Taxodiaceous conifers from the Upper Cretaceous of Sweden

By VIJAYALAKSHMI SRINIVASAN
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Abstract

A rich fossil assemblage of taxodiaceous conifers, comprising numerous leafy shoots, few seed cones, pollen cones and seeds has been recovered from Upper Cretaceous strata of Scania, southern Sweden. Based on differences in external leaf morphology and epidermal characters, three new genera *Elatidopsis* gen. nov., *Paracryptomeria* gen. nov. and *Quasisequoia* gen. nov. have been distinguished. The first two genera include one species each, while the third genus includes four. Although the species are mainly based on foliage shoots, *Quasisequoia florinii* gen. et sp. nov. includes seed cones as well. Leaf cuticle micromorphology of most species has been studied with light microscopy and scanning electron microscopy. The lanceolate, bifacially flattened, epistomatic leaves of *Elatidopsis* are compared with extinct *Elatides* Heer, while the rhomboidal to triangular, abaxially keeled and amphistomatic leaves of *Paracryptomeria* are compared with modern *Cryptomeria*. The elliptical to rhomboidal, appressed, amphistomatic leaves and ovoid seed cones of *Quasisequoia* are compared with extant *Sequoiadendron* and *Sequoia*. Comparisons are also made with relevant, fossil genera of the Taxodiaceae. A number of detached taxodiaceous seed cones, pollen cones and detached microsporophylls also discovered in the fossil assemblage but not assignable to any of the new species, are described separately. *In situ* papillate, taxodiaceous pollen are also recorded.

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Contents

Introduction

The Taxodiaceae are a small family of temperate to sub-tropical trees with a restricted distribution. Today the family contains ten genera and fifteen species mainly distributed in Asia and North America. Of these ten genera, seven are monotypic while two genera have three species each and one genus contains two species. The genus *Athrotaxis* Don which includes three species, is endemic to Tasmania and is the only genus of the family with a southern distribution (Sporne, 1965). Of the six genera confined to Asia five are monotypic and of these, *Metasequoia* Miki and *Glyptostrobus* Endlicher are native in China, *Sciadopitys* Siebold & Zuccarini is native to Japan and *Cryptomeria* Don is found in China and Japan. The genus *Taiwania* Hayata is native in Taiwan, China and northern Burma. *Cunninghamia* (Richard) Brown includes two species, of which one species is native in China and the other is confined to Taiwan. Of the remaining three genera distributed in North America, *Sequoia* Endlicher and *Sequoiadendron* Buchholz are monotypic and *Taxodium* Richard has three species, two of which are distributed in south-eastern United States and one in Mexico (Dallimore & Jackson, 1966).

Although most of these extant genera are considered to have sufficient number of characters in common to be united under a single family (Florin, 1952), an isolated position for *Metasequoia* (Hu & Cheng, 1948; Pulle, 1950) and *Sciadopitys* (Velenovský, 1905; Florin, 1922; Hayata, 1932; Christophel, 1976; Manum & Bose, 1988) has often been suggested. An isolation of *Sciadopitys* from the Taxodiaceae is further supported by cladistic analysis (Hart, 1987). A complete merging of the Taxodiaceae with the family Cupressaceae was proposed by Eckenwalder (1976), but according to Peters and Christophel (1978) the utility of such a change has not been established and intermediate taxa justifying the combination are absent.

Despite the limited number of extant genera and species, and their restricted geographical distribution, the family Taxodiaceae have an extensive fossil record. Although fossil evidence indicates the earliest appearance of the family in the Jurassic, they appear to have been diverse and widespread during the Cretaceous (Miller, 1977). Most seed cones and foliage shoots known from the Jurassic and Early Cretaceous have been placed in fossil genera and often show combined characters of more than one living genus of the Taxodiaceae. Records of several fossil seed cone genera such as *Nephrostrobus* La Pasha & Miller (1981), *Rhombostrobus* La Pasha & Miller (1981) from the Upper Cretaceous of New Jersey and *Austrosequoia* Peters & Christophel (1978) from the Upper Cretaceous of Australia support a Late Cretaceous diversification of the family. The Cretaceous fossil record also indicates the presence of the genera *Metasequoia, Taxodium, Glyptostrobus, Athrotaxis, Sequoia* and *Sciadopitys* mainly in the Northern Hemisphere.

While many fossil species, especially from the Tertiary, have been assigned to modern genera a large number of species have also been placed in fossil genera such as *Sequoiites* Brongniart (1849), *Sequoiopsis* Saporta (1884), *Parasequoia* Krassilov (1967), *Protosequoia* Miki (1969), *Austrosequoia* Peters & Christophel (1978) which show either *Sequoia*-like characters or combined characters of *Sequoia* and *Sequoiadendron.* The genus *Athrotaxites* Unger (1849) shows characters more like those of *Athrotaxis* than other Taxodiaceae. However, many of the species are preserved as poorly informative impressions that lack crucial epidermal characters. In many cases association with reproductive material is difficult to establish.

Extinct forms closely related to or included within the Taxodiaceae are described from Jurassic and Lower Cretaceous sediments and included in the extinct genera *Brachyphyllum* Brongniart (1828), *Pagiophyllum* Heer (1881), *Elatides* Heer (1876), *Sewardiodendron* Florin (1958) and *Sphenolepis* Schenk (1871).

In Sweden, only few conifers have been recorded from the Cretaceous based on megafossils, one of the most detailed works being that of Conwentz (1892) dealing with megafossils from the Holma-sandstone of Late Cretaceous age. Most of this material is assigned to the Pinaceae, although *Sequoiites holstii* (Nath.) Conwentz, an ill-preserved and doubtful species (Seward, 1919) has also been described. Nykvist (1957) reported conifer wood related to modern Pinaceae from the Åsen locality in southern Sweden.

The fossil taxodiaceous conifers described here are a part of the Upper Cretaceous flora of Scania, southern Sweden which is already well known for its rich angiosperm component (Friis & Skarby, 1981; 1982; Friis, 1983; 1985a, b; Friis, Crane & Pedersen, 1988). The fossil taxodiaceous material comprises numerous leafy shoots, few seed cones, pollen cones and seeds. These show distinct morphological characters which together with detailed cuticular observations indicate the presence of at least three distinct genera and several species.

The present work, describing six different kinds of taxodiaceous shoots, one attached seed cone, five types of associated seed cones, three types of associated male reproductive organs including one detached microsporophyll, lends further support to the theory of an Upper Cretaceous diversification of the family Taxodiaceae. The work includes short descriptions of the various living genera of Taxodiaceae (Appendix A); a tabular comparison of some characters of all the extant taxodiaceous species with the new fossil species described in the present work (Table I); a tabular comparison of the hitherto described fossil genera showing *Sequoia*-like characters or combined characters of *Sequoia* and *Sequoiadendron* with *Quasisequoia* (Table II), as well as a summarized survey of the hitherto described fossil genera of the Taxodiaceae (Appendix B).

Materials and Methods

The fossil material was collected from the Höganäs AB's kaolin quarry at the Åsen locality, Scania, southern Sweden (56°9'N, 14°30'E). Based on palynological and paleomagnetic evidence, the plant bearing beds are dated as of Late Santonian or Early Campanian age (Friis & Skarby, 1982; Mörner, 1983; Skarby, 1986). Within the sediments a distinct lower and an upper unit are recognised separated by a marked weathering horizon (Friis, 1985a). The rich fossil assemblage of taxodiaceous conifers was recovered from the clay gyttja layer of the lower unit (samples GI 32107, GI 32170, GI 32188, GI 32189). A number of angiospermous flowers, fruits, seeds and fragments of ferns were also recovered from these samples including *Actinocalyx bohrii* (Friis, 1985a) and several platanaceous species (Friis et al., 1988). The coniferous material composed of abundant leafy shoots, comparatively fewer seed cones, pollen cones, microsporophylls and seeds, is preserved mainly as compressed lignite fossils and rarely as charcoalifications. The excellent state of preservation of the fossil material permits the use of scanning electron microscopic studies in conjunction with light microscopy.

Cuticle and pollen preparations were obtained by macerating small pieces of the fossils in concentrated nitric acid for 5 minutes followed by a 5 percent solution of potassium hydroxide for 5-10 minutes. After repeated washing in water, preparations for light microscopy were allowed to dehydrate on glass slides and mounted in glycerine jelly. Preparations for SEM studies were mounted either directly on specimen stubs or on small round cover-glasses (10 mm diameter) which were then fixed to the specimen stubs. After dehydration the preparations were sputter-coated with silver palladium or gold. The occurrence of large number of fungal fruiting bodies, hyphae and spores often proved a hindrance to procuring clean and clear cuticles.

For scanning the outer surface of branchlets, open pollen cones and seeds, material was fixed directly on the specimen stubs with a thin coating of adhesive and sputter coated with silver palladium or gold and examined with Cambridge S2, Jeol JSM-35 and Jeol 800 Scanning electron microscopes. In the systematic description, terminology used by Florin (1958) has mainly been followed and for the interpretations of scanning electron micrographs, terminology used by Boulter (1971) has been adopted. The stomatal apparatus dimensions include guard cells and subsidiary cells as well as encircling cells in the case of dicyclic stomata.

For comparative reference, herbarium specimens and pollen slides, leaf-cuticle preparations of modern Taxodiaceae (Florin's collection) as well as fossil material were studied in the botanical and palaeobotanical collections in the Swedish Museum of Natural History, Stockholm.

The specimens and preparations from Scania used in this study are deposited in the palaeobotanical collections of the Swedish Museum of Natural History, Stockholm (S).

Systematics

GYMNOSPERMAE

Family TAXODIACEAE

Shoots and associated cones

Quasisequoia Srinivasan & Friis gen. nov.

Etymology: Derived from the Latin word 'quasi' (almost) and *'Sequoia'* indicating close resemblance of the fossil form to both *Sequoia* and *Sequoiadendron.*

Generic diagnosis: Foliage shoots with spirally arranged, appressed leaves. Leaves scale-like, elliptical to rhomboidal; free apical portions short or elongated, pointing straight or curved inwards or spreading outwards; leaf apex bluntly rounded to sub-acute to acute; leaf bases rhomboidal. Leaves amphistomatic. Seed cone ovoid; cone scales spirally arranged; about 33 in number; bract-scale and ovuliferous-scale completely fused; escutcheons mainly four-sided, rhomboidal, broader than long. Seeds inverted, winged; wings inconspicuous.

Remarks on the genus: To the genus *Quasisequoia* are attributed four species. It comprises foliage shoots and one species *Q. florinii* includes female cones as well. The monomorphic, spirally arranged, scale-like, appressed leaves of *Quasisequoia* are closely comparable with those of extant *Sequoiadendron,* but are not as sharply pointed as in the latter genus and also differ in the absence of tricyclic stomata. The seed cones assigned to *Quasisequoia* resemble the cones of both *Sequoiadendron* and *Sequoia* in shape and in the presence of four-sided or transversely rhomboidal, spirally arranged cone scales (see Table I), but are nevertheless distinct in the absence of the transverse median groove so characteristic of the cone scales of the two extant genera. The cones of *Quasisequoia* are more similar to *Sequoia* with respect to size, but are close to *Sequoiadendron* in the number of cone scales.

Several fossil genera previously established (e.g. *Sequoiites, Sequoiopsis, Parasequoia, Protosequoia* and *Austrosequoia*) are based either on superficial resemblance or on similarities in cuticular or anatomical features with *Sequoia* and/or *Sequoiadendron* (see Table II). *Sequoiites* and *Sequoiopsis* are based on impressions and lack epidermal characters for comparison with *Quasisequoia* (see Table II). Moreover, the genus *Sequoiites* is based on specimens earlier described as *Cupressites taxiformis* Unger (1841-1847), and which are considered best retained under *Cupressites* (Seward, 1919). With the cones of *C. taxiformis* now placed under *Athrotaxis taxiformis* (Unger) Dorofeev & Sveshnikova (1963), the valid use of the genus *Sequoiites* might well be questioned.

Parasequoia and *Protosequoia* are based on compression material, but the linear, hypostomatic leaves of *Parasequoia* with only longitudinally oriented stomata with 6-8 strongly cutinised subsidiary cells are distinct from those of *Quasisequoia.* The seed cones of *Protosequoia* are elliptic or orbicular with a short peduncle and the scaly foliage leaves have irregularly arranged stomata on their upper side and the epidermal cells have straight walls. Details regarding the number of cone scales or nature of stomata are not available for a closer comparison with *Quasisequoia. Austrosequoia* is based on petrified fertile shoots. The ellipsoidal cone has 29-49, peltate, transversely rhomboidal to hexagonal cone scales and each cone scale has a median transverse groove and transversely traversing resin duct on the abaxial and adaxial sides. Due to its petrified state and lack of epidermal features in the foliage shoot bearing the cone, the characters of *Austrosequoia* do not compare well with the compressed specimens of *Quasisequoia*.

Type species: Quasisequoia florinii Srinivasan & Friis sp. nov.

Quasisequoia florinii Srinivasan & Friis sp. nov. (Plate I, figs. 1-8; Plate VII, figs. 1-4).

Specific diagnosis: Shoots with crowded, spirally arranged, appressed, leaves. Leaves scale-like, nearly rhomboidal in shape; free apical portions short, apex bluntly rounded, leaf base almost rhomboidal. Leaves amphistomatic; stomata on abaxial surface in two zones separated by a median non-stomatal zone; stomata in each zone in short discontinuous rows or sparsely scattered in middle and basal parts of leaf; stomatal orientation mainly oblique or transverse or occasionally longitudinal; stomata mainly monocyclic, subsidiary cells generally 5-7, guard cells slightly sunken, cuticular flanges between guard cells and subsidiary cells and subsidiary cells and surrounding ordinary epidermal cells generally prominent; stomata on adaxial surface in 1-2 longitudinal rows along margins separated by a non-stomatal zone; stomatal orientation mainly oblique or transverse. Epidermal and subsidiary cell surfaces non-papillate. Seed cone solitary, terminal, ovoid; cone scales spirally arranged, about 33 in number, with short, bluntly rounded apex; escutcheon mainly four-sided, transversely rhomboidal, surface slightly convex or depressed fine transverse or radial ridges.

Dimensions: Flattened shoots including leaves 0.75-2.50 mm wide. Longest shoot 48.0 mm in length. Leaf length 0.70-3.75 mm, width 0.40-1.15 mm. Stomatal apparatus 52.5 (77) 100.0 μm long, 47.0 (67.1) 87.5 μm wide. Ordinary epidermal cells in the stomatal zone 25.0-50.0 μm × 22.5-50.0 μm Epidermal cells in the non-stomatal zone 30.0-70.0 μm × 15.0-35.0 μm. Almost completely preserved seed cone 20.0 mm long, 12.0 mm wide; escutcheon height 2.2-4.7 mm, breadth 5.0-7.5 mm; incomplete seed cone 10 mm in breadth (length unknown); escutcheon height 2.75-3.75 mm, transverse breadth 4.25-5.5 mm. Seed 2.7 mm long, 2.4 mm wide.

Holotype: S100193. Plate I, fig. 1 (sample GI 32189).

Type locality: Höganäs AB's quarry at Åsen, Scania, Sweden.

Type stratum: Lower unit (clay gyttja)

Age: Late Cretaceous, probably Late Santonian or Early Campanian.

Material: 50 leafy shoots (S100193, 100194, 100247, 100292, 100317), 2 seed cones (S 100197, 100198) and 1 dispersed seed (S100199). Cuticle preparations – S100195, 100196, 100197, 100264-1,2, 100285-1,2,3.

Etymology: In honour of the Swedish scientist, Rudolf Florin.

DESCRIPTION

External morphology of shoot: The leafy shoots are somewhat flattened. In the branched shoots, the angles of branching are usually small (Plate I, fig. 1), and less than 45°. The leaves are crowded, spirally arranged and appressed (Plate I, fig. 2). Individual leaves are scale-like and somewhat rhomboidal in shape. The free apical portions are short with a slightly convex surface (Plate I, fig. 3), and are sometimes curved inwards. The margins around the leaf apices are often membranous. The apex is bluntly rounded and the leaf base is somewhat rhomboidal. Young leaves on the slender branchlets are 0.70-1.0 mm long and 0.40-0.55 mm broad. Mature leaves are 2.0-3.75 mm long and 1.0-1.15 mm broad. The short, free apical portions are about 0.2-0.4 mm long.

Epidermal structure: The leaf cuticles are thin. The leaves are amphistomatic. On the abaxial surface, stomata are in two zones separated by a median non-stomatal zone (Plate I, fig. 4). Stomata in each zone are either sparsely scattered or in short discontinuous longitudinal rows and distributed mainly in the middle and basal parts of leaf. Stomatal orientation is occasionally longitudinal and is mainly oblique or transverse (Plate I, fig. 5).

On the inner surface of abaxial cuticle, the stomata are mainly monocyclic (Plate I, fig. 7). Stomatal apparatuses are 52.5 (77) 100.0 μm × 47.0 (67.1) 87.5 μm. There are generally 5-7 subsidiary cells surrounding the guard cells usually forming a complete ring (Plate I, fig. 7). Incomplete ring of subsidiary cells are uncommon (Plate I, fig. 8). Subsidiary cells are sometimes slightly thickwalled, but may sometimes also resemble the surrounding ordinary epidermal cells (Plate I, fig. 7). Guard cells are slightly sunken and the stomatal aperture which is well cutinized sometimes forms a narrow oval. Cuticular flanges between guard cells and subsidiary cells are particularly prominent in some stomata (Plate I, fig. 7), while in others, flanges between subsidiary cells and surrounding epidermal cells are more prominent. Flanges are rather irregular in outline with more or less smooth edges.

