INTRODUCTION

The late Professor Charles Bommer made a very extensive collection of fossil plants from the Wealden formation of Belgium. The fossils are preserved as lignite in a fine silt or clay and have rather the appearance of charcoal, being black and brittle but very little compressed; they are not however charred and when soaked in a dilute alkali they swell and soften and are then amenable to sectioning by the ordinary methods of celloidin embedding used for woody tissues. It is their preservation which gives these fossils their great importance for fossil plants with their internal structure preserved are rare at all periods, and an extensive flora preserved entirely in this way is almost unique.

Professor BOMMER not only collected the fossils and amassed the many thousands of fragments which are preserved in the Institut royal des Sciences naturelles de Belgique; he commenced their investigation. For this purpose he prepared a fine series of plates of photographs and drawings and these plates were duly printed. He also wrote voluminous notes about the flora and certain introductory sections may indeed represent final drafts, but virtually nothing was published, apart from some brief preliminary notes on certain species.

When I was asked by Professor V. VAN STRAELEN to prepare BOMMER's work for publication it was naturally my hope that I could in large measure draw directly on his work, and that it would be possible to publish large sections with little more than editing. Unluckily this proved quite impossible; his descriptive notes must indeed be regarded as a record of passing ideas and it would be quite unfair to BOMMER's memory as well as useless to a reader to attempt to print them. It is of course true also that with Botanical progress much of what was written as long ago as 1890, even though added to and emended during the next thirty years has become out of date. It has however been possible to make use of a good many of BOMMER's photographs which are excellent and of some of his spirited and characteristic drawings.

The collection consists in the main of pieces of woody tissue. It comprises a good many fern species, mostly represented by pieces of petiole and rhizome; excellent and abundant specimens of the fern-like plant *Weichselia*, a remarkable series of coniferous cones and enormous amounts of lignite (wood), probably largely of conifer origin.

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The investigation of this whole flora in detail worthy of its preservation will take many years. So far all that has been attempted has been the investigation of certain conifers. This paper contributes an account of two speceies of Taxodiaceous conifers bearing cones on their leafy twigs. A paper written by Mr. K. L. ALVIN of Birkbeck College, London, contributes a description of three Abietinean female cones. These two papers by no means complete the conifers; three or more species of possibly Abietinean cones remain as well as some leaves resembling *Pinus* and a vast material of wood fragments.

CONIFERS OF THE TAXODIACEÆ

FROM THE

WEALDEN FORMATION OF BELGIUM

Classe CONIFERÆ.

FAMILY TAXODIACEÆ.

Genus SPHENOLEPIS SCHENK.

Sphenolepis SCHENK, 1871, p. 243. Sphenolepidium HEER, 1881, p. 196.

The International rules of nomenclature require the use of the name Sphenolepis SCHENK and the rejection of Sphenolepidium HEER (which was proposed because of the earlier use of Sphenolepis by Agassis for a genus of fishes). The present rule uphoids the Botanical name Sphenolepis, ignoring its use in the animal kingdom.

The name Sphenolepis refers essentially to a type of female cone, but where attribution is clear it may be extended to include the whole plant. It has been much used for purely sterile twigs, some of very doubtful attribution. A different name should have been used.

The Type-species is S. kurrianus (DUNKER), but the position of this is not quite satisfactory. DUNKER described some small twigs without any fine details as *Thuites kurrianus* and SCHENK identified his specimens, which were the first good ones with DUNKER's species. This may be correct, but it cannot be considered convincing. Sterile twigs described by CARPENTIER (1939) and agreeing macroscopically with DUNKERS's specimens, as well as those of SCHENK and others, are so different in cuticle from the present ones that they must be not merely specifically but generically distinct.

Other specimens have been placed in Sphenolepis but their position is unsatisfactory. The name S. sternbergianum (DUNKER) has been used for specimens with slightly more spreading leaves. MICHAEL (1936) has described the cuticle

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of such leaves (under the name S. kurrianum forma sternbergiana). Their structure is again entirely unlike the present leaves, and apparently distinct from CARPENTIER's specimens. Certain sterile shoots described by FONTAINE 1889 as species of Sphenolepis or of Athrotaxopsis appear to represent promising material but are too little known to be discussed further.

Emended diagnosis of Sphenolepis. — Stems bearing spirally arranged leaves; leaves small, scale-like, forming the continuation of a well developed leaf-base cushion. Stomata forming two bands on the cushion and lower sides of the leaf, mostly placed transversely, monocyclic, adjacent stomata with separate subsidiary cells. Resin confined to a single short canal on the abaxial side of the leaf trace.

Wood of the *Cupressinoxylon*-type, without resin canals.

Female cone terminal, rather small and rounded, composed of numerous spirally arranged, persistent cone scales. Cone scale undivided, wedge-shaped, apex truncate. Upper surface lacking any ligular upgrowths, bearing about six seeds in two rows. Seeds small, flattened but not winged, attached basally with the micropyle facing the axis. Vascular system of cone scale consisting of a single basal strand which divides into a transverse row of normally orientated bundles from which very minute strands arise to supply the seeds, no other inverted system present. (Male cone and pollen unknown.)

Sphenolepis kurriana (Dunker) Schenk.

1. Select references.

Thuites (Cupressites?) Kurrianus DUNKER, 1846, p. 20, pl. VII, fig. 8. (Poor figure of vegetative shoots, the origin of the specific name.)

Sphenolepis Kurriana (DUNKER) SCHENK, 1871, p. 243, pl. XXXVII, fig. 5-8; pl. XXXVIII, fig. 1. (Good shoots and cones.)

Sphenolepidium Kurrianum (DUNKER) HEER, 1881, p. 19, pl. XII, fig. 1 b; pl. XIII, fig. 1 b, 8 b; pl. XVIII, fig. 1-8. (Shoots and ill preserved cone.) — (DUNKER) SEWARD, 1895, p. 200; pl. XVII, fig. 7, 8; pl. XVIII, fig. 1. (Good cones and shoots.)

2. Sterile twigs possibly identical with S. kurriana. (See DUNKER, 1846 above, and SEWARD, 1895, for references up to that date.)

Sphenolepidium Kurrianum (DUNKER) CARPENTIER, 1927, p. 70, pl. 20, fig. 4, 5. – MICHAEL, 1936, p. 56 in part (forma typica).

3. Specimens determined as S. kurriana but in my opinion distinct.

- Sphenolepidium Kurrianum (non DUNKER) SAPORTA, 1894, p. 115, pl. XXII, figs. 3-5. (Cones and shoots, both different.)
- Sphenolepidium Kurrianum forma Sternbergiana MICHAEL, 1936, p. 56, pl. III, fig. 3, 4. (Cuticle.)
- Sphenolepidium Kurrianum (non DUNKER) CARPENTIER, 1939, p. 157, pl. I. (Leaf and cuticle.)

Emended diagnosis of Spenolepis kurriana. — Tree or shrub, main stems bearing numerous slender ultimate branchlets on all sides. Leaves on branches of all orders minute and scale like, free part short, appressed, triangular in section, continuing uninterruptedly into a leaf-base cushion containing photosynthetic tissue. Resin confined to a short canal on the abaxial side of the leaf trace and confined to the upper part of the leaf cushion. Leaf and leaf base cushion with an epidermis composed of elongated rectangular cells with a non-papillate surface. Stomata occurring in two bands on the sides of the leaf base cushion and extending onto the leaf, nearly all transversely placed, rather crowded but adjacent stomata with separate though usually contiguous subsidiary cells. Guard cells moderately sunken in a rectangular pit; subsidiary cells often four, consisting of two large lateral ones and two small terminal ones; not papillate. Encircling cells normally absent. No hypodermal fibres present under the epidermis of the leaf-base cushion and leaf.

