail of lower surface showing dense indumentum with simple and glandular trichomes (S100719, x185).
5. Detail of lower surface of leaf showing elongated cells over vein, bases of simple trichomes and glandular trichomes (S100719, x400).
6. Details of lower surface of leaf showing densely spaced simple trichomes and straight anticlinal walls of lower epidermis (S100720, x1000).
7. Details of upper surface of leaf in an area with cuticle abraded showing epidermis cells with straight anticlinal walls and bases of simple trichomes (S100722, x700).



Title. – Titles should be kept as short as possible and with an emphasis on words useful for indexing and information retrieval.

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