Ordinary epidermal cells in the stomatal zone of abaxial surface vary in shape and size, being tetragonous, pentagonous or hexagonous, 25.0-50.0 μm × 22.5-50.0 μm. Cells may be isodiametric or vertically or transversely elongated. The surfaces of cells are granular, and the outlining cuticular flanges narrow, more or less smooth-edged and straight (Plate I, fig. 8). Epidermal cells in the median non-stomatal zone are short and vertically elongated, tetragonous, pentagonous or hexagonous. Outlining cuticular flanges are narrow and straight. The cells are 30.0-70.0 μm × 15.0-35.0 μm. Epidermal cells towards the margins of the surface are similar to the cells in the median non-stomatal zone.

Adaxially, the stomata are aligned in longitudinal rows along both margins and separated by a non-stomatal zone. Stomatal row along each margin is 1-2 stomata wide and the orientation of stomata is mainly oblique or transverse. Adjacent stomata are often contiguous (Plate I, fig. 6), but shared subsidiary cells are seldom observed. Stomatal details are almost similar to those of the abaxial surface, except that some adaxial stomata show lens-shaped pits or holes in the guard cell wall (Plate I, fig. 6). Epidermal cells in the non-stomatal zone are similar to the median non-stomatal epidermal cells of the abaxial surface.

Seed cone: The associated seed cone is solitary and borne terminally on the leafy shoot (Plate VII, fig. 1). The cone is ovoid, 20 mm long, 12 mm broad and except for two partially broken distal cone scales, it is completely preserved. There are about 33 spirally arranged cone scales with short obtuse apices and the ovuliferous and bract scales are completely fused. The escutcheons are mainly four sided and are typically broader than long, (5.0-7.5 mm broad and 2.2-4.7 mm high). The surface of the escutcheons is either slightly convex or slightly depressed in the middle with very fine transverse or radial ridges.

The cuticles of leaves from the lowermost part of the fertile shoot are rather thick. A comparative study of the epidermal characters and the leaf morphology of the fertile shoot indicates that it more closely resembles the foliage leaves of the present species than any other conifer from the Åsen locality.

The seed cone is also represented by a smaller incomplete specimen (Plate VII, figs. 2,3). This cone is 10 mm broad with an uncertain number of spirally arranged cone scales. The cone scale morphology is similar to that of the seed cone described above but the escutcheons are slightly smaller (4.25-5.5 mm broad, 2.75-3.75 mm high).

Seed: The incomplete cone (Plate VII, fig. 3), shows a partially exposed, inverted, flattened and comparatively large seed. Although the number of seeds could not be determined, they appear to be few per scale and arranged in a single row. A dispersed seed (Plate VII, fig. 4), similar to that in the cone clearly shows that the seed is flat and winged, even though the wings are inconspicuous. It is 2.7 mm long and 2.4 mm broad. The seed wall structure is unknown due to inadequate material.

Remarks: Quasisequoia florinii is the most abundant conifer species in the Åsen assemblage. The mature leaves of this species are distinguished from the other species of *Quasisequoia* by the presence of short free apical portions having bluntly rounded apex. It appears to be close to *Q. suecica* sp. nov. in the pattern of stomatal distribution, where the stomata on the abaxial surface are distributed in the central and basal part of leaf, but the stomata in *Q. florinii* differ in being mainly monocyclic and obliquely or transversely oriented. The monomorphic, scale-like and appressed leaves of *Q. florinii* compare more closely with those of extant *Sequoiadendron* than any other modern member of Taxodiaceae, but the leaf apices of the latter genus are sharply pointed and the stomata are mainly completely or incompletely dicyclic and occasionally incompletely tricyclic. The seed cones assigned to the former compare well with the cones of extant *Sequoia* and *Sequoiadendron* in shape and in the four-sided, transversely rhomboidal nature of escutcheons. The fossil cone is close to *Sequoia* in size, but is closer to *Sequoiadendron* in the number of cone scales. Flattened, winged, inverted seeds are characteristic of Recent taxodiaceous members and the seed assigned to *Q. florinii* may be compared with the seeds of modern *Sequoiadendron*.

A large number of fossil species have been assigned to the modern genus *Sequoia* based mainly on impression material. The most widely reported is *S. reichenbachii* recorded from several Cretaceous localities (Heer, 1874; Velenovsky, 1885). It was originally described as *Araucarites reichenbachii* Geinitz (1842) based on a piece of foliage shoot from the Lower Cretaceous of Saxony. It was subsequently transferred to the fossil genus *Geinitzia* Endlicher (1847) and later by Heer (1868) to *Sequoia*. Evidence supporting the generic identity with *Sequoia* was, however, lacking and the form genus *Geinitzia* was revived by Seward (1919). The foliage leaves of *Q. florinii* are quite distinct from those of *G. reichenbachii* figured in Doludenko, Kostina & Shilkina (1988), and in the absence of any cuticular characters no detailed comparison can be made.

Quasisequoia suecica Srinivasan & Friis sp. nov. (Plate II, figs. 1-8).

Specific diagnosis: Shoots with crowded, spirally arranged, loosely appressed leaves. Leaves scale-like, almost rhomboidal in shape; abaxial surface convex at broader basal part of leaf, free apical portions gradually tapering, slightly elongated, forming a triangular area, curved inwards or pointing straight; apex bluntly rounded or pointed; leaf base rhomboidal. Leaves amphistomatic; stomata on abaxial surface in two triangular zones in basal part of leaf, separated by a median non-stomatal zone; stomata occasionally irregularly placed, generally in short discontinuous rows; stomatal orientation occasionally diverse, mostly longitudinal in lower ends of leaf and transverse or oblique in central part; stomata on adaxial surface aligned in 1-2 rows closer to margins and separated by a non-stomatal zone; stomata completely or incompletely dicyclic, occasionally monocyclic; subsidiary cells large, generally 4. Ordinary epidermal cells in stomatal and non-stomatal zones mainly vertically elongated. Epidermal and subsidiary cell surfaces non-papillate; epidermal cell surfaces with small, round to irregular shaped crystal bodies.

Dimensions: Shoots including leaves 1.25-2.75 mm wide; longest shoot 15 mm long. Leaves 1.10-3.40 mm long, 0.75-1.92 mm wide at broad basal part. Stomatal apparatus 87.5 (117.0) 125.0 μm long, 62.5 (85.75) 112.5 μm wide. Ordinary epidermal cells in stomatal and non-stomatal zone 25.0-125.0 μm in length, 20.0-37.5 μm in breadth.

Holotype: S 100201. Plate II, fig. 2 (sample GI 32107).

Type locality: Höganäs AB's quarry at Åsen, Scania, Sweden.

Type stratum: Late Cretaceous, probably Late Santonian or Early Campanian.

Material: 50 fragments of shoots (S100200-100202, 100248, 100249). Cuticle preparations – S 100203-1, 100204, 100265, 100266, 100267-1 to 100267-4, 100305, 100306.

Etymology: Derived from 'Sweden' the country in which the fossil locality is situated.

DESCRIPTION

External morphology of shoot: The branchlets have crowded, spirally arranged, loosely appressed leaves (Plate II, fig. 2). Individual leaves are scale-like and rhomboidal in shape, 1.10-3.40 mm long and 0.75-1.92 mm broad (Plate II, fig. 3). The abaxial surface of the leaves is convex basally whereas the elongated free apical portions gradually taper to a bluntly rounded to pointed apex (Plate II, figs. 3,4). In some branchlets, young leaves appear to be crowded and more closely appressed and hence the free apical portions are less distinct (Plate II, fig. 1). In more mature leaves the elongated free apical portions are more prominent. The apical ends usually point upwards but may occasionally be curved inwards. The leaf base is rhomboidal. None of the shoots examined showed branching.

Epidermal structure: Leaf cuticles are thin and often infested with fungus, especially in the stomatal regions. Leaves are amphistomatic. On the abaxial surface, stomata are arranged in two triangular zones restricted to the basal part and separated by a median non-stomatal zone. The arrangement of stomata in these zones is variable in different leaves. Stomata may occasionally be irregularly scattered within the zone, but are more commonly in short discontinuous rows (Plate II, fig. 7). Orientation of stomata is also variable in different leaves. Occasionally it is diverse but is more often longitudinal in the lower parts of the leaf and transverse or oblique in the central part (Plate II, fig. 7). Guard cells are present on a few of the exposed leaf surfaces and the outer cuticle of subsidiary cells surrounding these guard cells sometimes form an inconspicuous ring (Plate II, fig. 8).

On the inner surface of abaxial cuticle, stomatal apparatuses are mostly completely or incompletely dicyclic and occasionally monocyclic. Stomata are comparatively large, 87.5 (117.0) 125.0 μm × 62.5 (85.75) 112.5 μm. Subsidiary cells are large and generally 4 in number (Plate II, fig. 5), but may sometimes be 5 or 6. In the former case, the subsidiary cells may be distributed as 2 polar and 2 lateral cells or as 2 lateral cells on either side of the guard cells. Sharing of subsidiary cells between adjacent stomata has not been observed although they may often be contiguous. Anticlinal walls of subsidiary cells as well as those of encircling cells are moderately thickened. Periclinal walls of these cells are devoid of papillae. Stomatal pit is long and the aperture is slit-like or forms a narrow oval. The guard cells are slightly sunken and thinly cutinized.

On the abaxial surface the ordinary epidermal cells both within and outside the stomatal zone are mostly tetragonous to pentagonous with straight walls (Plate II, figs. 5,6). The cells are 25.0-125.0 μm long and 20.00-37.5 μm broad, typically vertically elongated and tend to narrow towards one or both extremities. Anticlinal walls of these cells are moderately thickened. Periclinal walls of the epidermal cells are non-papillate, but small crystal bodies of different shapes are abundant on the ordinary epidermal cell surfaces (Plate II, fig. 6).

On the adaxial surface, stomata are aligned in longitudinal files parallel to the margins of the surface and separated by a non-stomatal zone. Stomatal files on either side are 1-2 stomata wide. The stomata are heavily infested with fungi and hence give no clear details of the number and nature of subsidiary cells and encircling cells. Stomatal orientation appears to vary in different leaves. Stomata may be mainly oblique or transversely oriented with a few being longitudinally oriented. Alternatively the stomata may be mostly oriented longitudinally towards apices and oblique and transverse in the lower ends. Epidermal cells in the stomatal as well as the non-stomatal zones are generally poorly preserved.

Remarks: Quasisequoia suecica is close to *Q. florinii* in the pattern of stomatal distribution, the stomata on the abaxial surface being mainly distributed in the central and basal parts of the leaf, but the leaves of the former species have longer, tapering free apical portions. The presence of mainly four subsidiary cells, numerous crystal bodies on the epidermal cell surfaces and the mostly vertically elongated nature of the ordinary epidermal cells in the stomatal zone are some characters that distinguish this species from the other species assigned to *Quasisequoia*. Although a few characters of *Q. suecica,* like the scale-like, monomorphic and spiral arrangement of leaves and the stomatal orientation, may be used for a general comparison with Recent *Sequoiadendron,* the fossil species does not closely resemble any modern species of Taxodiaceae.

Quasisequoia scanica Srinivasan & Friis sp. nov. (Plate III, figs. 1-8).

Specific diagnosis: Shoots with spirally arranged, closely appressed leaves. Leaves scale-like, elliptical to somewhat rhomboidal to hexagonal in shape, free apical portions short, pointing upwards, sometimes curved inwards, spreading outwards in young leaves, apex acute to sub-acute, leaf base nearly rhomboidal. Attachment of leaves to axis, angular. Space between adaxial surface and axis filled with resin secretion. Leaves amphistomatic; stomata on abaxial surface in two zones, separated by a median non-stomatal zone; stomata in each zone scattered, distributed almost upto apex in larger leaves; stomatal orientation diverse; stomata monocyclic, completely or incompletely dicyclic; subsidiary cells 5-6; guard cells slightly sunken; subsidiary and epidermal cell surfaces non-papillate; adaxial surface forming a narrow triangle; stomata on adaxial surface in longitudinal rows along margins and separated by a non-stomatal zone, stomata along each margin irregularly placed in a row or one stomata wide towards apex, 2-3 stomata wide along margins; stomatal orientation mainly oblique or transverse, occasionally longitudinal.

Dimensions: Stout shoots including leaves 3.5-5.0 mm wide; longest shoot 72 mm long; leaves 3.5-4.5 mm long, 1.5-2.0 mm wide. Less thicker branchlets including leaves 1.5-2.5 mm wide; leaves 2.0-2.9 mm long, 1.5-1.75 mm wide. Slender shoots with young leaves 1.25-1.50 mm wide; leaves 1.0-1.5 mm long, 0.40-0.5 mm wide. Stomatal apparatus 74.0 (92.5) 102.5 μm long, 53.0 (77.2) 105.0 μm wide. Ordinary epidermal cells in the stomatal zone 15.0-57.5 μm long, 17.5-32.5 μm broad. Epidermal cells in the non-stomatal zone 22.5-87.5 μm long, 15.0-25.0 μm broad.

Holotype: S100205. Plate III, fig. 1 (sample GI 32189).

Type locality: Höganäs AB's quarry at Åsen, Scania, Sweden.

Type stratum: Lower unit (clay gyttja).

Age: Late Cretaceous, probably Late Santonian or Early Campanian.

Material: Numerous leafy shoots (S100205-100208, 100250-100252, 100295, 100296). Cuticle preparations – S100209-100212, 100268-100274, 100286-1,2, 100287.

Etymology: Derived from the province 'Scania' in southern Sweden where the fossils were collected.

DESCRIPTION

External morphology of shoot: The leafy shoots are of three distinct sizes. Leaves on the stout shoots (Plate III, fig. 1), are distantly placed, spirally arranged and closely appressed to the axis. They are scale-like, almost elliptical to rhomboidal in shape with a distinct mid-rib (Plate III, fig. 3). The free apical portions are short. The apex is acute to sub-acute and the tips occasionally curve inwards. The leaf base is almost rhomboidal and leaves about 3.5-4.5 mm long and 1.5-2.0 mm broad. Leaves on the thinner branchlets are also spirally arranged and closely appressed. The scale-like leaves are narrowly rhomboidal to almost hexagonal in shape due to the angular attachment to the axis. The free apical portions are short and have acute to sub-acute apices (Plate III, fig. 4), with tips pointing upwards. The leaf base is almost rhomboidal and often concealed by overlapping leaves. These leaves are 2.0-2.9 mm long and 1.5-1.75 mm broad. The slender shoots with young leaves (Plate III, fig. 2), perhaps representing ultimate shoots have, spirally arranged, appressed leaves. The leaves are scale-like, almost rhomboidal to hexagonal in shape, 1.0-1.25 mm long and 0.4-0.5 mm broad. The short free apical portions distinctly spread outwards. The apex is acute to sub-acute and leaf base rhomboidal.

Carbonized resin secretions between the adaxial surface and the axis have been observed in all specimens (Plate III, fig. 4).

Epidermal structure: Leaf cuticles are moderately thick. Leaves are amphistomatic. On the abaxial surface, stomata are in two zones, separated by a median non-stomatal zone. Stomata in each zone are scattered (Plate III, fig. 5), distributed almost up to the apex in larger leaves. Adjacent stomata are occasionally contiguous. The stomatal orientation is diverse (Plate III, fig. 6), although the stomata tend to be more oblique and transversely oriented than longitudinal.

On the inner surface of abaxial cuticle, the stomatal apparatuses are quite well preserved. The stomatal pores are often occluded with fungal hyphae and spores. The stomatal apparatuses are 74.0 (92.5) 102.5 μm long and 53.0 (77.2) 105.0 μm broad. Stomata are monocyclic (Plate III, fig. 8), mostly completely dicyclic (Plate III, fig. 7), or occasionally incompletely dicyclic. There are generally 5-6 subsidiary cells. Guard cells are sunken and thinly cutinized. The guard cell wall surfaces of some stomata appear to have pits or holes. The stomatal aperture is slit-like or forms a narow oval.

On the abaxial surface, ordinary epidermal cells in the stomatal zone are variously shaped (Plate III, fig. 6), tetragonous, pentagonous or hexagonous and may be broader than long, isodiametric or slightly vertically elongated. The cells are 15.0-57.5 μm long and 17.5-32.5 μm broad. Anticlinal walls are slightly thickened and straight. Epidermal cells in the median non-stomatal zone are mainly tetragonous, more narrow and vertically elongated towards the middle and apical ends. The cells towards the base are also mainly tetragonous, but, intermixed with vertically elongated cells are also shorter cells. Anticlinal walls of these cells are moderately thickened and straight. The cells are 22.5-87.5 μm × 15.0-25.0 μm. Non-stomatal epidermal cells towards the margins of the surface are also vertically elongated and more or less similar to the cells in the median non-stomatal zone. The periclinal walls of the epidermal cells as well as the subsidiary cells are non-papillate. Oval to round shaped crystal bodies sometimes occur in the ordinary epidermal cells in the stomatal zone as well as the epidermal cells in the non-stomatal zone.

The adaxial surface forms a narrow triangle on which the stomata are arranged in 1-2 longitudinal rows along both margins separated by a non-stomatal zone. The stomata along each margin may be aligned irregularly in a row or the stomata may be 2-3 stomata wide along the margins and 1-2 stomata wide near the apical ends. Stomatal orientation is mainly oblique or transverse and occasionally longitudinal. The stomata details are more or less similar to those observed on the abaxial surface. The epidermal cells in the non-stomatal zone are mostly tetragonous, occasionally pentagonous, vertically elongated with slightly thickened and straight anticlinal walls. The cell dimensions are almost similar to those of the non-stomatal epidermal cells of the abaxial surface.

Remarks: Quasisequoia scanica is distinguished from the other species of *Quasisequoia* by the presence of elliptical to almost hexagonal shaped leaves with distinct mid-rib, short acute to sub-acute apices, and resin secretions between adaxial surface and axis. It resembles *Q. florinii* in the general pattern of stomatal distribution, but differs in having leaves with acute to sub-acute apices and monocyclic or completely to incompletely dicyclic stomata. Among the previously described fossil species, *Sphenolepis kurrianus* (Dunker) Schenk, figured in Seward (1895, Pl. XVIII, fig. 1), *Sequoiites concinna* Heer, figured in Seward (1926, Pl. 9, fig. 80) and the adult leaves of *Q. scanica* show some morphological similarity, but the epidermal characters of *Sphenolepis* are rather different (see Appendix B). *Q. scanica* is not identical to any living species of the Taxodiaceae.