Pith of branch stem narrow, composed of uniform, thick walled, pitted parenchyma. Annual rings developed, rather crowded in branch wood. Tracheids of secondary wood rather thick walled and narrow; pits of radial walls uniseriate, not in contact, almost confined to the two ends of the tracheids. Wood rays numerous but narrow, always uniseriate, mostly only one or two cells high, composed exclusively of ray parenchyma. Ray cells with thin walls, no pits apparent on walls between pairs of ray cells, but « field » formed by the contact of a ray and a tracheid showing a vertical row of two or three broadly oval, slightly bordered pits. Xylem parenchyma cells vertically elongated, scattered through the wood and not confined to the late wood. Resin canals entirely absent from the wood (not even developed in the wood formed from a wound callus).

Female cones borne terminally on a cluster of short branches. Cone oval, typically $12 \text{ mm} \times 7 \text{ mm}$, composed of numerous spirally arranged cone scales. Cone scale somewhat flattened and wedge shaped, $3 \text{ mm} \log 3 \text{ mm}$ wide at its distal end. Base narrow and terete, gradually becoming broader distally; and the whole scale also curving upwards. Under surface of scale continuing onto the distal end and ending in a slight transverse ridge raised at its centre to form a minute obtuse point. Distal end of scale thickened above the transverse ridge to make contact with the scales above.

Upper surface of scale concave, seed-bearing region limited distally by a slight curved ridge. Interior of scale composed largely of thick walled parenchyma, but no fibres. Three large resin canals usually present. Seeds forming two curved rows, sessile, attached to a minute scar on the scale. Seed typically 1 mm long, 1 mm wide, flat about 0.5 mm thick; micropyle slightly prominent, surface cells of integument elongated.

Description. — Leafy shoots are very numerous but most of them seem to have broken up in extraction or before deposition. Larger stems agreeing D





E

G





FIG. 1. — Sphenolepis kurriana (DUNKER) SCHENK.

- A: Cuticle of underside of cone scale showing four stomata and one trichome. The subsidiary cell cuticle is slightly thinner than the rest of the epidermis. $\times 200$.
- B: Fragment from epidermis of a leaf base showing a stomatal band. ×200.
- C: Fragment from the epidermis of a leaf base showing part of a stomatal band in which the stomata are scattered. The sides of the stomatal pit are striated. ×400.
- D: Longitudinal section of the epidermis of a leaf base showing three stomata in T.S.,

that on the left being pear the pole. $\times 600$. Same specimen as E-J.

- E-H: Selected sections from a transverse series through a small twig, showing the upper part of the leaf base cushion (E), the origin of the leaf (F, G) and its end (H). \times 12,5. Xylem black, resin duct shown as a ring. Pl. I, fig. 15 is from this series.
- I, J: Two sections from a slightly oblique longitudinal series through the same twig as E-H, showing the leaf base, resin duct (open cavity) and xylem (black). ×25.

in general structure with the twigs are also common. There are numerous isolated female cones and a few with the upper part of the peduncle attached.

Foliage. — The specimens lead me to suppose that while there are no categories of branches of definite and distinct orders, there was a tendency to produce weak lateral branches with only slight powers of growth, which in turn bore ultimate ramuli incapable of growth. No leader-shoots have been recognised in this material.

The ultimate ramuli are simple and barely 1 mm wide (Pl. I, fig. 5) and of unknown length. Their leaves are minute, only 0.7×0.5 mm including the cushion, and the pith likewise is slender, only 0.13 mm wide. Such ramuli however have fairly well developed wood which may even suggest a growth ring. They do not appear to have been shed naturally, but when they are missing from the branches of the next order, there are usually stumps suggesting that they were worn away during deposition (Pl. 1, figs. 3, 4, 6, 7).

The larger branchlets are of very varied size, and some of them show on sectioning clear evidence of secondary growth, but the larger size of their leaves and pith precludes the possibility of their having developed from the ultimate ramuli decribed above. The leaves are usually 1.0-1.5 mm long, occasionally 2.5 mm long and about 1.0 mm wide, and the pith is 0.3 mm wide.

The slenderest twigs, as has been said, are unbranched; slightly thicker ones branch occasionally and irregularly (Pl. I, fig. 9). Still thicker twigs branch very frequently, some showing a branch stump in almost every leaf axil (Pl. I, figs. 4, 5, 6, 7). In no case are the branches confined to one plane, nor do their free parts show flattening into one plane.

The leaves are always arranged in a spiral. In the slender twigs there are usually 2 + 3 contact parastichies, while in broader twigs (where the leaf is relatively smaller there are usually 3 + 5 contacts. The leaf is always scale-like and its apex varies from acute to rather obtuse (Pl. I, figs. 10, 11). Its free part is closely appressed to the stem (except where they subtend or formerly subtended a branch (Pl. I, figs. 9, 10). The free part of the leaf is very short only 1/5 of the total length of leaf and cushion and as it continues the cushion uninteruptedly, its extent is only recognisable in sections. The apex of the leaf varies from acute to rather obtuse (Pl. I, figs. 10, 11). The free part of the leaf is triangular in section, while the leaf base cushion is strongly convex in some specimens (Text-fig. 1, E-H), but flatter in others.

Anatomy of leaf and cushion. The vascular strand is minute and only passes out into the cushion at a level just below the free point. There is a short resin canal at about the same level, situated just outside the vascular bundle and beneath the assimilatory tissue. The vascular strand appears to be single and does not possess any strongly developed sheath, but other details could not be observed. The resin canal has often collapsed; the cavity is surrounded by delicate cells (not always preserved) and has no fibrous coat. The leaf and cushion contain a well developed assimilatory tissue consisting of a compact outer layer of palisade-like cells and a few layers of rounded cells underneath the palisade. There are no sclerids among the assimilatory cells, and no hypodermis is present.

The epidermis consists of thick walled rectangular cells 2-3 times as long as broad. The cuticle is probably well developed (but ill preserved in the present material) and shows the epidermal cells with rather thin, often slightly sinuous lateral walls and a flat, non-papillate surface. The stomata are confined to a band on either side of the leaf cushion, passing up onto the under sides of the leaf. The stomatal band is not very wide and has crowded stomata. The stomata are nearly all orientated transversely. Each usually has two small terminal subsidiary cells and 2-4 large lateral subsidiary cells; encircling cells are absent or at most occasional; they have not been recognised with certainty, and if present must be unspecialised. The subsidiary cells are non-papillate. Over most of the band the stomata appear to be rather regularly placed with the subsidiary cells of one opposite those of the next (Text-fig. 1, B) but in the fragment shown in Text-fig. 1, C they are irregular and some unspecialised cells lie among them.

The cuticles are most unsatisfactorily preserved in the present material and only occasional attempts gave preparations and these were tiny and poor looking fragments. However the stomata in these fragments agree with one another and the various planes of section of the epidermis studied all confirm the picture given by the cuticle preparations.

The leaf tissue appears to have been destroyed rather early as the stem grew in width and is scarcely recognisable on stems oved 2.5 mm wide.

The deep cortex of the smaller shoots consists of a very few layers of parenchyma cells, about twice as long as broad. Their walls are thin and unspecialised. In the older stems the surface is formed by a thin layer of periderm consisting of isodiametric cells 25μ wide with rather thick walls and entirely filled with a dark brown substance. The origin of this tissue was not traced, but it might be subepidermal.

Phloem. — The phloem is usually ill preserved, but certain specimens show it moderately well. In transverse section it shows alternate layers of less compact and of more compact tissue, with groups of thick walled cells 10μ wide presumed to be fibres. In longitudinal section elongated fibre-like cells were recognised and also parenchyma (much or all of it belonging to phloem rays). Sieve tubes were not seen.

The cambium is missing in the specimens examined.

Xylem. — The xylem was studied in various small twigs which were identified by their leaves, and in larger decorticated ones identified with the small stems by similarity of pith and xylem structure. Most of the microscopic detail is based on the study of the small twigs whose determination is more certain. The preservation is fairly good, but by no means perfect; very much less good than in the best petrified wood. It is presumed that all the xylem so far studied belongs to more or less weakly growing lateral branches (such as provide the greater part of the stem-litter of recent conifers). It may well be that the narrowness of the growth rings seen in the material described below is due to this position and is not characteristic of the tree as a whole.