Quasisequoia aasenensis Srinivasan & Friis sp. nov. (Plate IV, figs. 1-8).

Specific diagnosis: Shoots with spirally arranged, closely appressed leaves. Leaves scale-like, rhomboidal; free apical portions elongated, spreading

But, unlike the living genus the leaves of *Paracryptomeria* lack adaxial keel, have narrower leaf bases and have mainly monocyclic and transversely oriented stomata. The foliage leaves of modern *Araucaria* De Jussieu, especially *A. bernieri* Buchholz, are also comparable with *Paracryptomeria,* but the extant species is characterised by the presence of stomatal plugs, mainly obliquely oriented stomata with four subsidiary cells and numerous circular to lens shaped pits on the epidermal cell surfaces (Stockey & Ko, 1986). Although the reproductive organs of *Paracryptomeria* are not known, it is considered as being close to *Cryptomeria.*

Type species: Paracryptomeria elegans Srinivasan & Friis sp. nov.

Paracryptomeria elegans Srinivasan & Friis sp. nov. (Plate VI, figs. 1-7).

Specific diagnosis: Shoots with crowded, spirally arranged leaves. Leaves scale-like, rhomboidal to triangular in shape, keeled, not appressed; free apical portions tapering, incurved; apex acute to bluntly rounded, leaf base rhomboidal. Leaves amphistomatic; two distinct stomatal bands on abaxial surface, separated by a median non-stomatal zone; stomatal band 4-5 stomata wide proximally, gradually narrowing distally; stomatal bands on adaxial surface narrow, 1-2 stomata wide; stomata in discontinuous longitudinal files; stomatal orientation mainly transverse, less frequently oblique or longitudinal; guard cells depressed; stomata mainly monocyclic; subsidiary cells 5-7. Epidermal and subsidiary cell surfaces non-papillate. Leaves with single prominent median resin canal.

Dimensions: Shoot including leaves 2.0-4.5 mm wide. Longest shoot 25 mm long. Leaf length 2.0-5.0 mm, width 1.0-2.0 mm. Stomatal apparatus 75.0 (85) 92.5 μm long, 57.5 (61.2) 75.0 μm wide. Ordinary epidermal cells in the stomatal zone 17.5-35.0 μm long, 17.5-35.0 μm broad. Epidermal cells in the non-stomatal zone 27.5-67.5 μm long, 20.0-37.5 μm broad.

Holotype: S 100224. Plate VI, fig. 1 (sample GI 32189).

Type locality: Höganäs AB's quarry at Åsen, Scania, Sweden.

Type stratum: Lower unit (clay gyttja).

Age: Late Cretaceous, probably Late Santonian or Early Campanian.

Material: Numerous leafy shoots (S100224, 100227, 100228, 100256-100259, 100288-100291). Cuticle preparations – S100225, 100226, 100229, 100230, 100281-100284.

Etymology: Indicates elegant nature of the fossil form.

DESCRIPTION

External morphology of shoot: The leafy shoots are woody with crowded, spirally arranged leaves (Plate VI, fig. 1). The shoots are seldom branched and these are too fragmentary and few in number to be able to yield any details on the nature of branching. Some of the shoots show very small, scale-like leaves with obtuse apices basally. Individual mature leaves are scale-like and rhomboidal to triangular in shape, with gradually tapering incurved, free apical portions (Plate VI, fig. 4). Leaf bases are rhomboidal and apex is acute to bluntly rounded. Leaf bases are almost concealed by neighbouring overlapping leaves. Leaves are keeled on the abaxial surface, have a single prominent median resin canal, and are 2.0-5.0 mm long and 1.0-2.0 mm broad.

Epidermal structure: Leaf cuticles are moderately thick to thin and often infested with fungi. Leaves are amphistomatic. Stomata are arranged in two distinct bands on both abaxial and adaxial surfaces (Plate VI, fig. 2), and the two bands on each of the surfaces are separated by a median non-stomatal zone.

On the abaxial surface, each stomatal band is 4-5 stomata wide proximally but gradually tapers apically (Plate VI, fig. 2), where it is usually 2 stomata wide. The stomatal bands do not converge at the apex. Within each stomatal band, the stomata are more or less aligned in discontinuous longitudinal files (Plate VI, fig. 3). Orientation of stomata is

Holotype: S100218. Plate V, fig. 1 (sample GI 32170).

Type locality: Höganäs AB's quarry at Åsen, Scania, Sweden.

Type stratum: Lower unit (clay gyttja).

Age: Late Cretaceous, probably Late Santonian or Early Campanian.

Material: Numerous fragments of shoots (S 100218, 100219, 100221, 100222, 100254, 100255, 100293, 100294, 100313, 100314). Cuticle preparations – S100220, 100223, 100279, 100280, 100298.

Etymology: In honour of the Swedish scientist, Nils Nykvist.

DESCRIPTION

External morphology of shoot: The shoots have crowded, spirally arranged, loosely appressed leaves (Plate V, fig. 1). Individual leaves are lanceolate and narrow (Plate V, fig. 4), and bifacially flattened, 2.5-5.0 mm long and 0.75-0.90 mm broad. The basal part of leaf is loosely appressed to the axis. Free apical portions are long and gradually taper to an acute apex. The base is decurrent and often concealed by neighbouring overlapping leaves. Foliar buds are recognised in some shoots (Plate V, fig. 2). A prominent median resin canal is recognised in the leaves.

Epidermal structure: Leaf cuticles are moderately thick. Leaves are epistomatic. The two longitudinal bands of stomata close to margins of the adaxial surface appear to be narrow (Plate V, figs. 3,5). Each band is not more than one to two stomata wide. Adjacent stomata are rather contiguous. They are mainly transversely oriented and rarely oblique or longitudinal. Although more than 20 cuticle preparations were attempted, none of them showed any stomatal details like number of subsidiary cells and presence or absence of dicyclic stomata. This could be attributed to poor preservation perhaps attributable to fungal infestation in and around the stomatal regions. The subsidiary cell surfaces apparently lack papillae.

On the adaxial surface, epidermal cells in the median non-stomatal zone are tetragonous, narrow, vertically elongated and straightwalled, 37.5-62.5 μm × 12.5-15.0 μm. Epidermal cells at the margins of the adaxial surface are also vertically elongated but are narrower, being 5.0-7.5 μm broad. Epidermal cells of the entire abaxial surface are mainly tetragonous and vertically elongated, 37.5-87.5 μm × 7.5-22.5 μm. Few cells show a tendency to narrow towards either one of the extremities. Cuticular flanges outlining these cells are narrow, straight and smooth edged (Plate V, fig. 6). Epidermal cells of both abaxial and adaxial surfaces are devoid of papillae and are granular.

Remarks: Elatidopsis nykvistii is distinguished from the other species described in the present work by the presence of lanceolate, bifacially flattened and epistomatic leaves. Among fossil members, epistomatic leaves are present in some species of *Elatides* Heer, and the diagnostic characters of the latter genus also include seed cones and pollen cones. With a number of stomatal characters still lacking, this species has not been compared in detail with any living or fossil genus. It may be broadly compared with modern *Cunninghamia,* but is far removed from it.

Paracryptomeria Srinivasan & Friis gen. nov.

Etymology: Derived from the Greek word 'para' (near) and *Cryptomeria* indicating the close external resemblance to extant *Cryptomeria.*

Generic diagnosis: Woody shoots with spirally arranged, crowded leaves. Leaves scale-like, rhomboidal to triangular, bifacial, keeled, not appressed; free apical portions gradually tapering, incurved; leaf apex acute to bluntly rounded; leaf base rhomboidal. Leaves amphistomatic; stomata on each of the two surfaces in two distinct bands; stomatal bands on abaxial surface broader than on adaxial surface, narrowing from base to apex; stomatal orientation on both surfaces mainly transverse. Leaves with single prominent median resin canal.

Remarks on the genus: Paracryptomeria is based on foliage shoots and represented by a single species. It resembles modern *Cryptomeria* in gross morphology and arrangements of stomata in distinct bands.

non-stomatal zone are poorly preserved. Their anticlinal walls are also traversed by fungal hyphae. The cells, however, appear to be tetragonous to pentagonous and may tend to narrow towards either one of the extremities. Only a few cells could be measured and these are 45.0-87.5 μm × 25.0-30.0 μm. Epidermal cells along the margins of the surface are similar to the cells in the median non-stomatal zone. Periclinal wall of the epidermal and subsidiary cells are non-papillate.

On the adaxial surface, stomata are arranged in two longitudinal zones separated by a non-stomatal zone. Stomata in each zone are more or less aligned in 2-3 rows (Plate IV, fig. 7), and are often contiguous. Stomatal orientation is mainly oblique or transverse. Stomatal details are very similar to those of the abaxial surface. Epidermal cells in the non-stomatal zone are mainly tetragonous and vertically elongated and are similar to the epidermal cells of the median non-stomatal zone of the abaxial surface.

Remarks: The leaves of *Quasisequoia aasenensis* with elongated free apical portions generally spreading outwards, differ from the other species of *Quasisequoia* in leaf morphology and stomatal arrangement. They resemble the adult leaves of extant *Sequoiadendron,* but the leaf apices of the fossil species are not as sharply pointed, and also differ in epidermal characters such as stomatal orientation and number of subsidiary cells (see appendix A).

Elatidopsis Srinivasan & Friis gen. nov.

Etymology: Derived from '*Elatides*', indicating general resemblance to the extinct Jurassic genus *Elatides* Heer.

Generic diagnosis: Foliage shoots with spirally arranged, loosely appressed leaves. Leaves lanceolate, bifacially flattened; free apical portions gradually tapering; apex acute, base decurrent; leaf margin entire. Leaves epistomatic; stomata on adaxial surface in two narrow longitudinal bands separated by a median non-stomatal zone; subsidiary cells non-papillate. Prominent median resin canal.

Remarks on the genus: This genus is instituted for foliage shoots. The lanceolate, bifacially flattened leaves of *Elatidopsis* resemble the leaves of *Elatides* Heer (1876), in gross morphology, but do not diverge radially as in the latter genus and are not as elongated either. Further, the emended diagnosis of *Elatides* given by Harris (1979), states the presence of papillate subsidiary cells and includes characters of seed cones and pollen cones, and these are lacking in the present genus. The lanceolate leaves of modern *Cunninghamia* compare with those of *Elatidopsis,* but differ in having toothed margins and in being mainly amphistomatic. Although lanceolate leaves are of common occurrence in conifers, the presence of epistomatic leaves in modern and fossil conifers appears to be rather restricted. Among modern members they are characteristic of some podocarps and also occur rarely in *Athrotaxis* of Taxodiaceae (Florin, 1958), but the scale-like or awl shaped leaves of the latter genus are distinct from the lanceolate leaves of *Elatidopsis.*

Type species: Elatidopsis nykvistii Srinivasan & Friis sp. nov.

Elatidopsis nykvistii Srinivasan & Friis sp. nov. (Plate V, figs. 1-6).

Specific diagnosis: Shoots with crowded, spirally arranged leaves. Leaves lanceolate, narrow, bifacially flattened, appressed at basal ends, free apical portions gradually tapering; apex acute, base decurrent. Leaves epistomatic; stomata on adaxial surface in two narrow longitudinal bands separated by a median non-stomatal zone; each stomatal band 1-2 stomata wide; adjacent stomata contiguous, mainly transversely oriented; epidermal and subsidiary cell surfaces non-papillate.

Dimensions: Shoots with leaves 1.5-2.5 mm wide. Longest shoot 48 mm long. Leaf length 2.5-5.0 mm, breadth 0.75-0.90 mm. Epidermal cells in non-stomatal zone 37.5-62.5 μm long, 5.0-15.0 μm broad. Epidermal cells of abaxial surface 37.5-87.6 μm long, 7.5-22.5 μm broad.

outwards, occasionally curved inwards; apex bluntly rounded to pointed, leaf base rhomboidal; abaxial surface keeled. Leaves amphistomatic; stomata on abaxial surface in two zones separated by a median non-stomatal zone, stomata in each zone scattered in appressed part of leaf, arranged in a single row along elongated apical ends; stomatal orientation mainly oblique or transverse in appressed parts, mainly transverse and occasionally oblique in elongated apical region; stomata often contiguous, monocyclic to dicyclic; subsidiary cells 4-5, stomatal pit rectangular to oval, guard cells sunken, stomatal aperture as long as pit; stomata on adaxial surface in two zones along margins separated by a non-stomatal zone, stomata in each zone in 2-3 longitudinal rows; stomatal orientation mainly oblique or transverse, occasionally longitudinal. Epidermal and subsidiary cell surfaces non-papillate.

Dimensions: Stout shoot including leaves 5.5 mm wide. Longest shoot 71.0 mm in length; leaf length 4.6-5.5 mm, width 2.0-2.5 mm. Thinner branchlets including leaves 2.5-3.5 mm wide, longest shoot 50.0 mm in length, leaf length 3.9-4.5 mm, width 1.25-1.65 mm. Stomatal apparatus 55.0 (70.0) 87.5 μm long, 50.0 (52.9) 70.5 μm wide. Ordinary epidermal cells in the stomatal zone 20.0-90.0 μm in length, 22.5-42.5 μm in breadth. Epidermal cells in the non-stomatal zone 45.0-87.5 μm in length, 25.0-30.0 μm in breadth.

Holotype: S 100213. Plate IV, fig. 1 (sample GI 32189).

Type locality: Höganäs AB's quarry at Åsen, Scania, Sweden.

Type stratum: Lower unit (clay gyttja).

Age: Late Cretaceous, probably Late Santonian or Early Campanian.

Material: 11 leafy shoots (S100213-100215, 100217, 100253). Cuticle preparations – S100216, 100275-100278.

Etymology: Derived from 'Åsen', the fossil locality.

DESCRIPTION

External morphology of shoot: Leafy shoots are comparatively thick and appear to be woody. The thickest shoot is represented by a single specimen about 5.5 mm broad. Leaves on this shoot are spirally arranged, somewhat distantly placed, 4.6-5.5 mm long and 2.0-2.5 mm broad. Leaves on the thinner branchlets (Plate IV, 1), are also spirally arranged but are more closely placed, 3.9-4.5 mm long and 1.25-1.65 mm broad. Leaves on both these shoots are closely appressed to axis except apically and are scale-like, rhomboidal in shape. Free apical portions are elongated and generally spread outwards (Plate IV, fig. 2), but may also be curved inwards (Plate IV, fig. 3). Apex is bluntly rounded or pointed and the leaf base is rhomboidal. The abaxial surface is keeled.

Epidermal structure: Leaf cuticles are thin and infested with fungi. Leaves are amphistomatic. On the abaxial surface, stomata are in two zones separated by a median non-stomatal zone. Stomata in each zone are irregularly scattered in the appressed part of the leaves, gradually narrowing towards the apical region but are in a single row along the elongated, free apical portions (Plate IV, fig. 5). Stomatal orientation is mainly oblique or transverse in the appressed parts as well as in the region towards the apical ends (Plate IV, fig. 4), but is more often transverse than oblique along the elongated, free apical portions (Plate IV, fig. 5).

On the inner surface of the abaxial cuticle, stomata are monocyclic to dicyclic. The stomatal apparatuses are 55.0 (70.0) 87.5 μm × 50.0 (52.9) 70.5 μm. Subsidiary cells are generally 4, although due to bad preservation their number is often unclear. Encircling cells are also indistinct. Stomatal pit is rectangular to oval (Plate IV, fig. 6), and the thinly cutinized guard cells are slightly sunken. Flanges between the guard cells and subsidiary cells are narrow. Stomatal apertures are mostly slitlike (Plate IV, fig. 8).

On the abaxial surface, ordinary epidermal cells in the stomatal zone are tetragonous or pentagonous. The cells may be isodiametric, vertically elongated or broader than long, 20.0-90.0 μm × 22.5-42.5 μm. Anticlinal walls of these cells are traversed by fungal hyphae. Epidermal cells in the median mainly transverse (Plate VI, figs. 3,5), although oblique or longitudinally oriented stomata do occur at the apical ends. Guard cells are not preserved on most of the exposed leaf surfaces, but wherever present, appear to be slightly depressed.

On the inner surface of abaxial cuticle, stomatal apparatuses are poorly preserved. They are 75.0 (85) 92.5 μm long and 57.5 (61.2) 75.0 μm broad, and are mostly monocyclic with a ring of 5-6 subsidiary cells which have thinly cutinized anticlinal walls. Stomata may rarely be dicyclic but this is difficult to establish with certainty due to bad preservation. Although adjacent stomata are occasionally closely placed, shared subsidiary cells were not observed in any of the cuticle preparations. Subsidiary cells appear to be at leaf surface with depressed guard cells in their centre. Cuticular flanges between guard cells and subsidiary cells are not prominent. Guard cell walls appear to be more strongly cutinized than surrounding subsidiary and epidermal cells. Stomatal aperture is slit-like or oval with thickened poral walls (Plate VI, fig. 6).

On the abaxial surface, ordinary epidermal cells in the stomatal band are mainly tetragonous. They may be isodiametric or broader than long, 17.5-35.0 μm × 17.0-35.0 μm. These cells generally have straight walls but few may have slightly sinuous walls. Epidermal cells in the median non-stomatal zone are short or vertically elongated with an occasional tendency to narrow towards one or both extremities, and are 27.5-67.5 μm × 20.0-37.5 μm. Flanges outlining these epidermal cells are narrow and straight (Plate VI, fig. 7), but those towards the basal margins have slightly sinuous walls. Epidermal cells at the basal margins are darker than the rest of the epidermis and have strongly thickened anticlinal walls. Epidermal cells along lateral margins of the abaxial surface are irregular in shape and size. The cells may be tetragonous, being broader than long, 15.0-20.0 μm × 37.5-42.5 μm, or may be more irregular in shape, being 27.5-50,0 μm × 35.0-42.5 μm. Periclinal wall of the epidermal and subsidiary cells is non-papillate.

On the adaxial surface the stomatal bands are very narrow (Plate VI, fig. 2). Each stomatal band is not more than 1-2 stomata wide. The stomata are aligned in longitudinal files and are mainly transversely oriented. They are badly preserved and offer no details of the number of subsidiary cells or the nature of the surrounding ordinary epidermal cells and guard cells. Non-stomatal epidermal cells closer to the lateral margins are more or less similar to the median non-stomatal epidermal cells of the abaxial surface. Periclinal wall of the epidermal cells is non-papillate.

Remarks: Paracryptomeria elegans is close to extant *Cryptomeria japonica.* It resembles the latter in gross morphology, arrangement of stomata in distinct bands and in the non-papillate nature of subsidiary cells, but differs nevertheless in having much narrower stomatal bands and mainly transversely oriented, monocyclic stomata. The fossil species offers some morphological comparison with modern *Taiwania* which also has distinct stomatal bands on both leaf surfaces, but it differs from *Paracryptomeria* in having irregularly oriented, completely dicyclic to completely tricyclic stomata. Among the hitherto described fossil species, *Elatides bommeri* Harris (1953) resembles the Scanian species in gross morphology and in the non-papillate nature of subsidiary cells, but differs in being epistomatic.

Unassigned cones

Nine morphologically distinct types of seed cones and pollen cones are preserved in the Åsen assemblage. Except for the seed cones of *Quasisequoia florinii,* none of them yield sufficient information for a firm association with any of the vegetative shoots.

Unassigned seed cones and seeds (Plate VII, figs. 5-14).

Type 1: (Plate VII, figs. 5,6,10).

Material: 2 cones (S 100231, S 100232), few isolated seeds (S 100232), and several dispersed seeds (S 100260).

Description: The cones are incompletely preserved and the following description is based on the more complete specimen (Plate VII, fig. 5). It is elongate, about 21 mm long and 7.7 mm broad with spirally arranged cone scales. The number of cone scales is approximately 45. The other cone (Plate VII, fig. 6) is about 5.5 mm broad. The escutcheons appear to be four sided, are broader than long and each scale has an elongated spiny apex which is occasionally incurved. The escutcheons are 3.5-4.25 mm broad and 1.2-1.4 mm high. Leaves preserved at the base have somewhat elongated spiny apical portions.

A cone scale isolated from the incomplete cone (Plate VII, fig. 6), shows 10 seed scars arranged in a single row. The partially exposed seeds in the same cone show inverted attachment. A seed (Plate VII, fig. 10), isolated from this cone is 1.7 mm long and 1.3 mm broad and has narrow and thin lateral wings. The micropylar end is seen as an obtuse point.

Type 2: (Plate VII, fig. 7).

Material: 1 complete cone (S100233).

Description: The cone is ovoid and solitary, 18.0 mm long and 10.0 mm broad with about 22 spirally arranged cone scales (Plate VII, fig. 7). Ovuliferous and bract scales are completely fused and in a few cone scales, the short, almost subacute apices of the bract scales are recognised. Escutcheons appear to be distinctly pentagonous or hexagonous with unequal sides. They are 4.8-6.4 mm broad and 3.6-4.8 mm in height. They are commonly nearly isodiametric and rarely broader than long. The surface of the escutcheons is slightly convex or flat or somewhat cracked in the middle.

The shoot attached to the base of the cone is fragmentary and has a few partially preserved leaves. Although they closely resemble the foliage leaves of *Quasisequoia scanica* Srinivasan & Friis sp. nov. (Plate III) in general morphology, lack of epidermal characters prevent an assignment of the cone to this species. No seeds have been observed in the cone.

Type 3: (Plate VII, figs. 8,9).

Material: 2 cones (S100234, S100235).

Description: The cones are ovoid in shape. One cone (Plate VII, fig. 8), is incomplete, about 11.25 mm broad with escutcheons 3.10-3.75 mm high and 4.0-5.0 mm broad. The other (Plate VII, fig. 9) is 23.2 mm long and 12.8 mm broad and has about 26 cone scales. The escutcheons are slightly larger, 3.25-4.25 mm in height and 5.25-6.25 mm in breadth. Cone scales are spirally arranged and have short spiny apices. Ovuliferous scales and bract scales are fused. Escutcheons appear to be distinctly four-sided and are usually broader than long. The surface of escutcheons is slightly convex or slightly depressed in the middle. These cones may resemble those of *Quasisequoia florinii* Srinivasan & Friis sp. nov. (Plate VII), but are slightly larger. Seeds appear to be inverted (Plate VII, fig, 8), but are not sufficiently exposed for a detailed comparison with *Q. florinii*.

Type 4: (Plate VII, figs. 11,12).

Material: 2 incompletely preserved cones (S 100236, S100237); dispersed cone scales (S100299, 100315).

Description: The cones are incomplete, lacking a few scales in the distal part. They appear globose to sub-globose, and have spirally arranged cone scales. One cone (Plate VII, fig. 11), is 7.0 mm long and 6.4 mm broad with escutcheons 2.0-2.8 mm high and 2.4-3.5 mm broad. The other (Plate VII, fig. 12), is 5.4 mm broad with escutcheons 1.8-2.4 mm high and 2.2-3.0 mm broad. Since both cones are incomplete, the number of cone scales could not be determined. Ovuliferous and bract scales are completely fused. Escutcheons are distinctly pentagonous or hexagonous with unequal sides, usually isodiametric or rarely transversely elongate. The surface of the escutcheons is sometimes slightly depressed in the middle, occasionally with fine transverse or radial ridges. In one of the cones (Plate VII, fig. 11), a poorly preserved seed is exposed at the distal end and it appears to be inverted. The number of seeds per scale could not be determined.

Type 5: (Plate VII, figs. 13,14).

Material: 1 cone (S100238), several dispersed seeds (S 100239, 100261, 100262, 100301).

Description: The cone is incomplete, but appears to be globose (Plate VII, fig. 13) and is about 7.4 mm in diameter. It is resinous and cone scales are spirally arranged. Since the cone is incomplete, the number of cone scales could not be determined but probably do not exceed 45. The cone scales have minute, sharp tips which are sometimes incurved. Escutcheons are four-sided and about 2.2-3.1 mm broad and 1.4-1.8 mm high. Their surface are deeply cracked.

The seeds observed in the cone show inverted attachment. No seeds were isolated from the cone but, a large number of dispersed seeds of similar type have been recovered. The seeds are wingless and somewhat triangular (Plate VII, fig. 14), 1.05-1.25 mm long and 0.5-0.75 mm broad. The micropylar end is slightly elongated and occasionally curved.

Discussion on unassigned seed cones: All five types of female cones are characterised by spirally arranged cone scales and cone scale complexes with completely fused bract and ovuliferous scales. The cone types are distinct in form and number of cone scales. The shape of the cones varies from globose to ovoid to elongate and the escutcheons vary in shape, being four-sided or rhomboidal to pentagonous or hexagonous with unequal sides. The latter feature is observed in cone type 2 and 4, but these two cone types differ in shape and size and the partially preserved leaves at the proximal ends of these cones are also morphologically distinct. Cone types 1 and 3 have four-sided or somewhat rhomboidal escutcheons and may be closely comparable. Cone type 3 is distinctly ovoid and has cone scales with shorter spiny apices. Cone type 1 is more elongate and narrow. The cone scales have extended spiny apices and the partially preserved leaves at the proximal end of this cone type also have extended, almost spiny apices. Cone type 5 is distinct from all the other cone types in being small and globose. The cone is resinous and cone scales have minute sharp tips which are occasionally incurved. The small, wingless, triangular seeds of this cone type are unlike the flattened, winged seeds of cone type 1 as well as other winged, dispersed seeds found in the taxodiaceous assemblage.

The various cone types have been segregated mainly on the basis of cone morphology. While cone types 1,2,3 and 4 may be said to be 'sequoioid' in nature, and closely comparable with the cones of extant *Sequoia* and *Sequoiadendron,* they differ in size and number of cone scales. The seeds of two cone types are known and of these the seeds of cone type 1 resemble the winged seeds of *Sequoia* and *Sequoiadendron* as well as *Quasisequoia florinii* Srinivasan & Friis sp. nov., but are much smaller in size. Cone type 5 is distinctly 'taxodioid' in nature in the degree of fusion of ovuliferous and bract scales but does not compare closely with the cones of any modern genus of Taxodiaceae.

Unassigned pollen cones (Plate VIII, figs. 1-9).

Pollen cone type 1: (Plate VIII, fig. 6).

Material: 1 specimen (S100245).

Description and remarks: The cones are small and appear to be attached to the shoot in a cluster of three. Each cone has few tightly packed microsporophylls and details like number of pollen sacs per microsporophyll are not discernible. The cluster of cones is about 1.6 mm long and 2.0 mm broad. Pollen grains are more or less spheroidal, thin walled, asaccate and orbiculate, measuring approximately 20 μm in diameter. The shoot attached to the cones has lanceolate leaves about 1.4 mm long. The leaves are basally appressed to the axis while the free apical portions with convex surface and incurved rounded tips are elongated and spread outwards.

The leaves of the attached shoot are quite unlike any of the foliage shoots described in this work. The material being fragmentary no attempts were made to obtain leaf cuticle preparations. The details revealed by the specimen being insufficient, no generic assignment was possible. However, a comparison with the pollen cones of extant taxodiaceous genera shows the fossil material to be quite distinct. The thin-walled, almost spheroidal and orbiculate pollen grains are comparable with those of extant *Athrotaxis* and *Taxodium.*

Pollen cone type 2: (Plate VIII, figs. 1-5).

Material: 2 detached pollen cones (S100240, S 100241), several detached microsporophylls with pollen sacs (S100242, 100243, 100263, 100302-100304, 100308-100310, and pollen (S100244).

Description and remarks: The complete cone (Plate VIII, fig. 1) is 1.9 mm long and 1.1 mm broad. The incomplete cone (Plate VIII, fig. 2) is open in the longitudinal plane. Microsporophylls are spirally arranged and have almost triangular heads with membranous margins. They are attached to the cone axis by a stalk at an angle of 60°-90°. In the cones, the number of pollen sacs per microsporophyll is not determinable. But detached microsporophylls (Plate VIII, fig. 3), show at least eight basal pollen sacs. The outer wall of pollen sac is composed of cells with thick, undulated walls (Plate VIII, fig. 4). Pollen sacs dehisce longitudinally. Pollen grains (Plate VIII, fig. 5), are more or less spheroidal, thin walled and orbiculate measuring about 17 μm in diameter.

The cones as well as the more commonly occurring detached microsporophylls evidently belonging to the pollen cones of this type, compare closely with the pollen cones of extant *Sequoia* and *Sequoiadendron.* In the number of pollen sacs per microsporophyll and in the spheroidal, thin-walled and orbiculate nature of the pollen grains, the fossil material may, in addition to the two above mentioned modern genera, be compared with *Taxodium.* But, in the absence of any attached foliage shoots no generic assignment is made.

Pollen cone type 3: (Plate VIII, figs. 7-9).

Material: 1 detached cone S 100246 (now macerated), pollen slides S 100246-1 to 100246-11.

Description and remarks: The considerably flattened pollen cone (Plate VIII, fig. 7), was completely macerated for obtaining pollen. The cone, partly broken at the proximal end was about 1.8 mm broad. Pollen *in situ* are small, more or less spheroidal, thin-walled, orbiculate and papillate (Plate VIII, fig. 8), measuring 25 μm in equatorial diameter. The papilla is not prominent and is seen as a small conical projection. Longitudinally split pollen are also observed (Plate VIII, fig. 9).

The fragmentary and compressed cone offers no distinct morphological characters for comparison, but, the pollen *in situ* are characterised by the presence of a papilla. Such papillate pollen are characteristic of most modern genera of Taxodiaceae. The prominence and degree of curvature of papilla varies in the different genera. The fossil papillate pollen although comparable with the pollen of extant *Sequoia, Sequoiadendron, Glyptostrobus, Metasequoia* and *Taxodium,* agrees more closely with the pollen of *Taxodium* in the rather inconspicuous nature of the papilla. Papillate pollen assigned to the genus *Sequoia-pollenites* Thiergart (1937), have been recorded from the Cretaceous deposits of Siberia, United States and Canada (Singh, 1983). The Cretaceous records of such pollen are comparatively fewer than the Tertiary records.

Conclusions

The spiral phyllotaxy, morphological and cuticular characters of the foliage leaves, morphology of attached as well as associated seed cones, details of microsporophylls and pollen, strongly support the assignment of the fossil conifers from Scania to the family Taxodiaceae. However, epidermal characters and morphology of the fossils distinguish them from all the other members of the family, both living and fossil, and three genera *Elatidopsis, Paracryptomeria* and *Quasisequoia* have been established to accommodate some of the fossils. Some seed cones and pollen cones are due to insufficient material, unassigned.

A large number of the hitherto described taxodiaceous taxa are based mainly on impression fossils and these are hardly comparable with the present material. Further,. many modern taxodiaceous species are generally similar in gross morphology and epidermal features are crucial for distinguishing not only genera and suprageneric taxa, but also species (Meyen, 1987). A separation of impression and compression fossils was suggested by Meyen (1969), for other plant groups where epidermal features were considered of systematic importance. Following this suggestion, no attempts have been made to compare the Åsen material with the large number of mainly impression fossils recorded from the Cretaceous (e.g. Heer, 1868, 1874, 1883; Velenovský, 1885, 1887; Velenovský Viniklář, 1926-1931).

The diversity of the Taxodiaceae during the Upper Cretaceous is further evident from the unique Scanian material. The three new genera, *Elatidopsis, Paracryptomeria* and *Quasisequoia* are regarded as extinct members of Taxodiaceae. Although they are not considered as being directly ancestral to any modern genus of Taxodiaceae, they may have played an important role in the evolution of some of the modern members of the family.

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Appendix A: Extant genera of Taxodiaceae

The following descriptions of the genera are based on information from Basinger (1981), Dallimore and Jackson (1966), Erdtman (1943, 1957, 1965), Florin (1931, 1952, 1958), De Laubenfels (1953) as well as personal observations.

Athrotaxis Don: This genus of evergreen trees is endemic to Tasmania and is the only genus of the family with a southern distribution. It includes three species, *Athrotaxis cupressoides* Don, *A. selaginoides* Don and *A. taxifolia* Hooker. The leafy shoots have crowded, spirally arranged leaves which are small, scale-like, appressed or awl shaped to lanceolate and unappressed. The leaves are amphistomatic and only rarely do epistomatic leaves occur together with amphistomatic leaves. The stomata are more or less irregularly oriented on the abaxial surface and are monocyclic or incompletely dicyclic. The subsidiary cells are 4-7 and slightly papillose. Adjacent stomata very frequently share subsidiary cells. The epidermal cells in the non-stomatal zone have straight walls.

The seed cones are globose, solitary and terminal and have 10-25 spirally arranged cone scales. The cone scales are woody and wedge shaped at the proximal ends and have a triangular spiny process at the distal ends. The seeds a re 3-6 per scale and inverted, with two narrow wings. The pollen cones are catkin-like with spirally arranged microsporophylls. Each microsporophyll has 2 pollen sacs. The pollen grains are spheroidal (diameter, 27-30 μm), orbiculate and provided with a small pouting leptoma.

Cryptomeria Don: This genus of evergreen trees is monotypic and native to China and Japan. The single species, *C. japonica* (Linn) Don, has leafy shoots with spirally arranged leaves. The leaves are scale-like, incurved, with apex tapering to a blunt point, keeled and amphistomatic. The stomata are arranged in bands and within the bands the orientation of stomata is more or less irregular. They are completely to incompletely dicyclic. The subsidiary cells are 4-7. Subsidiary cells are rarely shared by adjacent stomata. The epidermal cells in the non-stomatal zone have straight walls.

The seed cones are globose, solitary with 20-30 spirally arranged cone scales. Each cone scale has 3-4 curved, spiny processes at the apex. The bract scale which is partially fused with the cone scale has a free, exerted, reflexed, triangular apex. The growing shoot is sometimes prolonged from the apex of the cone. The seeds are somewhat triangular with very narrow wings and are erect. The pollen cones are in clusters of 20 or more. The microsporophylls are spirally arranged. Each microsporophyll generally has 3 pollen sacs. The pollen grains are spheroidal (diameter, 23.9-39.0 μm), orbiculate and papillate. The papilla is prominent, slightly bent or straight.

TABLE I. Comparison of the fossil species from scania with extant species of Taxodiaceae.

	Athrotaxis cupressoides	Athrotaxis laxifolia	Athrotaxis selaginoides	Cryptomeria japonica	Cunninghamia lanceolata	Cunninghamia konishii	Glyptostrobus lineatus	Metasequoia glyptostroboides	Sciadopitys verticillata	Sequoia sempervirens	Sequoiadendron giganteum	Taiwania cryptomeroides	Taxodium ascendens	Taxodium distichum	Taxodium mucronatum	Quasisequoia florinii sp. nov.	Quasisequoia suecica sp. nov.	Quasisequoia scanica sp. nov.	Quasisequoia aasenensis sp. nov.	Elatidopsis nykvistii sp. nov.	Paracryptomeria elegans sp. nov.
Leaves																					
Spiral	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x
Decussate								x													
In whorls									x												
Dimorphic							x		x	x											
Scale-like	x	x		x			x		x	x	x					x	x	x	x		x
Linear							x	x	x				x	x	x						
Lanceolate			x		x	x				x										x	
Basally twisted					x			x		x				x							
Keeled			x	x								x							x		x
Stomata																					
Amphistomatic	x	x	x	x	x	x	x			x	x	x	x	x	x	x	x	x	x		x
Epistomatic	x																			x	
Hypostomatic					x			x	x												
Stomatal arrangement & orientation on 1.																					
In bands		x	x	x	x	x		x	x	x		x	x	x	x						x
Scattered	x						x				x					x	x	x	x		
Oblique													x	x		x			x		
Transverse													x	x		x			x		x
Longitudinal					x			x	x	x											
Longitudinal basally, oblique or transverse centrally											x						x				
Diverse	x	x	x	x	x		x			x		x					x	x			
Stomatal structure																					
Mainly a									x							x					x
a to incompl. b	x	x	x					x													
a, incompl. to compl. b																	x	x	x		
a, incompl. to compl. b & occasionally incompl. c					x	x															
Incompl. to compl. b				x			x							x							
Compl. b to compl. c												x									
Seed cone																					
Globose	x	x	x	x	x	x		x		x		x	x	x							
Ovoid									x	x	x					x					
Scales																					
Number per cone	10-25	10-25	10-25	20-30	30-40		10-15	20-30	20-35	15-20	35-40		10-15	10-15		33					
Spirally arranged	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x					
Decussately arranged								x													
Four-sided								x		x	x		x	x		x					
With exserted triangular apex	x	x	x																		
With sub-apical teeth							x														
With 3-4 apical spines				x																	

(1 = abaxial surface; a = monocyclic; b = dicyclic; c = tricyclic) Source of information: Dallimore & Jackson (1966), Florin (1931, 1952, 1958) and personal observations.