Macroscopic characteristics of the xylem in transverse section include its compact structure with crowded and often complex growth rings which are not however specially conspicuous (Pl. III, figs. 1, 2). Tangential longitudinal sections of small stems show the minute leaf trace (or rather the disturbed area around it) (Pl. I, fig. 15) or else the rounded axillary branch traces which are characteristic (Pl. VII, fig. 2).

Details of the xylem. — In transverse section, the annual ring is marked by a more or less gradual change in the dimensions of the tracheids :

	Total radial width	Radial width of lumen	Total tangential width	Tangential width of lumen	
Well developed early tracheid	14 μ.	10 μ	16 µ	12 μ	
Well developed late tracheid	10 µ	5 μ	16 µ	10 µ	

Many tracheids in both early and late wood appear to be smaller than this. It is noteworthy that nearly all tracheids are broader tangentially than radially.

Resin canals are entirely absent from all parts of the wood, even from the highly disturbed and ill-formed wood formed around severe wounds, and also from the less disturbed areas around leaf and branch traces. Scattered cells with dark contents (here termed resin) occur in all parts of the growth ring, but are possibly more numerous in late wood : it may be however that some of these cells are ordinary tracheids pathologically filled up. The rays are narrow and inconspicuous, but the pits in the adjacent tracheid walls are easily recognised.

In the tangential longitudinal section, tracheids, in general, show no pits at all on their tangential walls; even in those from the late wood. Occasional cells showing oval, slightly bordered pits on the tangential walls are presumed to be resin-containing xylem parenchyma cells, but the possibility was not excluded that they might be exceptional tracheids. The tracheids show their length clearly (typically about 0.6-1.2 mm) and the fact that their bordered pits occur almost exclusively on the walls of the tapering ends, within about 100 μ of the point, while none occur in the parallel-sided middle part.



FIG. 2. — Sphenolepis kurriana (DUNKER) SCHENK. Wood structure, all from stem C, ×600.

Wood structure, all from stem C, x000. A: R.L.S. showing a ray and a cell of doubtful nature with resinous contents, slide 6 B: R.L.S. showing another resin-filled cell, apparently divided transversely, slide 6 C: T.L.S. showing a xylem parenchyma cell. The rays are interesting : they are invariably uniseriate and on the whole remarkably low, though numerous. The following data gives the percentages of rays of different numbers of cells high. (140 rays from two twigs were counted.)

Number of cells high	1	2	3	4	5	6
Percentage having this number	32	34	19	9	3	2

In addition one ray appeared to be nine cells high, but this may have been a mistaken observation of two rays close together. The rays are composed exclusively of ray parenchyma cells, most of them appear empty but occasional ones are filled with resin. There is nothing to suggest that the resinous ray cells were originally different. The ray-cell walls in this and in other planes were carefully examined for pits, but in no case was a pit observed on either the end (or tangential) wall nor on the upper and lower walls. It can be stated therefore that pits are either absent from the walls of neighbouring cells, or if present they are very inconspicuous : the preservation is not good enough to give convincing evidence of their absence. Bordered pits of the tracheid wall adjacent to a ray cell are conspicuous. Radial section : the distribution of the pits on the tapering ends of the tracheids causes an uneven distribution of bordered pits in the section; four fifths of the section lacks them entirely, but in transverse streaks (where the tapering ends of a radial file of tracheids occur) pits are very numerous. The pits are oval or rounded, about 6 µ wide in the early wood, 4μ wide in the late wood. Neighbouring pits may be well spaced or rather close, but are never in contact or flattened. Rims of SANIO were not seen and so must at best be inconspicuous. In the late wood the pits are fewer as well as smaller and rounder. Many of the tracheids show oblique striation, and often oblique elongation of their pits, but it was presumed that these features are produced by partial decay.

The ray cells are conspicuous, although their walls are thin. The individual cells are long enough to cross about 3 tracheids of the early wood. The horizontal walls of the ray cells are by no means always straight, but often bulge at the middle and are often hollowed at the corners, but no intercellular air spaces exist at corners. The ray « field » (the area marked by the crossing of a ray cell and a tracheid) usually shows two oval pits (sometimes one, sometimes three). Where there are two or three they occur one above another. The pits always show a narrow oblique border (except in rotted areas where the pits form oblique slits right across the field). The tracheids of the late wood differ only in having slightly smaller pits in the ray fields.

A good many scattered cells have resinous contents, and these are presumed to be mostly xylem parenchyma though some may be tracheids pathologically

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filled with resin. These cells are vertically elongated, and are either as long as the tracheids, or more probably are divided occasionally but the transverse septa are obscured. The resinous contents adheres to the walls in varying amounts and may have exactly the same appearance as the wall substance, there being no boundary recognisable between the original solid wall and the originally liquid contents. The resin occurs either as numerous small drops along the walls, or else as larger drops with a concave meniscus extending from side to side and alternating with bubbles (Text-fig. 2A, B). Intermediate types of filling occur. The transverse drops make the recognition of transverse walls uncertain; it is thought that transverse walls do appear to occur at rather long intervals. The pitting of the walls is hopelessly obscured by the resin.

In a wounded region (where the cambium had apparently been destroyed, but a callus had developed and formed new wood) the first wood consists of short irregular cells, some with brown resinous contents, others with bordered pits, and this abnormal wood is soon replaced by normal wood.

Protoxylem. — No features of special interest were observed, but narrow spirally thickened tracheids were seen. The ray cells in this region are often irregular, and a good deal broader than usual (i.e. increased in the longitudinal plane of the stem.

Pith. — The pith forms a 3-5 rayed core. In the stronger twigs an inner zone of rather larger cells is distinguishable. The whole pith in transverse section is solid and compact and the inner part is composed of uniform rather thick walled parenchyma cells with numerous simple pits (the pits are often obliterated by the resinous contents). In the longitudinal section, the inner region shows longitudinal files of almost isodiametric cells. The outer region of the pith, and the whole pith of the smallest twigs differs in its smaller and narrower cells. The pith forms the readiest means of distinguishing a section of a twig of Sphenolepis kurriana from one of Elatides bommeri, where it is much less compact.

Female cone. — In this material the female cones are either isolated, or at best attached to the top few mm of the peduncle; fortunately it is known from the specimen described by SEWARD that the cones form a cluster on short peduncles (as for example in Sequoia sempervirens).

The cone peduncle is rather stout (2-5 mm wide) and has the best developed leaves so far known in S. kurriana, they are 3 mm long \times 2 mm wide but normal in shape. At the base of the cone they form a transition to the cone scales, becoming broader and shorter. In the cone shown in Pl. 2, fig. 16 some interesting further transitional organs occur apparently consisting of a pad-like body borne immediately above a broad bract, but separate from it. No internal details are available.

The cone is oval and typically $12 \text{ mm} \times 7 \text{ mm}$, the largest measured $14 \text{ mm} \times 10 \text{ mm}$. The cone scales are spiral and 5 + 8 chief contact parastichies were recognised. The cone scales are persistent, but are easily broken away from the central axis; when this happens they take all the outer tissue leaving only a conical core of xylem marked by conspicuous scars. In the unripe cone the cone scales stood obliquely at about 60° to the vertical cone axis, but in the ripe cone they diverge more almost to 90° to the axis and so separate.

The cone scale (except possibly in the transitional bodies at the base of the cone, mentioned above) is externally simple. Its basal part is stalk-like, rounded in section, and when pulled off its single vascular bundle may be obvious. The cone scale gradually becomes broader to its final width of about 3 mm, and at the same time curves upwords, so that the upper surface is concave, the lower convex : in the mature cone it becomes straighter and flatter. The lower surface usually passes uninteruptedly to the distal end where it ends in a ridge, arched in the middle to form a more or less conspicuous but very obtuse point. In other specimens the under surface is not curved but bent in an obtuse angle (Pl. II, fig. 10) the inner part being entirely concealed, the outer part being exposed on the surface of the cone.