Cunninghamia (Richard) Brown: This extant genus includes two species, *C. lanceolata* (Lamb) Hooker and *C. konishii* Hayata. The latter species is native in Taiwan, while the former is native to China. The leafy shoots have spirally arranged, narrow, lanceolate leaves with finely toothed margins. They are without stalks and are often twisted at the base. The leaves are amphistomatic, although a mixed occurrence of hypostomatic and amphistomatic leaves is seen in this genus. The stomata are arranged in distinct bands and within the bands the stomata are more frequently longitudinal. The stomata are monocyclic or incompletely to completely dicyclic and very rarely incompletely tricyclic. The subsidiary cells are 4-7. Adjacent stomata rarely share subsidiary cells. The epidermal cells in the non-stomatal zone have undulating anticlinal walls.

The seed cones are globose or ovoid, solitary or several together. The cone scales have toothed margins and a long, spiny apex. The seeds are 3 per scale, narrowly winged and inverted. The pollen cones are in clusters of 10-12. The microsporophylls are spirally arranged and each microsporophyll has 2-3 pollen sacs. The pollen grains are somewhat spheroidal (diameter, 30-50 μm), orbiculate and provided with a pore-like aperture.

Glyptostrobus Endlicher: This genus is native to China. It is monotypic, being represented by a single species *G. lineatus* (Poiret) Druce. The leafy shoots have spirally arranged, dimorphic leaves. On the terminal branchlets, the leaves are linear and those on the fertile shoots and persistent vegetative branchlets, are scale-like and overlapping. The leaves are amphistomatic. The stomata are rather irregularly oriented. They are incompletely to completely dicyclic. The subsidiary cells are 4-7. Adjacent stomata rarely share subsidiary cells. The epidermal cells in the non-stomatal zone have straight walls.

The seed cones are pear-shaped and stalked and have 10-15 cone scales. Each cone scale is obovate, with wart-like sub-apical teeth and a central triangular mucro. The seeds are oblong, with a terminal, thin wing, inverted and are 2 per scale. The pollen cones are solitary and ovoid, with spirally arranged microsporophylls. Each microsporophyll has 3-4 pollen sacs. The pollen grains are somewhat spheroidal (diameter, 29-31 μm), orbiculate and papillate. The pollen grains are more or less similar to those of *Cryptomeria* and *Metasequoia*.

Metasequoia Miki: This genus was first established on fossil material by Miki (1941), from the Pliocene deposits of Japan. The living species, *M. glyptostroboides* Hu et Cheng. was discovered later (Hu, 1948). The branchlets are of two kinds, persistent and deciduous. The foliage leaves are decussately arranged, uninerved, with a bifacially flattened, linear lamina and a decurrent base. The leaves are hypostomatic. The stomata are arranged in two broad bands on the abaxial surface and within the band, the stomata are mainly longitudinally oriented. The stomata are monocyclic or incompletely dicyclic. The subsidiary cells are 4-8. Adjacent stomata rarely share subsidiary cells. The epidermal cells in the non-stomatal zone have undulating walls.

The seed cones are terminal, solitary and subglobose. The cone scales are 20-30 in number, decussately arranged, ovate to shield-shaped. The seeds are 2-9 per scale, inverted and have thin wings. The pollen cones are axillary, decussate on long spikes or panicles. Each pollen cone is ovoid, with 15-20 microsporophylls, not strictly decussate in arrangement. Each microsporophyll has 2-3 pollen sacs. The pollen grains are spheroidal (diameter, 19-30 μm), orbiculate and papillate. The papilla forms a small conical projection which has a sharply curved tip.

Sciadopitys Siebold & Zuccarini: This monotypic genus is native to Japan and is quite distinct from all the other extant genera of the Taxodiaceae. The species *S. verticillata* (Thunberg) Siebold & Zuccarini, has dimorphic leaves. The small scalelike leaves are distantly placed and spirally arranged, whereas, the linear, grooved leaves which consist of 2 leaves fused together, are arranged in whorls and subtended by a ring of scale leaves. The mature leaves are hypostomatic. The orientation of stomata in the stomatal band is mainly longitudinal. The stomata are monocyclic. The subsidiary cells are 4-8 and are strongly papillose and cutinized. Adjacent stomata very frequently share subsidiary cells. The epidermal cells in the non-stomatal zone generally have straight walls.

The seed cones are large, terminal, oblong to ovoid, on short stalks. The cone scales (? 20-35) are spirally arranged, woody, wedge-shaped, with a furrowed surface. The seeds are 5-9 per scale and are oblong, inverted, with narrow wings. The pollen cones are in compact clusters. Each microsporophyll has 2 pollen sacs. The pollen grains are spheroidal (diameter, 27.7-44 μm), and the thick ektexine is provided with densely placed rounded warts. The pollen grains are morphologically distinct from those of other extant taxodiaceous genera.

Sequoia Endlicher: This monotypic genus is confined to the coastal region of California, U.S.A. The species *S. sempervirens* (D. Don) Endlicher, has spirally arranged, dimorphic leaves. The leaves are lanceolate and twisted at the base on the lateral branchlets. On the fertile shoots the leaves are loosely appressed or slightly spread outwards. The leaves are amphistomatic and the stomata occur in irregular files. In the adult leaves the stomatal orientation is longitudinal in the decurrent part, mostly transverse in the basal and central part and rather irregular in the apical part. The stomata are completely dicyclic or occasionally incompletely tricyclic. The subsidiary cells are 4-6. Adjacent stomata rarely share subsidiary cells. The epidermal cells in the non-stomatal zone have straight walls.

The seed cones are terminal, ovoid to globose with 15-20 spirally arranged cone scales. The cone scales are peltate, wrinkled and hard. The seeds are inverted, winged and 5-7 per scale. The pollen cones are terminal and axillary and have spirally arranged microsporophylls. Each microsporophyll has 2-5 (usually 3) pollen sacs. The pollen grains are spheroidal (diameter, 25-35 μm), orbiculate and papillate. The papilla is distinct but shorter than in *Sequoiadendron.*

Sequoiadendron Buchholz: This monotypic genus represented by a single species *S. giganteum* (Lindley) Buchholz, is confined to California, U.S.A. The leafy shoots have spirally arranged leaves. The leaves are scale-like and amphistomatic. The stomatal orientation is longitudinal in the basal part of the leaf, and oblique or transverse in the central and apical parts of the leaf. The stomata are completely dicyclic or very seldom incompletely tricyclic. The subsidiary cells are 4-6. Adjacent stomata rarely share subsidiary cells. The epidermal cells in the non-stomatal zone have straight walls.

The seed cones are solitary, terminal and ovoid, with 35-40 spirally arranged cone scales. The scales are four-sided with a central depression. The seeds are numerous per scale. They are flat, oblong, winged and inverted. The pollen cones are terminal, with spirally arranged microsporophylls. Each microsporophyll has 2-5 (usually 3) pollen sacs. The pollen grains are spheroidal (diameter, 28-41 μm), orbiculate and papillate. The papilla is prominent and sometimes has a curved tip.

Taiwania Hayata: This genus is represented by a single species, *T. cryptomeroides* Hayata, and is native to Taiwan, China and N. Burma. The leafy shoots have spirally arranged leaves. Mature leaves are leathery, triangular and keeled and have incurved, pointed apex and are amphistomatic. The stomata are in bands and within the bands they are irregularly oriented. The stomata are completely dicyclic to completely tricyclic. The subsidiary cells are 4-7 and are rarely shared by adjacent stomata. The epidermal cells in the non-stomatal zone have straight walls.

The seed cones are sub-globose with numerous, spirally arranged, overlapping cone scales. Each scale has a minute bract at the base. The seeds are broadly winged, inverted and are 2 per scale. Pollen cones are small and sub-globose. There are usually 2 pollen sacs per microsporophyll. The pollen grains are spheroidal (diameter, 20-32 μm), orbiculate and papillate. The papilla is not prominent and forms a small conical projection.

Taxodium Richard: This genus is represented by three species, *T. ascendens* Brongniart, *T. distichum* (L.) Richards and *T. mucronatum* Tenore. The first two species are native to N. America while the third is native to Mexico. The trees are deciduous. The leaves are spirally arranged to alternate, flat, with a basal twist or awl shaped, incurved and pressed to the axis and are amphistomatic with mainly transversely or obliquely oriented, incompletely to completely dicyclic stomata. The subsidiary cells are 4-7 and are rarely shared by adjacent stomata. The epidermal cells in the non-stomatal zone have straight walls.

The seed cones are globose to ovoid with short stalks and have 10-15 spirally arranged, hard, peltate, four-sided cone scales. Each scale has 2 seeds which are triangular, erect and 3-winged. The pollen cones are in long, terminal panicles. Individual pollen cones are small, globose with few spirally arranged microsporophylls. There are 5-9 pollen sacs per microsporophyll. The pollen grains are somewhat spheroidal (diameter, 25-37 μm), orbiculate and papillate. The papilla is not prominent as in *Cryptomeria* or *Sequoiadendron,* but forms a small conical projection.

Appendix B:
Fossil genera of Taxodiaceae

Athrotaxites Unger (1849): This genus was instituted for a branched fertile shoot from the Upper Jurassic of Solenhofen, Bavaria resembling extant *Athrotaxis*. The type species *A. lycopodioides* Unger (1849) agrees closely with Recent *Athrotaxis cupressoides* in its crowded, imbricate leaves and the globose cones. The cone scales have thick spinous distal ends similar to those of the recent genus (Seward, 1919). *Athrotaxites ungeri* Halle (1913a) is based on fertile specimens from San Martin flora of Patagonia, probably of Late Jurassic or Wealden age. The species *Athrotaxites berryi* was first described from the Lower Cretaceous of Canada by Bell (1956). Following the discovery of compressions and impressions

TABLE II. Comparison of Quasisequoia with other fossil genera showing sequoioid characters.

	SEQUOIITES	SEQUOIOPSIS	PARASEQUOIA	PROTOSEQUOIA	AUSTROSEQUOIA	QUASISEQUOIA present work
LOCALITY	Haering (Austria)	Crue, Saint Mihiel (France)	Primorie (U.S.S.R.)	Honshu (Japan)	Winton (Australia)	Åsen (Sweden)
Age	Early Tertiary	Jurassic	Early Cretaceous	Late Tertiary	probably Late Cretaceous	Late Cretaceous
Mode of preservation	Impression	Impression	Compression	Compression	Petrifaction	Compression
Parts known	Foliage + seed cone	Foliage shoot	Foliage shoot	Foliage shoot + seed cone + pollen cone	Shoot with seed cone attached	Foliage shoot + seed cone
Leaf arrangement	-	Spiral	Alternate	Spiral	Spiral	Spiral
Leaf shape	Squamiform (scale-like) - linear	Squamiform (scale-like)	Linear	Scale-like	Scale-like	Rhomboidal (scale-like)
Leaf apex	Acuminate	Acuminate	Acute	-	Acute-acuminate	Bluntly rounded -sub-acute/acute
Stomatal distribution	-	-	Hypostomatic	On upper side	-	Amphistomatic
Shape of seed cone	Sub-conical	-	-	Elliptic or orbicular (ovoid-round)	Ellipsoidal (ovoid)	Ovoid
Number of cone scales	-	-	-	-	29-49	About 33
Shape of cone scales/escutcheon	Peltate	-	-	-	Transversely rhomboidal - hexagonal	Transversely rhomboidal
Median transverse groove on cone scales	-	-	-	-	Present	Absent
Seeds	-	-	-	Wings inconspicuous	-	Winged, wings inconspicuous

of leafy twigs, pollen cones and seed cones of this species from the Lower Cretaceous of Montana, an emended diagnosis was provided by Miller and LaPasha (1983). According to Miller and LaPasha (1984), the leaves in *A. berryi* Bell, are scale-like and hypostomatic and the stomata are arranged in longitudinal rows. Each microsporophyll of the pollen cone has two or more pollen sacs. Each seed cone has at least 20 spirally arranged bract-scale complexes. According to the latter authors *A. berryi* shows many but not all characters of the extant *Athrotaxis cupressoides*.

Athrotaxopsis Fontaine (1889): This genus was proposed for some fertile coniferous shoots from the Lower Cretaceous of Fredericksburg and near Brooke, N. America. According to Fontaine (1889), the leaves of *Athrotaxopsis* are thin, scale-like, elliptical, rhombic or oblong and the spirally arranged cone scales are woody, thick, wedge-shaped in the basal part and expanded at the free ends and the elliptical seeds are one per scale and many of these characters are strikingly similar to the extant *Athrotaxis*. Of the four species, *Athrotaxopsis grandis, A. tenicaulis, A. pachyphylla* and *A. expansa,* described by Fontaine (1889), Berry (1911) considers *A. tenicaulis* and *A. pachyphylla* to be identical with *A. grandis* and based on Seward's suggestion (1895), considers *A. expansa* to include specimens of *Sphenolepis kurrianus* (Dunker) Schenk (1871) and *Sequoia ambigua* Heer (1874).

Austrosequoia Peters & Christophel (1978): This genus is based on a petrified fertile shoot from Queensland, Australia and believed to be from the Upper Cretaceous. The single species *A. wintonensis* Peters and Christophel (1978) has an ellipsoidal seed cone with about 29-49 spirally arranged cone scales. The cone scales are peltate, transversely rhomboidal to hexagonal in dorsal view. The ovules are 4-7, in a single row and inverted. The leaves of the shoot bearing the cone are rhomboidal with acute-acuminate apex and keeled. The cone is considered to be more similar to those of extant *Sequoia sempervirens* and *Sequoiadendron giganteum* than *Athrotaxis*.

Cryptomeriopsis Stopes & Fujii (1910): The genus was instituted for petrified twigs from the Upper Cretaceous of Japan, that resemble modern *Cryptomeria* in their structural features. In the type species *C. antiqua* Stopes and Fujii, the axis is devoid of resin canals and xylem parenchyma, and the tracheids have uniseriate, circular, separate bordered pits. Although Jeffrey (1910) strongly favoured the inclusion of *Cryptomeriopsis* in the Araucarineae, Stopes (1911) considered the vegetative shoots to be comparable with *Cryptomeria* rather than *Araucaria* (Seward, 1919).

Cryptomerites Bunbury (1851): This name was provisionally proposed for branched vegetative shoots from the Jurassic of Scarborough and Whitby, England. Bunbury (1851) considered the species *C. divaricatus* to resemble modern *Cryptomeria, Araucaria* and *Cunninghamia* in leaf morphology. The leaves of the fossil species are two-ranked, alternate to nearly opposite, and taper from the decurrent base to a sharp point. The leaves on the main axis are more distantly placed and stiff and almost spinous in appearance. No fructifications are known. Harris (1951) included *C. divaricatus* in *Elatides*. But, based on cuticle differences between the two genera, Harris (1979), placed *Cryptomerites* in *Geinitzia*, restricting the genus *Elatides* to species with female cones like those of *Elatides williamsonii*. An emended diagnosis of *Geinitzia divaricata* has been provided by Harris (1979). The spirally arranged leaves taper evenly from base to an acute apex and the larger leaves arise perpendicular to the axis. The imperfectly known cuticles do not reveal the stomatal arrangement, but most stomata are transversely oriented with slightly sunken guard cells and not much specialized subsidiary cells. The genus *Cryptomerites* was also proposed by Brongniart (1849) for *Cupressites ulmanni* Bronn (1837).

Cunninghamiostrobus Stopes & Fujii (1910): This genus including a single species *C. yubariensis* was first reported from the Upper Cretaceous of Japan by Stopes and Fujii (1910). The genus is based on petrified specimens resembling the cones of extant *Cunninghamia* in their size, form and anatomical features. Another species *C. hueberi* has been reported by Miller (1975) from the Lower Cretaceous of California, U.S.A. This species is based on petrified seed cones and needle bearing twigs, earlier described as species of *Abietites, A. californicus* Fontaine and *A. ellipticus* Fontaine, (Miller, 1975). The seed cones of *C. hueberi* are ellipsoid, borne laterally and terminally with spirally arranged cone scale complexes. The bract is conspicuous and the ovuliferous scale is reduced to a pad of tissue. The seeds are round and flat, and are three per scale.

Cunninghamites Presl (1838) in Sternberg 1838 (1820-1838): Another genus for coniferous shoots resembling extant *Cunninghamia* is *Cunninghamites* Presl, from the Jurassic and Lower Cretaceous of Saxony, Germany. According to Seward (1919), this genus does not afford any real evidence of affinity to the recent conifer, although the vegetative shoots assigned to *Cunninghamites* by several authors have linear-lanceolate leaves with a distinct mid-rib and finely serrate margins as in extant *Cunninghamia*. Some specimens have been transferred to *Elatocladus* by Halle (1913b) and according to Seward (1919), some may be allied to *Araucaria* De Jussieu.

Elatides Heer (1876): This coniferous genus is abundant from the Middle Jurassic to Lower Cretaceous. Nathorst (1897) revised Heer's type species *E. ovalis* Heer (1876) and renamed it as *E. curvifolia* (Dunker) Nathorst. An emended diagnosis of the genus *Elatides* is given by Harris (1979) and is based on information from *E. williamsonii* (Lindley & Hutton) Nathorst and *E. bommeri* Harris (1953). The leaves are persistent and spirally arranged and diverge radially from decurrent cushion. The presence of a single abaxial resin canal, stomata crowded in bands on the flat sides and transversely or irregularly oriented, papillate subsidiary cells; oval, terminal female cone with spirally arranged cone scales; oval, unwinged, flattened seeds; terminal clusters of pollen cones with spirally arranged microsporophylls, 3 fused pollen sacs per microsporophyll and spheroidal pollen grains with an inconspicuous pore are some of the important characters of this genus. According to Harris (1979) these characters match that of one or more extant genera of Taxodiaceae, *Cunninghamia* being the closest in cuticular anatomy, although not in leaf morphology. Other species of this genus include *E. thomasii* Harris (1979) from the Jurassic of Yorkshire, England, *E. falcifolia* Teixeira (1948) from the Lower Cretaceous of Portugal, *E. asiatica* (Yokoyama) Krassilov (1967) from the Lower Cretaceous of eastern Asia, and *E. harrisii* Zhou Zhiyan (1987) from the Lower Cretaceous beds of Liaoning, China.

Farndalea Bose (1955a): This genus was first established by Bose based on cuticle fragments obtained from macerating rock samples from various Jurassic localities in Yorkshire. According to Bose (1955a), the affinities of this genus are taxodiaceous and the cuticle are comparable with those of *Sequoia sempervirens* and *Cryptomeria japonica*. This genus has been discarded and placed under *Pagiophyllum fragilis* by Harris (1979) who provides a slightly modified diagnosis. The characters of *P. fragilis* (Bose) Harris include triangular, bifacial, non-petiolate leaves with acute to obtuse apices, two well marked adaxial stomatal bands and few abaxial stomata in larger leaves.

Kanevia Doludenko, Kostina & Shilkina (1988): This coniferous genus is based on silicified leafy shoots and female cone from the Late Albian of the Ukraine and represented by two species *K. pimenoviae* and *K. teslenkoi*. The spirally arranged leaves are awl shaped, keeled and rhomboidal to triangular in transverse section. The outer wall of the epidermal cells of the leaves are strongly thickened. The hypodermis is 3-4 layered and the mesophyll consists of undifferentiated, rounded parenchyma cells. Besides central resin canals there may also be smaller laterally distributed resin canals. The axis has primary and secondary cortex which contain large resin canals and sclerenchymatous fibres. Primary and secondary phloem are also present. The female cone is terminal, oval, 35-40 mm long and 30 mm in diameter. The cone scales are thick and dense and have a beak-like or spiny apex which is incurved. Based on leaf morphology, the genus *Kanevia* is considered as resembling extant *Araucaria* and *Cryptomeria* and the type species *K. pimenoviae* which was earlier described as *Cryptomeria pimenoviae* (Doludenko & Shilkina, 1985), is considered to be close to *Elatides bommeri* Harris, and may possibly belong to one and the same genus.

Margeriella Page (1973): *M. cretacea* Page (1973), is based on silicified wood and leaves from the Upper Cretaceous (Maastrichtian) of California. The leaves are spirally arranged, apetiolate and amphistomatic. The monocyclic stomata are arranged in two longitudinal bands on the abaxial surface and clusters of thickwalled fibres are scattered throughout the leaf. The wood is composed of tracheids with a single row of bordered pits on the radial walls and low uniseriate rays. The cortex of the wood is thick and contains resin canals and leaf traces. The pith cells are irregular in shape and size. The epidermis of the leaves is considered to be similar to some Recent Taxodiaceae like *Sequoia, Sequoiadendron, Taiwania, Glyptostrobus* and *Cryptomeria,* and the wood is classified as the *Cupressinoxylon* type.

Nephrostrobus LaPasha & Miller (1981): This is a petrified seed cone genus described from the Upper Cretaceous of New Jersey, U.S.A. and includes two species *N. cliffwoodiensis* and *N. bifurcatus*. The seed cones are oblong with spirally arranged cone scales and the bract scale complexes are peltate. The vascular cylinder of the cone axis is surrounded by a single ring of resin canals. There is atleast one flattened and possibly winged seed per scale. The fossil cone is considered to be comparable with the cones of modern *Sequoia, Sequoiadendron* and *Metasequoia* in its internal characters.

Pararaucaria Wieland (1935), Stockey (1977): This genus is based on petrified seed cones from the Middle Jurassic Cerro Cuadrado beds of Patagonia, Argentina. The species *P. patagonica,* is composed of nearly 40 bract-scale complexes arranged spirally on the cone axis. There is a single, winged, inverted seed per scale. The cone shows a combination of characters of both Taxodiaceae and Pinaceae. Its polyembryonic character is comparable with *Sequoia* and *Taxodium,* single seeded ovuliferous scale is comparable with that of *Taiwania,* and the degree of fusion of bract and scale is comparable with *Cryptomeria,* but, its winged seeds and vascularization of the bract-scale complexes suggest a relationship to the Pinaceae (Calder, 1953).

Parasequoia Krassilov (1967): The genus *Parasequoia* Krassilov includes a single species *P. cretacea* from the Lower Cretaceous of Primorja, U.S.S.R. The species is characterised by shoots with alternately distributed linear leaves with acute apices and decurrent bases. The leaves are hypostomatic, predominantly with longitudinally oriented stomata. The fossil genus is considered to be comparable with extant *Sequoia sempervirens.*

Parataxodium Arnold & Lowther (1955): This genus was instituted for leafy shoots, seed and pollen cones from the Upper Cretaceous of Alaska, U.S.A. The genus is represented by a single species *P. wigginsi* Arnold and Lowther and has also been reported from the Cretaceous beds of Russia (Krassilov, 1971) and Spitsbergen (Schweitzer, 1974). Although the leaves, seed cones and pollen cones of *Parataxodium* are morphologically similar to extant *Metasequoia,* the phyllotaxy of the fossil genus is spiral as in extant *Taxodium.*

Protosequoia (Miki) Miki (1969): This genus was established for compressed foliage shoots and fertile shoots from the Tertiary beds of Honshu, Japan which were earlier described as *Sequoiadendron primarium* Miki (1965). The cones are elliptic or orbicular with a short peduncle, borne terminally on lateral twigs. The convex cone scales are spirally arranged and have many stomata on their surface. The seeds are obovate and without distinct wings. The leaves on the shoots are scaly with irregularly arranged stomata on the upper face. While some characteristics of this fossil genus are considered close to the extant *Sequoia* and *Sequoiadendron,* it is not identical to them.

Rhombostrobus LaPasha & Miller (1981): The single species *R. cliffwoodiensis* LaPasha and Miller (1981) is based on petrified material from the Upper Cretaceous of New Jersey, U.S.A. The seed cones are oblong and have spirally arranged cone scales. The bract-scale complexes are wedge-shaped and rhombic in cross section. The seeds are inverted and laterally winged. The fossil cone is considered to resemble extant *Cunninghamia* in the arrangement of the vascular strands and *Sequoia* in the relative amount of bract and ovuliferous scale making up the cone-scale complex.

Romeroites Spegazzini (1924): *R. argentinensis* is a petrified seed cone from the Jurassic of Patagonia, Argentina with about 25 spirally arranged bract-scale complexes. The peltate heads formed by the fusion of bract and ovuliferous scale resemble those of modern *Sequoia,* but, the thin ovuliferous scales bear many erect seeds.

Sciadopitophyllum Christophel (1973): This genus is based on compressed specimens of shoots and leaves from the Late Cretaceous of western Canada. It is represented by a single species *S. canadense* which has foliar shoots bearing whorls of lanceolate leaves, each whorl being subtended by a group of scale leaves also arranged in a whorl. The epidermal details of the fossil leaves are not known but the fossils are considered to be strikingly similar to the modern *Sciadopitys* in leaf morphology.

Sciadopitytes Goeppert & Menge (1883): *Sciadopitys*-like leaves have been described from the Middle Miocene of the Baltics by Goeppert and Menge (1883), under two species, *S. linearis* and *S. glaucescens.* The leaves preserved in the Baltic amber are described as having a single vein on the upper surface and two veins on the lower surface, although the morphological feature represented by these 'veins' is not clear (Seward, 1919). Halle (1915) described two species of *Sciadopitytes, S. nathorsti* and *S. crameri,* of which the latter was originally described as *Pinus crameri* Heer (1868). The leaves of these species are reported to have epidermal characters almost similar to extant *Sciadopitys.* In the fossil leaves the dorsal groove is protected by elongated papillae and the stomata in the groove are large and may or may not be crowded. Florin (1922) described several species of *Sciadopitytes* from the Early Cretaceous of Greenland, Mid-Jurassic of Norway and the Late Jurassic of Scotland.

Sciadopitytes variabilis Bose (1955b) from the Lower Cretaceous of Arctic Canada includes leaves and pollen. The leaves are linear and have slightly swollen base. The stomata are in bands in a groove on the lower surface. The thickened guard cells are not sunken beneath the surface and papillae are present along the stomatal groove. Pollen grains from the macerated samples are spherical and almost identical to the pollen of extant *Sciadopitys.* However, all known Mesozoic leaf species hitherto included in *Sciadopitytes* and *Sciadopitys* have been transferred to the genus *Scaidopityoides* Sveshnikova (1981). This genus is included in Pinopsida, but is not assigned to any family.

Sequoiopsis Saporta (1884): The genus was instituted for branched leafy shoots from the Jurassic of France. According to Saporta (1884), the shoots with spirally arranged, imbricate and squamiform leaves are comparable with extant *Sequoia.* The genus is represented by three species, *S. buvignieri* and *S. echinata* described by Saporta (1884) and *S. perucensis* described by Velenovský and Viniclář (1926) from the Early Cretaceous of Bohemia.

Sequoi(i)tes Brongniart (1849): This genus is based on impressions of foliage and cones from the Tertiary beds of Haering, Austria, and which were described as *Cupressites taxiformis* Unger (1841-1847).

According to Brongniart (1849) the specimens of *C. taxiformis* resemble closely the extant *Sequoia sempervirens* and *Sequoia (Sequoiadendron) giganteum*. Based on superficial resemblance of the cones of *C. taxiformis* to the cones of extant *Cupressus,* Seward (1919) favours a retention of the genus *Cupressites,* and at the same time adopts the generic name *Sequoiites* for several fossil species originally described as *Sequoia giganteoides* Stopes (1915), *S. concinna* Heer (1883) and *S. couttsiae* Heer (1862). Dorofeev and Sveshnikova (1963) have included Unger's *Cupressites taxiformis* (Unger, 1841-1847; Pl. 9, fig. 1 & 2) under *Athrotaxis taxiformis.*

Sewardiodendron Florin (1958): This Jurassic genus was established for vegetative coniferous shoots from the Middle Deltaic Gristhorpe bed and few localities of the Yorkshire Lower Deltaic flora. Combined under the species *S. laxum* (Phillips) Florin (1958) are *Taxites podocarpoides* Brongniart (1828), *Taxites laxus* Phillips (1875) and *Taxites brevifolius* Nathorst (1880). According to Florin (1958), the leaf morphology and epidermal characters of *S. laxum* are comparable with *Cunninghamia* of the Taxodiaceae and are not related to any member of the Taxopsida. The leaves of *S. laxum* are spirally disposed, appearing two-ranked on stronger shoots, spreading in all directions and are twisted at the base. The bifacial, linear-lanceolate to triangular-lanceolate leaves are hypostomatic with well-marked stomatal band on either side of mid-rib. The non-papillose subsidiary cells slightly overarch the periphery of the stomatal pit. Although agreeing to the taxodiaceous affinities of the species, Harris (1979) places *S. laxum* under *Elatocladus laxus* (Phillips) Harris. Many other species of *Elatocladus* Halle (1913a) have been placed in the Cephalotaxaceae.

Sphenolepis Schenk (1871): This genus was instituted for coniferous shoots and cones from the Wealden Formation of Germany. The generic name was changed to *Sphenolepidium* by Heer (1881). The International Rules of Botanical nomenclature require the use of the earlier name *Sphenolepis* Schenk, and Harris (1953) provided an emended diagnosis. The shoots of *Sphenolepis* have spirally arranged scale-like leaves. The monocyclic stomata are mostly transversely placed and form two bands on the cushion and lower sides of the leaf. A single short resin canal is present on the abaxial side. The small, globose female cones are terminal and have numerous spirally arranged cone scales with truncate apices. There are six seeds per scale, arranged in two rows and the seeds are small, flattened, unwinged and inverted. The type species *S. kurrianus* (Dunker) Schenk 1871, principally exhibits characters of *Sequoia, Athrotaxis, Taiwania* and *Cunninghamia* (Harris, 1953).

Taxodiophyllum Van der Burgh & Van Konijnenburg-van Cittert (1984): *Taxodiophyllum scoticum* Van der Burgh & Van Konijnenburg-van Cittert (1984) described from the Upper Jurassic of Sutherland, Scotland, is based on flat, linear, single veined leaves that are hypostomatic. The lower cuticle has more than one stomatal band on either side of the vein and the stomata are longitudinally oriented. The subsidiary cells rarely show papillae. The cuticles of the fossil species have been compared with those of several extant species of Taxodiaceae. *T. scoticum* and *Masculostrobus zeilleri* Seward (1911), are believed to belong to the same plant (Van Konijnenburg-van Cittert, 1988).

In addition to the above fossil genera, there are a large number of fossil species attributed to various modern genera like *Athrotaxis, Cryptomeria, Glyptostrobus, Metasequoia, Sciadopitys, Sequoia, Sequoiadendron, Taiwania* and *Taxodium.* Most of these have been described from the Late Cretaceous onwards and mainly from the Northern Hemisphere. Many of the species are based on impressions but several species have been described with cuticular details (Boulter, 1969; Kilpper, 1968; Sveshnikova 1967).

The two Jurassic species of *Sequoia, S. jeholensis* Endo (1951) from Manchuria and *S. problematica* Fliche & Zeiller (Seward, 1919) from France, are based on impressions of foliage shoots and cone respectively. In both these species, affinity with extant *Sequoia* is based on superficial appearance of the fossil (Miller, 1977). Velenovský (1885, 1887) described several species of *Sequoia* from various Lower Cretaceous localities of Bohemia. *S. crispa, S. microcarpa, S. heterophylla* described by Velenovský (1885), *S. minor, S. major* described by Velenovský (1886 and 1887) and *S. affinis* and *S. cylindrica* recorded by Velenovský and Viniklář (1926-1931), are based merely on superficial resemblance of the fossils to extant *Sequoia* and do not afford any evidence of affinity to the modern genus.

Heer, in his voluminous works "Flora Fossilis Arctica" (1868, 1871, 1874, 1877, 1878, 1880, 1883), involving a study of the Cretaceous and Tertiary floras of the Arctic, described a large number of *Sequoia* species based mainly on impressions of foliage shoots and cones. Following the discovery of the living *Metasequoia* in 1945, Chaney (1951) undertook a revision of fossil *Sequoia* and *Taxodium* in western North America and at the same time made a survey of the *Sequoia* and *Taxodium* species in Heer's "Flora Fossilis Arctica". Chaney (1951) suggested that the Cretaceous *Sequoia langsdorfi* (Brongniart) Heer and *S. smittiana* Heer (in part) from Greenland, may well be assignable to *Metasequoia* and that *S. ambigua* Heer, *S. fastigiata* (Sternberg) Heer, *S. concinna* Heer, all from Cretaceous of Greenland and *S. gracilis* Heer and *S. reichenbachi* (Geinitz) Heer, from Greenland and Spitzbergen are conspecific and resemble the extant *Sequoiadendron giganteum*. Seward (1926) has placed several specimens of *Sequoia fastigiata, S. reichenbachi,* and *S. subulata* described by Heer from Greenland, under the species *Sequoia concinna*. According to Chaney (1951), the Arctic Tertiary species of *Sequoia* recorded by Heer, *Sequoia langsdorfii* (Brongniart) Heer, *S. brevifolia* Heer, and *S. disticha* Heer show foliage characters of *Metasequoia,* whereas, *S. couttsiae* Heer, *S. sternbergi* (Goeppert) Heer, *S. sibirica* Heer resemble extant *Sequoiadendron giganteum* and *S. nordenskiöldi* may be referable to *Glyptostrobus*.

From among the hitherto described North American fossil species of *Sequoia,* Chaney (1951) retained two species, *Sequoia dakotensis* Brown (1935) from the Upper Cretaceous and *S. affinis* Lesquereux (1876) from the Tertiary and included in the latter species all the Tertiary material of *Sequoia* from western North America. From a survey of the "Upper Cretaceous flora of Alaska" described by Hollick (1930), Chaney (1951) considered the probable presence of a single species of *Sequoia, S. reichenbachi* characterised by foliage with scale-like leaves and placed the Alaskan Tertiary species of *Sequoia* described by Hollick (1936) under two main genera *Taxodium* and *Metasequoia*. Foliage and peltate cone scales referred to *Sequoia reichenbachi* have also been reported from the Lower Cretaceous beds of Bohemia by Velenovský (1885). According to Seward (1919), many of the *Sequoia* species from the Jurassic and especially the Lower Cretaceous strata do not withstand close scrutiny.

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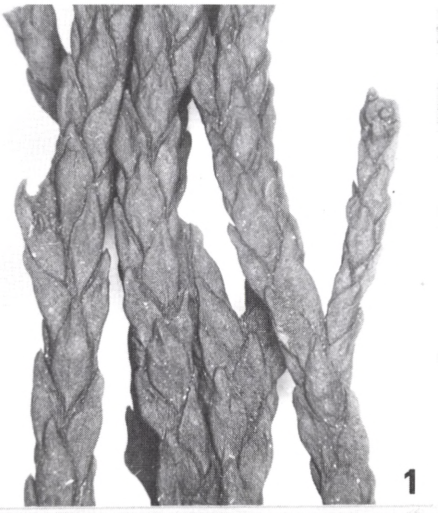
Plates I-VIII

PLATE I

Fossil *Quasisequoia florinii* Srinivasan & Friis sp. nov. from the Santonian/ Campanian of Scania, Sweden.