Above the distal ridge mentioned just above, the upper surface of the scale forms a thickened edge or crest where the scale has a total thickness of 1 mm. These three parts — the upturned lower surface, the distal ridge and the « crest » of the upper surface form the exposed surface of the cone and in each cone scale this is a rhomboidal area 3 mm broad, nearly 2 mm high. This exposed surface is never flat as for example in *Sequoia* but always strongly convex.

The « crest » is closely pressed against the under surface of the scales above and thus seals the cone. In many specimens it appears to be stuck to this surface with resin and when the scales are separated, fragments of the scale above adhere to it.

The upper or adaxial surface of the cone scale shows a large hollowed area where the seeds are borne; this area is bounded distally by the « crest ». In some the crest forms a definite rim but nothing more (Pl. II, figs. 5, 6); in others the crest forms a prominent angle, as in the specimen shown in Pl. II, figs. 9, 10 where its development is exceptionally strang. Very frequently fragments of the lower epidermis of the scales above break off and remain attached along this angle and I suspect that this is the nature of the upgrowths shown in Pl. II, figs. 7, 8 (BOMMER's drawings). In no scale examined by me was there such a definite « ligule » like upgrowth.

It is natural to regard this crest in Spenolepis as of the same nature as the similar crest in *Elatides bommeri*, that is as a mere swelling of the cone scale surface which seals the cone. There is nothing corresponding to the « ligule » of *Elatides* of *Cunninghamia*.

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The seed-bearing depression may be a single hollow (Pl. II, figs. 5, 6) or this may be divided by a number of ridges and groves (Pl. II, figs. 8, 9, 11). The groves house the seeds, there being a placental scar at the top of each grove, and often another further down, but the relation is not strict for one of the proximal row of placentae was noticed on a ridge.

Very commonly there are six placentae in two rows of three, the upper row in particular being strongly curved (Pl. II, figs. 5, 6). The number and arrangement is however variable. There may be fewer than six, one scale showed two side by side, another a curved row of three. There may be more than six, one scale showed an outer strongly curved row of five and an inner of two. It is possible that there may be more than two rows, for a particular scale in addition to the usual two rows of three placentae showed two additional scars of similar appearance but smaller size outside the outer three.

The placentae are distinguished as very slightly raised areas usually of a darker colour than the rest of the scale. They measure about $150 \mu \log \times 80 \mu$ wide, and are only raised to a minute extent, perhaps $15-30 \mu$. In a few cases they were not raised at all or even slightly sunken.

The seed-bearing part of the scale is distinguished from the rest by its fine surface markings. It shows distinct longitudinal cell-striae, whereas the rest of the upper surface scarcely shows the cells at all and there are no striae.

A few immature cones were studied. Some of these appear to have aborted at an early stage and although they are nearly 1 cm long, showed no ovules at all. The scales are thin in substance and nearly flat. Others however are better developed and do show young ovules. One of these is figured (Pl. II, fig. 17). The upper scales have broken away exposing the cone axis and the upper surface of a scale. Five young ovules are seen, three in the distal row, two in the proximal row. There are deep cracks one just above the ovules, and another further out, but these cracks are largely if not entirely caused by shrinkage on drying (after cleaning away the matrix with HF).

Structure of the cone scale. — A cone was successfully macerated and yielded some moderately good cuticles. The cuticle of the conescale is fairly thick. The lower surface shows numerous stomata, sometimes scattered, sometimes tending to be grouped in longitudinal rows, but always widespread over a large area. The stomata are monocyclic, with a ring of almost equal sized subsidiary cells. The guard cells are sunken in a rounded or rectangular pit which is variously orientated but often transverse. A few trichomes occur on the under surface of some scales but their number and distribution is most inconstant. They consist of a bulging cell surrounded by a ring almost exactly like subsidiary cells and their appearance suggests a stoma diverted in its development (Text-fig. 1A). The epidermal cells are isodiametric or slightly elongated and in parts of the scale form rows. Their lateral and end walls are from the main ones and pass upwards, towards the placentae. They disappear before reaching the surface. These strands are so small that they are obscure and only recognisable in the better sections, but one was traced from its origin from the inner side of a lateral bundle near the protoxylem. This strand runs



FIG. 3. — Sphenolepis cone scale.

Series of transverse sections through a cone scale, A, near the base, O, near the apex All $\times 12,5$.

In A, two resin ducts have appeared, in B, the bundle is dividing and the third duct has appeared. In C, D, E, F, the bundles are dividing further and the minute strands supplying seeds are seen; it was only possible to recognize one resin duct in F, but the others may be present. In sections F-O a certain amount of tissue on the left is missing (edge of section shown by broken line). In section I a supplementary resin duct appears above and the three main ones move downwards.

for 0.5 mm near the strand of its origin and was then lost. Another of these small strands lay just above the central main strand, but it did not originate from it but from one of the lateral strands, very near the point of origin of the other small strand mentioned above.

fairly broad, straight and strongly marked and their surface is strongly granular, the middle of the cell being sometimes rather thickened.

The upper surface of the scale shows no stomata or trichomes, but rather uniform isodiametric or elongated cells.

One internal feature is often very obvious on the surface, namely the resin ducts. There are of varied size. When large, the scale may split to expose them (Pl. II, fig. 18) when usually three spindle shaped masses of resin are seen, they run most of the length of the scale.

Many scales were sectioned, but the resin causes difficulty as when abundant it swells so strongly as to cause the scale to break up; and the successful sections are therefore of scales where there is little resin.

A natomy of the cone scale. — The cone scale is mainly composed of thick walled parenchyma. This parenchyma is rather sharply divided into two regions; above the vascular bundles it is composed of small cells with pale contents, while below it is composed of much larger cells, many of which have dark contents. No fibres occur and there is no cork or similar secondary tissue, but there are three resin ducts in the lower parenchyma. In the proximal region where the vascular strand is near the upper surface, there is very little of the small celled tissue, but gradually the vascular strands pass deeper into the scale, and towards the distal end the small celled tissue predominates, but a little of the large celled tissue persists almost to the apex.

There is a single large vascular strand which leaves the axis and passes without change into the base of the scale. This strand in an ordinary collateral bundle composed of about three fifths xylem, two fifths delicate tissue presumed to be ordinary secondary phloem. The xylem shows rays and the position of the protoxylem is clear. There is no centripetal xylem, nor associated resin duct.

In the lower part of the scale this bundle grows broader and then divides into three, the middle strand being the smallest (Text-fig. 3). The three strands form a straight row and their orientation is unchanged here as indeed in all parts of the scale. The outer bundles then divide again giving five of which the middle is still the smallest. The lateral strands divide again and again to give a row of about thirteen and all of them become very small, but they still remain in a line. As the bundles become smaller their phloem becomes less well preserved, being at first represented by a gap, and then not even by a gap, but the rows of tracheids can still be seen and it is clear that they always remain nearly vertical. At the end of the scale the bundles become very small indeed and hard to recognise. Several of them converge towards the apex, it is not clear whether all of them do so, but it is possible.

The seeds are borne in the middle three fifths of the scale where there are from three to five bundles. In this region a system of minute strands arises These strands consist of a few — about six — small tracheids placed in two rows. Neither protoxylem nor phloem were seen, and all that can be said of their orientation is that the tracheid rows are vertical, parallel with the rows in the main bundles. Comparison with other conifers however strongly suggests that these strands should be inverted, and in the discussion this is assumed.

Seed. — The ripe seed (Pl. II, figs. 13-15) is rounded and flattened with a small basal hilum and a very small apical micropylar projection. The margins of the seed are flattened to a slight rim, but this is never sufficiently prominent to be described as a wing. The surface shows one or two ribs which are varied in position and are probably produced by pressure of neighbouring seeds and the ridges on the scale.

At a younger stage (Pl. II, fig. 17) the seeds are oblong and the micropyle which faces the cone axis is already full sized and therefore appears relatively larger than in the mature seed. The young seed often shows a distinct but narrow marginal wing, but this is considered to be caused by compression of an epidermis surrounding a soft layer in the outer part of the integument. No mature seeds were available for anatomical study, but a few rather ill preserved young ones were successfully macerated. The following membranes were obtained.