1. Holotype. Branched foliage shoot with spirally arranged leaves (S 100193, x 5).
2. Holotype. Scale-like, appressed leaves (S 100193, x 10).
3. Appressed leaves with bluntly rounded apex (S 100194, x 25).
4. Leaf enlarged to show stomatal distribution on abaxial surface (S 100194, x 100).
5. Inner surface of abaxial cuticle showing mainly obliquely or transversely oriented stomata (S 100195, x 200).
6. Inner surface of adaxial cuticle showing contiguous stomata with some showing lens-shaped pits in the guard cell wall (S 100195, x 600).
7. Inner surface of abaxial cuticle showing stomatal apparatus with six subsidiary cells (S 100195, x 600).
8. Inner surface of abaxial cuticle showing stomatal apparatus and granular surface of ordinary epidermal cells in the stomatal zone (S 100196, x 600).

Figs. 1,2 reflected light micrographs, figs. 3-8 SEM.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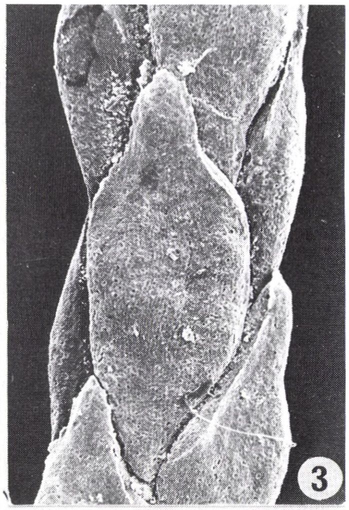
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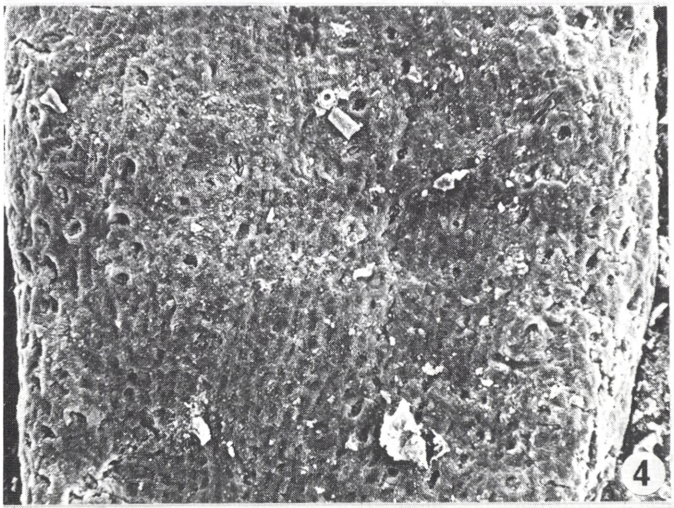
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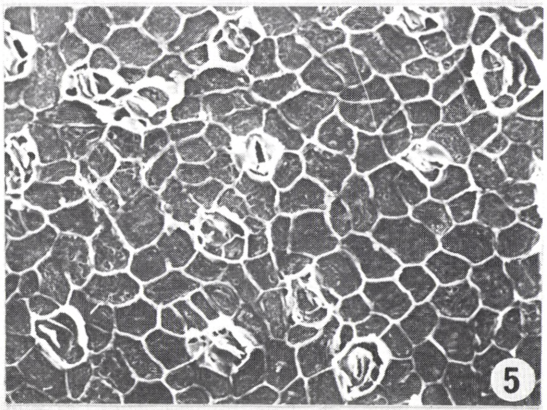
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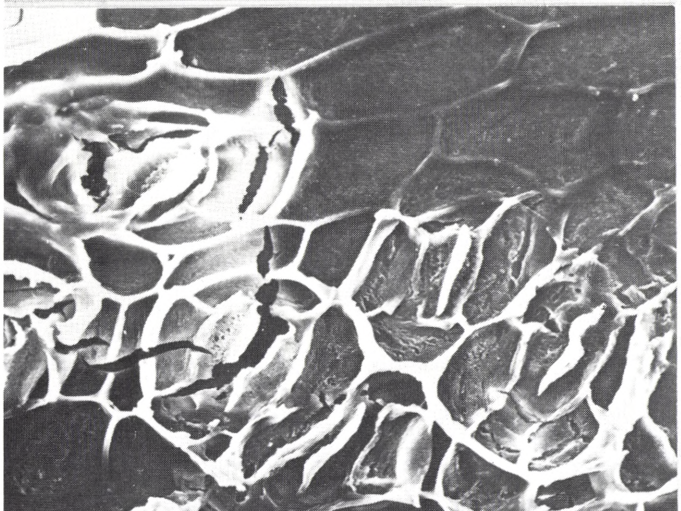
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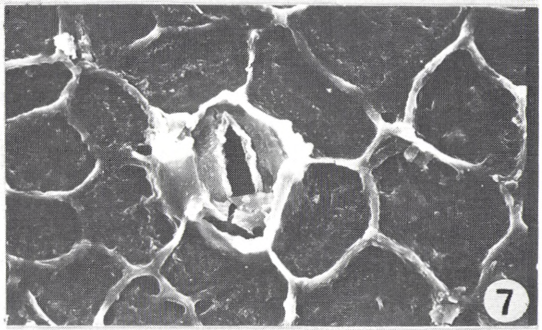
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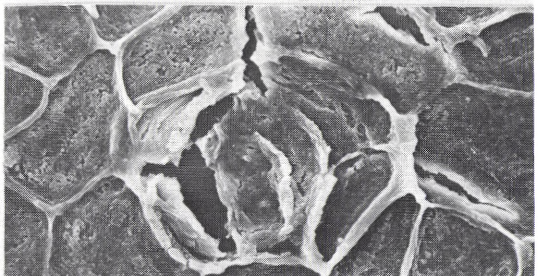
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PLATE II

Fossil *Quasisequoia suecica* Srinivasan & Friis sp. nov. from the Santonian/ Campanian of Scania, Sweden.

1. Shoot with spirally arranged, young appressed leaves (S 100200, x 10).
2. Holotype. Shoot with scale-like leaves having slightly incurved, free apical portions (S 100201, x 10).
3. Leaves with gradually tapering free apical portions (S 100202, x 25).
4. Cuticle of abaxial surface of leaf (S 100203, x 25).
5. Inner surface of abaxial cuticle showing stomata with four large subsidiary cells (S 100204, x 600).
6. Inner surface of abaxial cuticle showing crystal bodies on the epidermal cells of non-stomatal zone (S 100204, x 600).
7. Leaf enlarged to show stomatal arrangement and orientation on outer abaxial surface (S 100202, x 200).
8. Outer cuticle of subsidiary cells forming an inconspicuous ring around the guard cells (S 100202, x 600).

Figs. 1,2 reflected light micrographs, figs. 3,7,8 SEM, figs. 4-6 transmitted light micrographs.


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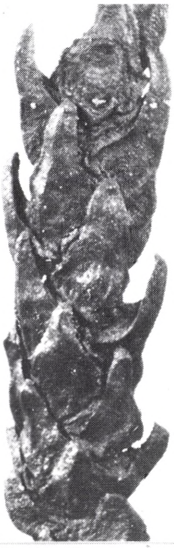
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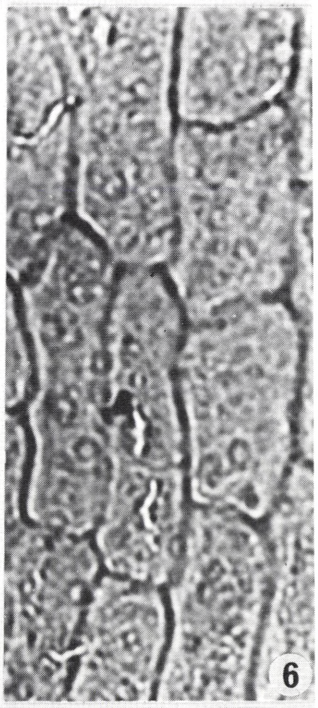
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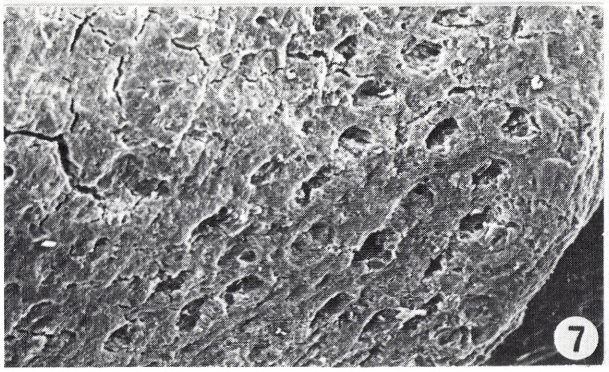
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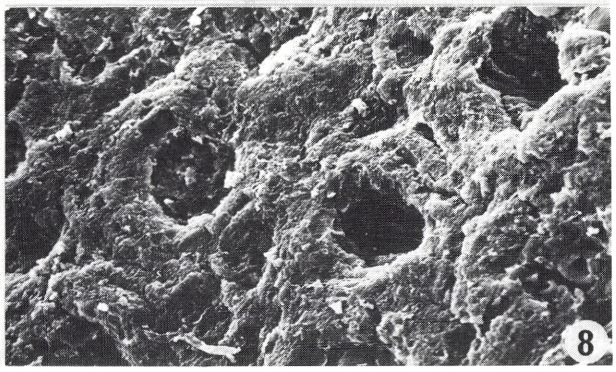
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PLATE III

Fossil *Quasisequoia scanica* Srinivasan & Friis sp. nov. from the Santonian/ Campanian of Scania, Sweden.

1. Holotype. Stout shoot with distantly placed, appressed leaves (S 100205, x 10).
2. Shoot with young leaves (S 100206, x 10).
3. Leaf of stout shoot showing distinct mid-rib and short free apical portion (S 100207, x 25).
4. Slightly thick shoot with spirally arranged, appressed leaves with acute apices and resin secretions (arrow) in the space between adaxial surface and axis (S 100208, x 25).
5. Abaxial cuticle of a mature leaf showing sparsely scattered stomata (S 100209, x 25).
6. Inner surface of abaxial cuticle with diversely oriented stomata and variously shaped epidermal cells in the stomatal zone (S 100210, x 375).
7. Inner surface of abaxial cuticle showing dicyclic stomata (S 100211, x 600).
8. Inner surface of abaxial cuticle showing monocyclic stomata (S 100212, x 1000).

Figs. 1,2 reflected light micrographs, figs. 3,4,7,8 SEM, figs. 5,6 transmitted light micrographs.


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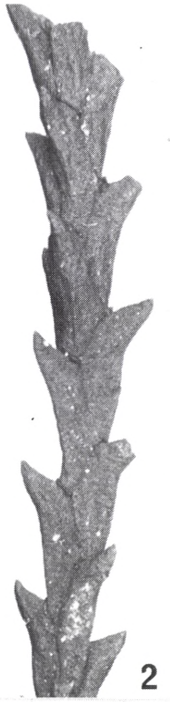
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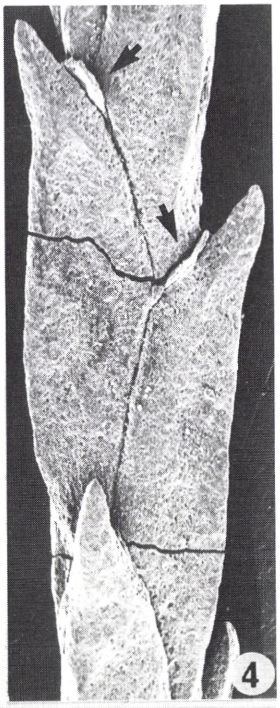
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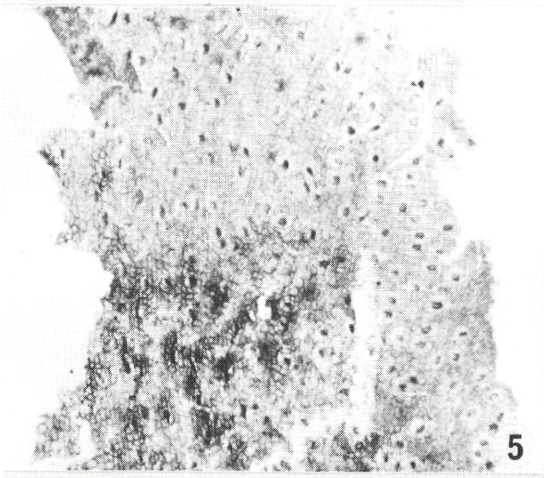
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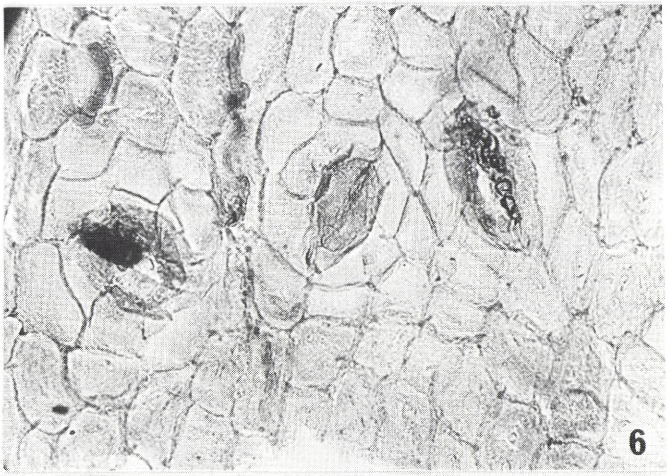
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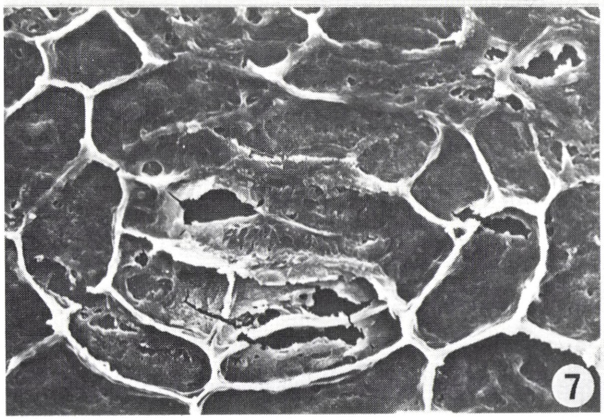
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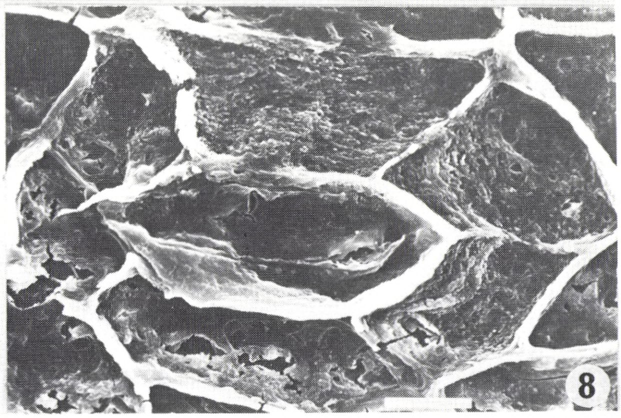
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PLATE IV

Fossil *Quasisequoia aasenensis* Srinivasan & Friis sp. nov. from the Santonian/Campanian of Scania, Sweden.

1. Holotype. Branched shoot with spirally arranged, appressed, keeled leaves (S 100213, x 5).
2. Leaves with elongated free apical portions spreading outwards (S 100214, x 10).
3. Leaves with elongated free apical portions slightly curved inwards (S 100215, x 25).
4. Outer abaxial surface close to apical region showing mainly transversely or obliquely oriented stomata (S 100215, x 200).
5. Outer abaxial surface showing a single row of transversely oriented stomata along the elongated apical region (S 100215, x 200).
6. Inner surface of abaxial cuticle showing stomata with rectangular or oval stomatal pits (S 100216, x 375).
7. Outer adaxial surface showing 2-3 longitudinal rows of stomata along each margin (S 100217, x 150).
8. Inner surface of abaxial cuticle, stomata enlarged to show stomatal aperture (S 100216, x 600).

Figs. 1,2 reflected light micrographs, figs. 3-8 SEM.