1. The rather thick outer cuticle of the integument. Cell outlines are very indistinct, but there is some indication of elongated cells. In addition there are numerous scattered ring shaped thickennings 6μ wide of unknown nature.

2. A delicate collapsed cuticle (of the free part of the nucellus) showing more or less isodiametric cells 30μ wide with nearly straight, fine but clearly marked walls. This delicate cuticle is rather extensive, so that in the young seed at least, a considerable portion of the nucellus must be free.

3. A non-cellular rounded sac of moderately thick cuticle, the megaspore membrane. As is usually the case in fossil conifer megaspore membranes, it is strongly creased and its substance is finely granular.

Discussion. — Sphenolepis is known in its foliage, its wood and in its female cone and seed; missing parts are the male cone and of course the game-tophytes and young stages. The lack of the male cone is unfortunate, but a search in good material should supply it. It must be borne in mind that the missing parts might be so aberrant as to make nonsense of all suggestions of affinity given below, I can only proceed on the assumption that they do not.

In its female cone, as well as in its wood and its foliage, Sphenolepis agrees with the Taxodiaceæ, of which it appears to be a typical member. Its cone in particular precludes its belonging to any other existing family, and no other possible affinities will be discussed.

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Its foliage is not exceptional in appearance. Similar shoots are seen in the Taxodiaceæ (e.g. in Athrotaxis cupressoides and in Glyptostrobus) and nearly similar scale-leaves occur at the end of a years growth in many Taxodiaceæ in which the normal leaves are larger. Similar shoots occur also in several genera of Podocarps (with which Sphenolepis can have no affinity), and in the Cupressaceæ the individual leaves are often very similar, though of course always opposite. Its cuticle is however more characteristic, and there is indeed no living genus which closely matches it. Transversely orientated stomata are rare in the Conifers. They occur in certain Taxodiaceæ (Sequoia and Taxodium and occasionally in Cryptomeria).

The female cone is by far the most influential organ in the comparative morphology of a conifer. In its general aspect, the cone of Sphenolepis agrees with that of Sequoia sempervirens, and it is not very different from those seen in some other genera e.g. Athrotaxis. The cone scale is in external form intermediate between those of Sequoia and Athrotaxis, being less truncate than in Sequoia, but more so than in Atrotaxis. In bearing ovules in two rows, Sphenolepis is unusual, it agrees with Sequoia gigantea but no other member of the Taxodiaceæ. I do not regard this character however as one of special weight.

The anatomy of the cone scale seems to me very important. In the Taxodiaceæ two types of cone scale anatomy can be distinguished; in Sequoia, Taxodium and several other genera the scale has a double system of bundles, of which the upper, inverted, members supply the seeds and also non-reproductive tissue representing the sterile scales of the « seed-scale-complex ». In the other section, comprising Cunninghamia, Taiwana and Athrotaxis selaginoides, the inverted system is very feeble and limited to supplying the ovules. The conescale consists of a dominant bract scale and only the feeblest vestiges of the sterile parts of the seed scale complex. Sphenolepis clearly belongs to this second group and differs greatly from Sequoia. The fact that in Athrotaxis cupressoides there is a well developed inverted system makes it impossible to divide the Taxodiaceæ on this one character; but it by no means removes its morphological and phylogenetic interest. In the Taxodiaceæ there seems to be a widespread tendency for reduction in the sterile part of the seed-scale-complex both in its external development and in its vascular supply. Where this part has been almost eliminated as in Sphenolepis the cone scale must be considered advanced in this respect and it cannot well be regarded as ancestral to a less advanced type e.g. Sequoia. In its way Sphenolepis is one of the most advanced (i.e. reduced) genera of the Taxodiaceæ.

The seeds of the Taxodiaceae are rather uniform, except in size. Sphenolepis has a typical Taxodiaceous seed, but it is the smallest known, though those of Athrotaxis cupressoides are only slightly larger.

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Limiting the comparison to the *Taxodiaceæ* we have :

Leaf form, Athrotaxis cupressoides, Glyptostrobus.
Cuticle : transverse stomata, Sequoia sempervirens, Taxodium.
Cuticle : monocyclic stomata, Athrotaxis.
Wood, most : Taxodiaceæ (especially Sequoia, Athrotaxis).
Cone form, Sequoia, Athrotaxis.
Cone scale : 2 rows of ovules, Sequoia gigantea.
Vascular anatomy of cone scale, Cunninghamia, Taiwana, Athrotaxis selaginoides.
Inverted seed, Cunninghamia, Athrotaxis, Sequoia, Sciadopitys.
Small size of seed, Athrotaxis.

We can state that every feature of Sphenolepis can be matched in the living Taxodiaceæ, but the grouping of characters is peculiar to itself. If it is to be regarded as closely related to a particular living genus, it must be because greater weight is assigned to certain characters e.g. cone scale anatomy and less to others e.g. leaf cuticle. I do not consider that knowledge of the Taxodiaceæ is yet complete enough to make this possible to do usefully at present but it is of interest to mention that BOMMER in his notes was much impressed by points of agreement with Athrotaxis.

For my part, I regard the existing *Taxodiaceæ* as the scattered survivors of a once great family, which perhaps in the early Mesozoic, was morphologically coherent, but so much extinction has occurred as to make coherence now doubtfully recognisable. Improvement in understanding will come gradually with the description of numerous extinct types. Till then we should be very reluctant to regard two genera as particularly closely related when they differ unaccountably in any aspect.

Genus ELATIDES HEER.

Elatides HEER, 1876, p. 77.

Elatides is primarily a genus of female cones. It is correctly extended to cover the other organs of the plant where their attribution is certain, but where it is not certain other names should be used.

HEER (1876) described two species of cones, E. ovalis and E. brandtiana, and E. ovalis is here chosen as the Type. Later BRONGNIART'S Lycopodites williamsonis was placed in *Elatides* and this species has become much more fully known, but HEER'S species have never been closely investigated. Thus while E. williamsoni and E. bommeri decribed here agree closely with one another, their reference to *Elatides* depends on their superficial agreement with the Type in cone and foliage, and a reinvestigation of the type might well show important differences.

E. ovalis HEER and E. brandtiana HEER are from the Upper Jurassic of Siberia; where in addition there are sterile shoots named E. falcata HEER. Another species is E. curvifolia DUNKER of the Lower Cretaceous; and this species

I suspect may be composite, for the specimens described from different localities are very varied. The best specimens are the shoots and cones described by NATHORST (1897) from Spitzbergen.

Elatides thus ranges from the Lower Oolites (Bajocian) of Yorkshire through the Uppermost Oolites (or Lower Cretaceous) of Spitzbergen and Siberia to the Lower Cretaceous (Wealden) of various parts of N. Europe. It has been suggested (SEWARD, 1919, p. 270; HARRIS, 1943, that Palyssia or Ontheodendron sternbergi (NILSSON) from the Rhaetic of Sweden and Greenland may belong to Elatides but this is doubtful.

Revised diagnosis of Elatides (Based on E. ovalis, E. williamsoni and E. bommeri). — Coniferous tree. Lateral shoots irregularly branched. Leaves borne spirally, short, incurved, rhomboidal in section, arising from a raised cushion. Leaf with a single vascular bundle and abaxial resin canal. Stomata crowded in narrow bands, transversely or irregularly orientated. Guard-cells sunken in a shallow rectangular pit formed by large lateral and small terminal subsidiary cells. Subsidiary cells not papillate, encircling cells forming an incomplete ring or absent. Subsidiary cells of adjacent stomata not shared. Ordinary epidermal cells without papillae. Hypodermis present.

Stem cortex containing resin ducts. Xylem of Cupressinoxylon type.

Female cone borne singly, terminal, medium sized, oval; composed of persistent spirally arranged scales. Scales flattened, not very woody, composed of a stalk expanding above and then contracting into a sharp spine. Upper surface bearing a broad more or less lobed membranous « ligule » and 3-5 seeds. Seeds flattened but not winged, orthotropous, micropyle facing the cone axis. Integument free from the nucellus. Archegonial group apical; pollen received in micropyle.

Male cones borne in a terminal cluster, cylindrical. Microsporophylls borne spirally, consisting of a slender stalk expanding into an imbricating scale. Pollen sacs three, probably fused to one another and to the stalk; walls delicate. Pollen grains round-oval with one furrow.

The systematic position of *Elatides* is discussed on p. 35 and the conclusion is reached that it is a typical member of the *Taxodiaceæ*. It is closely allied to the fossil genus *Sphenolepis*, but not to any one living genus, though it is least different from *Cunninghamia*. Its various characters are all found among the existing genera of the *Taxodiaceæ*, making it, although extinct seem a modern and by no means archaic type.

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Elatides bommeri sp. n. (Type specimen Pl. IV, fig. 3.)

Diagnosis. --- Shoots irregularly branched. Leaves borne spirally, short, up to 3 mm long, rhomboidal in section, arising from the middle of a raised cushion. Leaf possessing a single large resin canal and an almost complete fibrous hypodermis. Stomata limited to a single band on each adaxial Stomata rather crowded, mostly transversely orientated, aperture surface. sunken in a rectangular pit formed by 2-4 lateral subsidiary cells and 2 small terminal ones. Papillae absent from subsidiary cells. Ordinary epidermal cells elongated, rectangular, lateral walls straight, surface not papillate.

Cortex of stem containing resin canals. Secondary phloem fibrous. Pith rather narrow. Xylem showing annual rings. Tracheids rather narrow, with uniseriate bordered pits on their radial walls. Pits not in contact, distributed along the whole length of the tracheid but tending to be absent from the middle region. Wood rays numerous, always uniseriate, mostly 2 or 3 cells high, composed exclusively of ray parenchyma. Ray cells with thin walls, pits not apparent on walls between ray cells, but « field » of contact of ray cell and tracheid showing usually two broadly oval pits, one above the other. Field pits very slightly bordered. Xylem parenchyma cells vertically elongated, scattered through the wood and not confined to the late wood. Resin canals entirely absent from the wood (not even developed in disturbed areas or near leaf and branch traces).

Female cones terminal and solitary on ordinary leafy branches. Cone oval about 1.1 mm wide, 1-2 cm long. Cone scales consisting of a stalk 2 mm long expanding rather suddenly into a flat part 5 mm wide, 2 mm long and then contracting to a sharp spine about 1 mm long. Tissue of cone scale partly fibrous and containing a single large abaxial resin canal. « Ligule » of cone scale membranous, rectangular, divided by two groves into three lobes, concealing the three slightly prominent placentae.

Seeds oval, flat, not winged, length 2-3 mm, breadth 1.9 mm, micropyle slightly prominent.

Male cones and pollen not known.

Description. — Tha material is fairly abundant but brittle and much broken up, and it appears that many of the specimens were broken since they were collected. The preservation of the internal tissues is very unequal in the different specimens, perhaps as a result of rotting before preservation. Many specimens are permeated by fungus hyphae.

Stem and leaf surface. — The leafy shoots branch occasionally and irregularly. Apart from some unexpanded bud-like branches, the various shoots all agree fairly well except in thickness and it is presumed that there are no definite categories of branches of different orders, but that all were equally capable of unlimited growth.

In the narrowest shoots, the stem is nearly 2 mm wide, and bears incurved leaves giving the shoot a total width of about 5 mm. In wider shoots with the stem about 4 mm wide, the leaves are unaltered, but still wider stems have their leaves broken off. The unexpanded, bud-like branch figured in Pl. VII, fig. 11 is regarded as a shoot arested in growth. Its outer leaves appear to be normally robust (though unusual in certain respects); the inner part where young leaves were no doubt situated is not preserved. Comparable regions of feeble growth are found in most conifers at the beginning and end of a seasons growth.

The leaves are borne in a spiral. In slender stems there are 3 + 5 contact parastichies suggesting a phyllotaxis of about %. The stem is covered with very prominent diamond shaped leaf-base cushions. These cushions are 1.3 mm wide in slender stems but their length varies a good deal. The shortest are seen in regions of arrested elongation e.g. the lateral branch on Pl. VII, fig. 11, where they are barely 1 mm long; usually they are about 2 mm long; one shoot shows them 3 mm long. Their width increases in thickened stems. Where the leafbase cushions are short, they are scarcely distinguished from the leaf, which expands only a little towards its attachment to the stem. Leaf-cushions 2 mm or more long are fairly well marked off from their leaves by the change in the direction of the surface, though the surface cells (and the underlying tissue in sections) are only gradually changed; and the cushion was probably just as green as the leaf. In lateral view the stomatal bands are seen to end abruptly at about the level of the leaf base cushion. In front or back view the lateral margins of the leaf are suddenly constricted at about the same level. On a well developed cushion, the leaf arises from the middle or very slightly below the middle, and never from above the middle of the cushion; this position is unusual but by no means unique in conifers. Leaves on well developed cushions are typically square in section (many specimens showing them broken off). Often however the sides are concave, making the angles more prominent but this is probably due to decay and collapse. Leaves on short cushions (where the stem growth is arrested) are just as strongly curved as usual, but are much flatter in section and instead of being square are broadly rhomboidal. The lateral width is 1 mm as in normal leaves but the front to back width is only 0.5 mm or even less. Such leaves consequently have obtuse front and back angles but sharp lateral ones.

Anatomy of leaf. — All the leaves studied had suffered through rotting. In transverse section the leaf shows a small vascular bundle above and a large resin duct just below its geometric centre. At the sides of the vascular bundle are two patches of thick walled transfusion cells, some with bordered pits. The vascular bundle is sometimes cracked through its middle, presumably along a line of weakness, but it is not divided into two separated strands as for example in *Cunninghamia*. The bundle has no fibrous sheath.

The mesophyll consists of an inner layer of rounded or irregular parenchyma cells and an outer layer of cylindrical palisade like cells which are better differentiated on the abaxial side. In longitudinal section the mesophyll forms nearly transverse plates separated by intercellular air spaces. Similar tissue extends down into the leaf base cushion, but after cork formation it is altered, the cells being filled with a brown resinous matter.

The leaf has a hypodermis of a single layer of thick conpact cells which cover it completely except under the stomata. The hypodermal cells are much more conspicuous than the epidermis in most sections. They extend down over all sides of the leaf base cushion. Their shape is nearly isodiametric polygons.

The epidermis was studied entirely in sections, since cuticle preparations failed (no doubt because of poor preservation). The cells over most of the leaf are elongated, about $20\,\mu$ wide with straight lateral walls and transverse or oblique ends. The stomata are confined to a band on each adaxial face; they were seen in leaf sections and are also plainly visible, though without details, in surface views of the intact leaf. The stomatal bands are not very broad, only occupying about $\frac{1}{3}$ of each adaxial face.

In the region of the stomatal bands Text-figure 4 the epidermal cells are roughly isodiametric and their surface bulges somewhat but does not form a definite papilla. The stomata are rather crowded in the band and are mostly orientated transversely but some lie obliquely. They do not form definite rows or any other regular pattern. Each stoma has two small terminal subsidiary cells and usually four lateral subsidiary cells, or sometimes a single long cell running the whole length of the guard cells. The aperture of the guard cells is only very slightly sunken to form an elongated pit and the poles of the guard cells are at the surface level. The subsidiary cells do not overhang the aperture at all and they are scarcely papillate although their outer surfaces are bulging. No encircling cells are present around any of the stomata examined.

Anatomy of stem. — The primary cortex consists of a thin inner layer of even thickness and an outer very uneven layer forming the leaf-base cushions. The inner layer contains about ten large resin ducts and cork arises between the two layers, thus cutting off the whole of the leaf-base tissues. After they have been cut off, the outer cortical cells mostly become filled with a brownish substance, but previously they appear to form an ordinary, rather parenchymatous assimilatory tissue.