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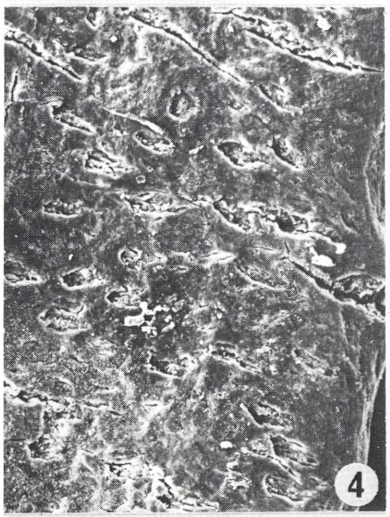
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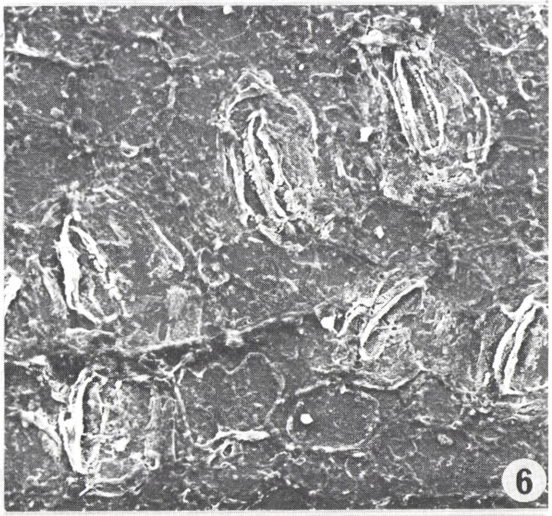
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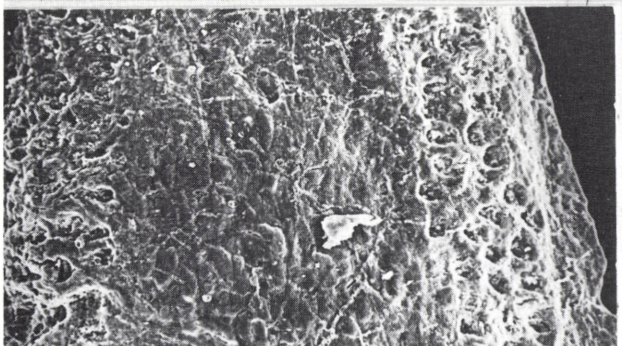
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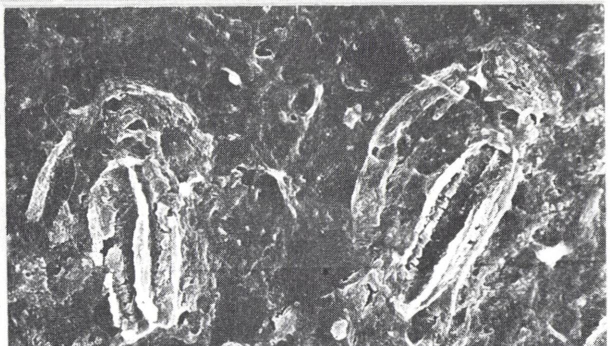
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PLATE V

Fossil *Elatidopsis nykvistii* Srinivasan & Friis sp. nov. from the Santonian/Campanian of Scania, Sweden.

1. Holotype. Branched shoot with spirally arranged, appressed leaves (S 100218, x 10).
2. Fragment of shoot with foliar bud (S 100219, x 15).
3. Cuticle of leaf showing two adaxial stomatal bands (arrow) aligned close to margins (S 100220, x 40).
4. Shoot enlarged to show lanceolate leaves with acute apices (S 100221, x 25).
5. Outer adaxial surface with narrow stomatal bands (arrow) along margins (S 100222, x 40).
6. Inner surface of abaxial cuticle showing vertically elongated epidermal cells with straight walls (S 100223, x 600).

Figs. 1,2 reflected light micrographs, figs. 4,5,6 SEM, fig. 3 transmitted light micrograph.

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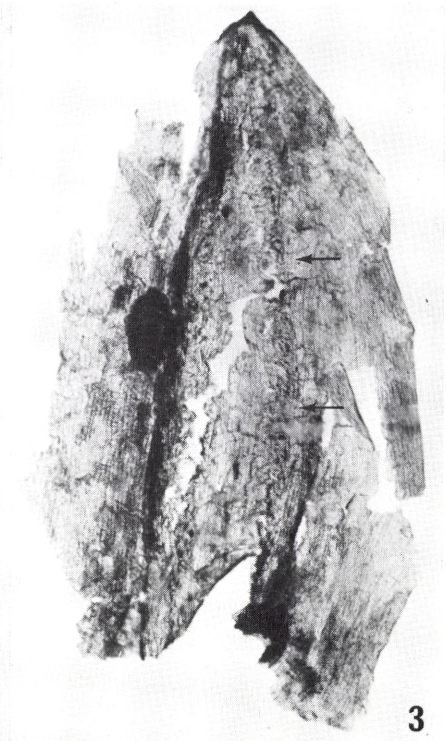

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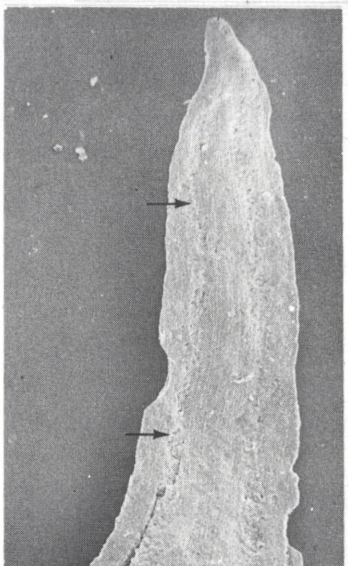

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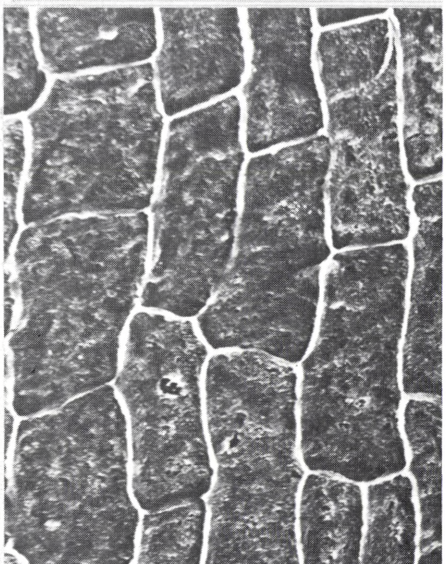

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PLATE VI

Fossil *Paracryptomeria elegans* Srinivasan & Friis sp. nov. from the Santonian/ Campanian of Scania, Sweden.

1. Holotype. Shoot with spirally arranged, crowded, scale-like leaves (S 100224, x 10).
2. Cuticle of leaf showing stomatal bands on abaxial and adaxial (arrow) surfaces (S 100225, x 25).
3. Inner surface of abaxial cuticle showing discontinuous longitudinal files of stomata in the stomatal band (S 100226, x 200).
4. A mature leaf with gradually tapering, incurved free apical portions (S 100227, x 25).
5. Outer abaxial surface showing stomatal band with mainly transversely oriented stomata (S 100228, x 200).
6. Inner surface of abaxial cuticle, guard cells enlarged (S 100229, x 1200).
7. Inner surface of abaxial cuticle, epidermal cells in the non-stomatal zone (S 100230, x 1200).

Fig. 1 reflected light micrograph, figs. 2,3 transmitted light micrographs, figs. 4-7 SEM.


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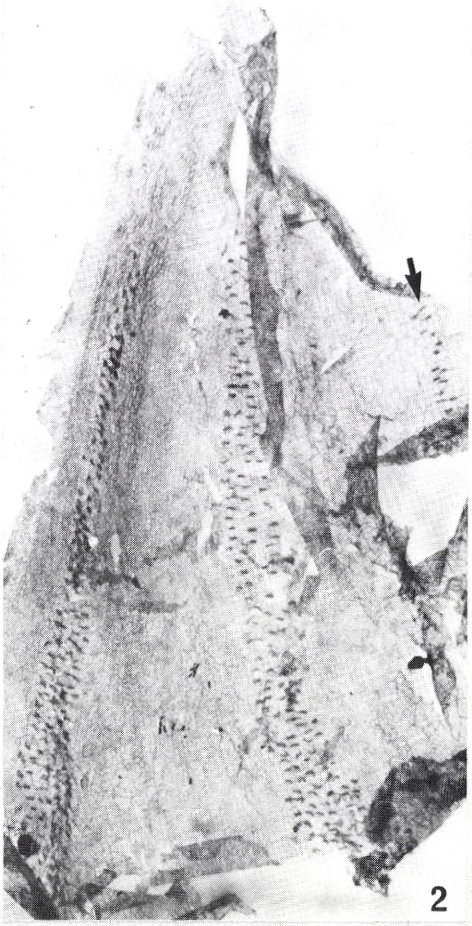
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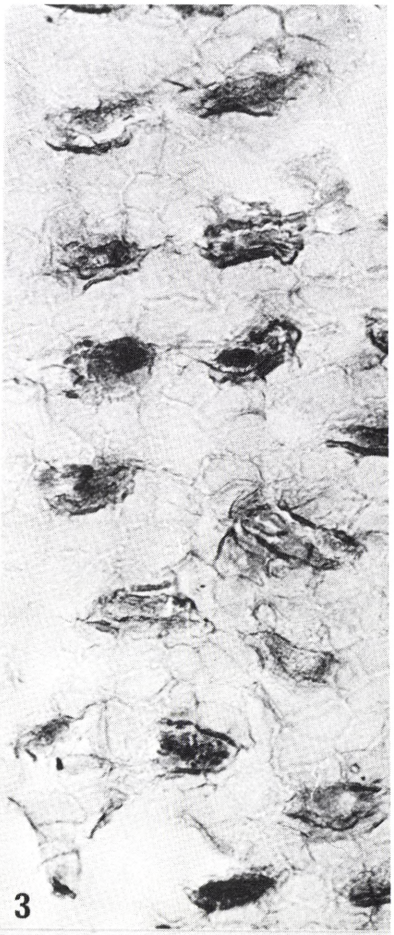
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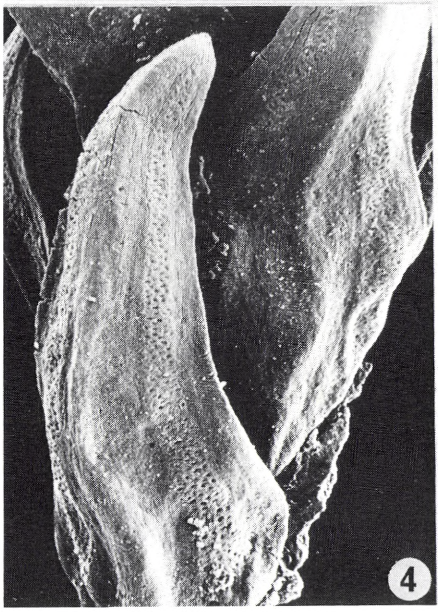
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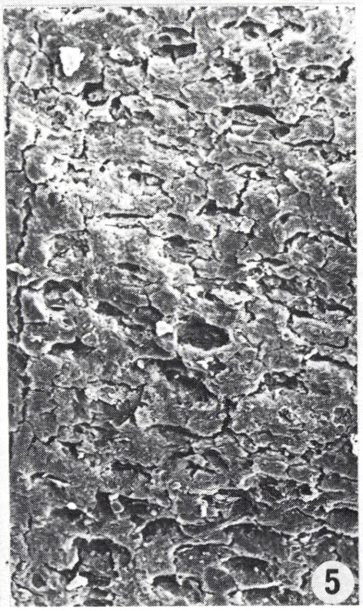
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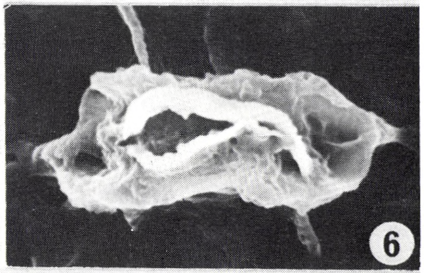
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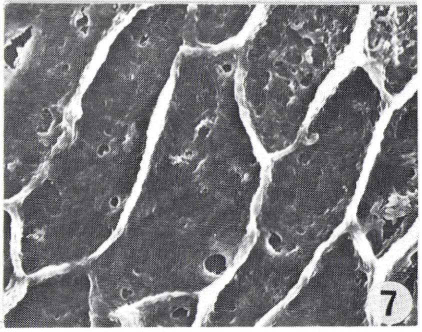
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PLATE VII

Assigned and unassigned fossil seed cones and seeds from the Santonian/Campanian of Scania, Sweden.

1. Seed cone, *Quasisequoia florinii* sp. nov. (S 100197, x 3).
2. Incomplete cone assigned to *Q. florinii,* (S. 100198, x 3).
3. Same as above, viewed from another side (S 100198, x 3).
4. Dispersed seed assigned to *Q. florinii,* (S 100199, x 15).
5. Cone type 1 (S 100231, x 3).
6. Cone type 1 (S 100232, x 3).
7. Cone type 2 (S 100233, x 3).
8. Cone type 3 (S 100234, x 3).
9. Cone type 3 (S 100235, x 3)
10. Isolated seed from specimen shown in fig. 6 (S 100232-1, x 15).
11. Cone type 4 (S 100236, x 3).
12. Cone type 4 (S 100237, x 3).
13. Cone type 5 (S 100238, x 3).
14. Dispersed seed similar to seeds observed in specimen shown in fig. 13 (S 100239, x 30).

Figs. 1-9, 11-13 reflected light micrographs, figs. 10, 14 SEM.


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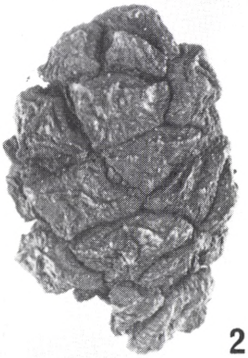
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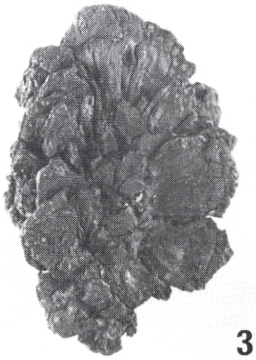
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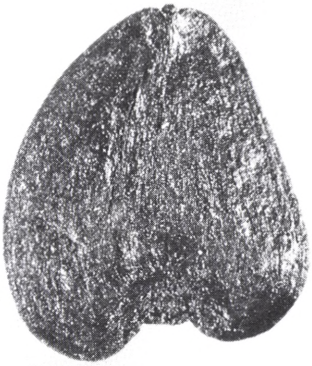
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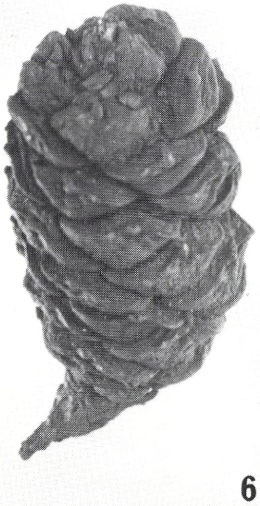
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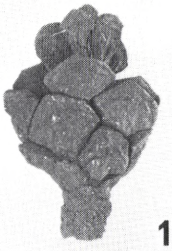
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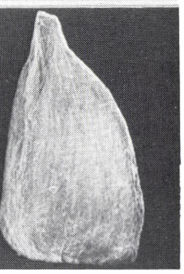
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PLATE VIII

Unassigned fossil pollen cones from the Santonian/Campanian of Scania, Sweden.

1. Pollen cone type 2 (S 100240, x 33).
2. Pollen cone type 2 (S 100241, x 35).
3. Detached microsporophyll with several pollen sacs (S 100242, x 83).
4. Pollen sac epidermal cells with undulated walls (S 100243, x 500).
5. Orbiculate pollen (S 100244, x 2000).
6. Pollen cone type 1, a cluster of three pollen cones (arrow) towards distal end (S 100245, x 20).
7. Pollen cone type 3 (S 100246, x 25).
8. Pollen with short papilla, from specimen shown in fig. 7 (S 100246-2, x 2000).
9. Longitudinally split pollen from specimen shown in fig. 7 (S 100246-7, x 2000).

Figs. 1-6 SEM, fig. 7 reflected light micrograph, figs. 8,9 transmitted light micrographs.


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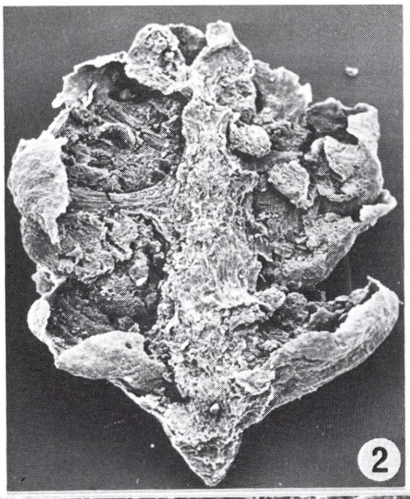
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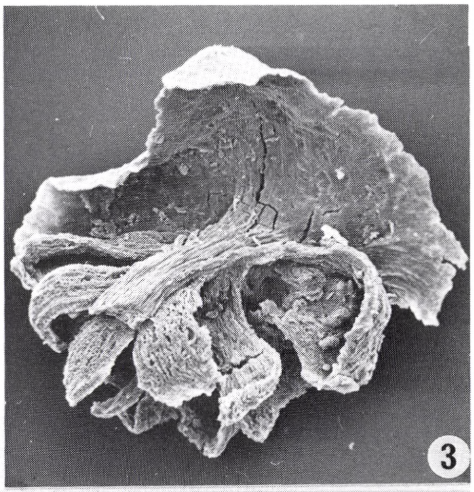
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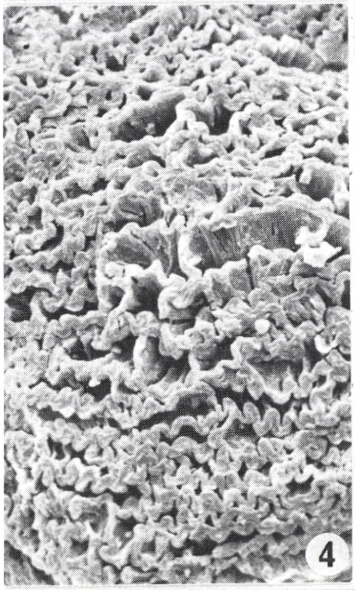
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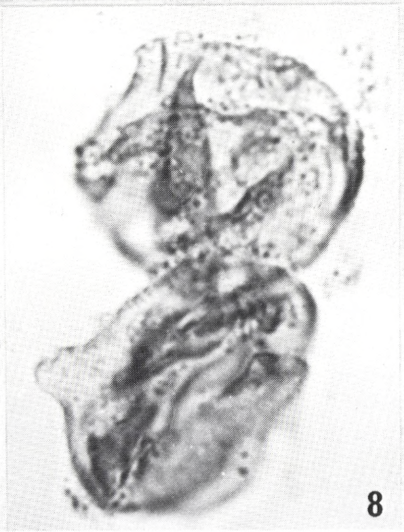
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