The cork (which was recognised in a stem with only one year's wood) arises from a cambium which persists for some time (in a stem with three growth rings). The cork of the three year old stem consists of alternate layers of robust and delicate tissue; first about four thick walled cells full of brown matter, then about two delicate walled, crushed and empty cells.



FIG. 4. — Elatides bommeri sp. n. · Leaf structure.

A, nearly transverse section of a leaf showing stomata in longitudinal section. (Fungal hyphae are seen outside both.) The dark bodies in the internal cells appear to be resin drops. Leaf series B, $\times 200$. B, section of a leaf parallel with the surface, showing a stomatal band. The ordinary epidermal celles are to the left (two hypodermal cells at the base). The section passes beneath the epidermis on the right and some mesophyll cells are seen at the top right corner. Stem series A, Slide 8, $\times 200$. C, stoma in transverse section from a nearly longitudinal section of a leaf. The epidermis has partly rotted away, Leaf C, $\times 200$. D, stomatal region as in B but $\times 400$. On the right the section passes outside the lateral cell walls and just catches the bulging outer walls. Stem A, Slide 8.

The resin ducts persist in the older stem but are flattened.

The secondary phloem is a thin but complex tissue, unfortunately not very well preserved in the specimens studied. It consists of layers of crushed cells (presumed to be sieve tubes) mixed with uncollapsed small parenchyma cells and a few small, thick walled fibres.

The cambium is missing in all specimens studied.

Secondary xylem. Macroscopic features include fairly well developed growth rings which are not particularly conspicuous, having very little late wood, and in tangential section the occasional rather characteristic leaf traces. The tracheid walls are not particularly thick. In transverse section the annual ring is marked by the following changes in the dimensions of the tracheids (figures are means for several well developed tracheids on either side of the end of the year's growth).

	Total	Radial width	Total	Tangential
	radial width	of lumen	tangential width	width of lumen
Early tracheid	11 μ	9μ	11 μ.	9μ
	6 μ	4μ	11 μ.	8,5μ

Many of the earlier tracheids are almost square in transverse section.

Resin canals are absent from the wood, even from regions showing slight disturbance. Very many cells however contain brown, resinous matter, and many or these are probably xylem parenchyma. Such cells occur everywhere in the annual ring, but are particularly abundant at the end of the late wood. The wood rays are fairly conspicuous in the transverse section. Their cells are rather long extending past 4-8 ordinary tracheids. The horizontal wall of each ray cell (the one separating it from another cell immediately above it in the same ray) usually appears unpitted but some rays show conspicuous round pits.

In the tangential section, the rays are seen to be rather numerous and invariably uniseriate.

The height of the ray is given in the following table (percentage from a count of over 200).

Number of cells high	1	2	3	4	5	6
Percentage having this number	18	42	18	16	4	1



FIG. 5. — Elatides bommeri sp. n. Wood structure.

A: R.L.S. showing two small rays. One of the tracheids shows faint spiral cracks.
B: T.L.S. showing cells partly filled with resin (presumed to be xylem parenchyma).
C: T.L.S. showing two cells (probably tracheids), containing some resinous matter.
A, B, C all ×600, from stem C, slides 6, 1.

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Higher rays were met (but not during this count); one had seven cells, one ten, one eleven.

The tangential walls of the ray cells (the wall separating it from the next cell in the same radial row) usually appears without pits, but occasionally seems to show very conspicuous pits of small or rather large size. I think it likely however that some at least of the pit-like appearance is due to the preservation of cavities, originally water drops, in a resinous cell filling (Text-fig. 5C).

Where the section is sufficiently longitudinal to show them fully, the tracheids appear to be just over 1 mm long. The ordinary pits of the tracheids are well seen; they are more numerous towards the pointed ends of the tracheids but occur also along the whole length. No tracheid showed pits on its tangential wall.

In the radial section, the tracheids show their bordered pits in a single row. The pits are never crowded or in contact, but Sanio's rims could not be seen. The late and early tracheids are very similar except in radial width. The rays are very conspicuous, but chiefly because their cells are apt to be full of resin. The ray cell horizontal walls are moderately thick and occasionally pitted, the ends of ray cells are thinner and slightly contracted. The ray field shows usually two pits, occasionally three always one above another; but occasionally there is only one. The pits are broad oval or sometimes nearly round and have a narrow border (Taxodioid pitting).

The cells regarded as xylem parenchyma resemble tracheids in shape and thickness of wall but are occupied by large quantities of resin. Some appear to show cross walls at long intervals but these were not distinguished with certainty from transverse trabeculae such as may occur in tracheids. The resin takes the form of discontinuous brown drops, or of a continuous brown mass containing dispersed clear cavities, formed presumably from water droplets. These cavities may be large, or small when they often look like pits.

Pith. — The pith is rather narrow and not particularly well preserved in the shoots studied. It is composed of apparently uniform parenchyma cells about 15μ wide and 60μ long. The walls are probably thin but often appear thick because of resinous deposits and the whole interior of the cell is often full of resin (Pl. VII, fig. 4).

Female cone. — There are rather numerous female cones, all but one of which had been broken off before preservation or when collected. This specimen is borne terminally on a short leafy branch among other leafy branches, as in other species of *Elatides*, not in a compact cluster as in some conifers. The detached cones have irregularly broken bases and it seems likely that they have all been broken off before or after preservation, not shed naturally.

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The cone scales are persistent. Several cones, it is true, have lost some scales and show the cone axis, but I am certain that this was all due to dissection after the material was collected. Some of the cones show gaps between the scales; perhaps these were wider when the ripe cone dried naturally and allowed the seeds to escape.

In the cone shown in Pl. V, fig. 3 the cone scales diverge from the cone axis at an angle of about 45° , but in others (perhaps representing a riper state) they diverge at about 60° . The cone axis when exposed by dissection either appears as a slender woody core (Pl. V, figs. 1, 2) or else if it retains its cortex is a stout, rough structure (Pl. V, fig. 5). The crowded stalks of the cone scales seem to cover its surface completely.

A typical cone scale from the middle of the cone is about 6 mm long, 5 mm broad and the following parts are distinguished for description : the stalk, the distal expansion, the terminal point, the « ligule », the placentae. The longitudinal axis of the cone scale is often straight, or it may be slightly but never strongly curved upwards. The terminal point is the part most often bent upwards.

The cone-scale stalk is typically about 2 mm long, 1 mm broad and 0.6 mm thick in section. Its expansion may occupy 0.5 mm or may be quite abrupt, and sometimes it is asymmetric. The distal expansion is about 5 mm wide, up to 2 mm long and 0.6 mm thick in the middle but thins off towards the sides. Its thickness increases distally to a maximum of 0.7 or 0.8 mm from where it thins off rapidly. This region of greatest thickness forms an obtuse angle called the « crest » in this description (Pl. V, figs. 3, 7). From this crest the scale thins off to a sharp distal edge. The « terminal point » is of varied size, but is always recognisable. It is most commonly 1 mm long, it must sometimes be longer, perhaps 2 mm but then is always broken off. At its smallest it forms a mere obtuse point (Pl. V, fig. 7). The terminal point is about 0.3 mm wide at its base and the free part is conical.

The « ligule » is a band of tissue situated just above the stalk. It measures nearly 1 mm long \times 3 mm wide, and though continuous is divided by groves into three bulging lobes. All its edges appear free because it is attached by an area in the middle region. The tissue of the ligule is always thin in section. In many scales it has broken away, but fragments are often found sticking to the scales above. No doubt the ligule was broken when the cone was dissected. The three placentae are hidden under the edge of the ligule; in some scales they are flat, but in others they form small bulges.

In a purely lateral view of the complete cone the exposed surface is formed entirely by the under surfaces of the cone scales (and their terminal points), but when seen from above, a little of the upper surface is visible, as far as the « crest ». In the cones studied the « crest » was slightly separated from the scales above, but its form is always moulded to fit their backs and I have no doubt that during the growth of the cone they were pressed closely together, sealing the cone. There is usually a good deal of free resin outside the scales which must have made the seal more effective. Ch. BOMMER, in his notes, insists that the « ligule » was an important sealing organ, and it may have been so, particularly during early stages of growth, but I know no evidence for this.

Scales from the apex and base of the cone are smaller and often imperfectly formed. They may lack both ligule and placentae. There seems to be a transition to foliage leaves at the base of the cone, while at the apex the reduced scales also become somewhat leaf-like.

A n a t o m y. — A good many cone scales were sectioned. Those first studied were disappointing because the tissues were almost black, and consolidated in patches into homogeneous coal. This made the complicated and crushed tissues look chaotic. However other cone scales were found which were unconsolidated, and it was found possible to bleach the sections with sodium hypochlorite to make them fairly transparent. When bleached, it was even possible to stain them effectively.

The tissues will first be described as seen in a transverse section through the region of the ligule.

The main mass of the scale is a rather spongy looking parenchyma. The cells are mostly about 50μ wide, and their walls are fairly thick, but usually rather distorted. The cells have brownish contents which often makes it difficult to make out individual cells. This parenchyma is chiefly developed below the bundles, while above them it soon gives place to the different parenchyma of the ligule. Among the parenchyma cells there are occasional fibres which seem to wind about irregularly, but in the distal part of the scale the fibres collect in the region below the lower epidermis.

The vascular bundles show groups of ordinary small xylem tracheids separated by broad bands of secondary parenchyma somewhat resembling woodray tissue. In the distal part of the scale, the ray-like tissue increases and the tracheids diminish in numbers. The phloem is poorly preserved in even the best sections, but is no doubt represented by several layers of collapsed cells; or else by a mere space. In one specimen there are a few small fibres in the secondary phloem.

The ligule is composed of a rather different parenchyma. The cells are thinner walled than in the rest of the scale, but they have not collapsed. The walls are pale and there is no brown contents in these cells. Fibres occur here also. In the proximal part of the ligule they are scattered, but they collect above and in the distal part form an almost continuous hypodermal layer under the upper or exposed epidermis. It is noteworthy that in the « crest » of the scale, very similar parenchyma to that of the ligule occurs.

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The placentae (Pl. VI, figs. 8, 10) are composed of many small, thin walled parenchyma cells forming a cushion of soft-looking tissue. There is no internal differentiation in this tissue, though one or two of the fibres may occur in the deeper parts. Below the two lateral placentae there are two small areas of cork. This cork is present in all scales studied, but its extent varies : the patches may be very small indeed, or may extend nearly to meet in the middle. The cork consists of vertical rows of very thin walled almost cubical cells completely filled with a transparent yellow substance (Pl. VIII, figs. 5, 9). No other areas of cork occur in the scale.

The resin duct is a fairly large cavity below the midrib; rather flattened in the series shown in text figure 6. It is only partly filled with resin. Its walls (which are rather poorly preserved in all specimens) appear to consist of small, non-fibrous cells.

The epidermis of the cone scale is composed of rather small cells in this region. It was not possible to isolate the cuticle, though a cuticle is seen in the sections.

The structure of other levels will now be considered.

The stalk, near its base has a single, compact vascular bundle, round in section. The xylem consists almost entirely of rows of small metaxylem tracheids, with very little ray tissue; these rows indicate the position of the protoxylem. The phloem forms a cap of ill preserved tissue round the lower side of the bundle. A little further out (Text-fig. 6 A) the bundle becomes slightly broader and a small resin canal appears below the phloem. This resin canal occupies this position for the whole length of the scale, but it becomes much enlarged at about the middle of the scale. The rest of the tissue of the stalk consists of the spongy parenchyma with scattered fibres that has already been mentioned.

At higher levels in the stalk (6 B, C) the vascular bundle becomes wider and its area increased considerably. This increase is largely caused by the appearance of rows of ray parenchyma cells between the xylem tracheids; but there is some increase in the number of tracheids. The tracheids still form vertical rows and the phloem remains in the same position. At this level, the top of the stalk, the patches of cork below the lateral placentae first appear.

In the distal expansion of the cone scale (6 D onwards) the vascular mass becomes broader still. In the series drawn this expansion is gradual, but in some of the others it is more abrupt, so that at a certain level vascular tissue is seen in the transverse section running longitudinally outwards towards the sides. In this expansion the vascular tissue breaks up into separate bundles of tracheids and phloem, but these are united laterally by bands of secondary parenchyma, forming ray like tissue. The central vascular bundle remains a compact mass of tracheids, but the lateral ones become more and more parenchymatous. The number of these lateral bundles increases by new ones arising from the sides of the central strand, and also by division of the earlier formed lateral ones. Those at the extreme edge on the other hand die away; this occurs simply by their tracheids becoming very few and then ceasing at higher levels so that the identity of the bundle is lost in the ray like tissue which persists around it.



FIG. 6. — Elatides bommeri sp. n.

Selected members of a series of sections through the cone-scale, from base to apex. The plane is slightly oblique (the left side being lower). In all sections xylem is solid black, phloem a white border to the xylem. The resin canal is represented as a space below the xylem. In C, D, E, the corky tissue is crosshaded and in D-G the placentae are marked with an arrow. The extent of the ray-like tissue connecting bundles is indicated by a dotted line. $\times 12,5$.

indicated by a dotted line. x12,5. The numbers of the sections are A-14, B-43, C-56, D-69, E-75, F-82, G-86, H-90, I-97, J-101, K-107, L-118, M-128, N-148, O-157, P-163, Q-170.

Towards the end of the distal expansion this happens to all of the lateral bundles which thus end blindly; but the midrib persists as a very small strand, passing into the terminal point. All of the bundles described above have maintained their orientation which is the normal orientation of a leaf bundle.

There are however some extremely minute bundles which are thought to form an inverted system. In the stalk, at level 6B, a tiny strand is seen immediately above the main bundle. The origin of this bundle was traced from the protoxylem of the main bundle a few sections earlier. In later sections this small bundle becomes still smaller, and then is lost; its whole recognisable course being about 0.25 mm. At its largest point, near its origin, it consists of about seven very small tracheids. No phloem was recognised. No other small strands than this were recognised in this series, but they may have been missed through the difficulty in seeing them.

In another series, where because of some unexplained difference of preservation the xylem stands out well though other tissues are poor, two, and perhaps more of these minute strands arise. Two arise separately in the stalk region from the protoxylem of the single vascular bundle, and then at a higher level, at the base of the distal expansion another small strand arises from the end of the vascular mass which in giving rise to it bends round in a hook. It is possible that a fourth small bundle arises from the other end of the vascular mass, but there are fibres which obscure that region. These small bundles persist for about 0.5 mm but are then lost without their having ever actually entered the placenta or ligule. The placentae and ligule are entirely non-vascular in the sections examined.

Seeds. — The mature seeds are oval or oval-triangular with the micropyle forming an obtuse point. The length is about 1.3 mm the width 0.8 mm, the thickness about 0.4 mm. The surfaces are marked with ridges which differ in different seeds and are no doubt due to pressure of neighbouring seeds and scales. Although the seed is flat and its edges are sharp it is not at all winged. The hilum in the specimen figured (Pl. V, fig. 10) forms a fairly large shallow cavity.

Several seeds were studied in section (Pl. VIII, figs. 2, 7, 8, 11). The testa or integument forms a compact layer varying from $35\,\mu$ or less to $65\,\mu$ thick in different parts of the seed. Its surface layer of cells is very conspicuous forming an epidemis of cup shaped cavities in transverse section. Apparently the inner and radial walls of the cells are very thick but the outer wall is either missing, or collapsed against the robust walls. Some seeds show a little yellow material just outside this layer, but I suppose that it is extraneous. The inner layers of the integument appear homogeneous in some seeds, but shows scattered and small cell cavities in others. Evidently it consists of a few layers of very thick walled fibrous cells. In the parts where the testa is thin, it is these inner layers of fibres that are missing.

Inside the stone layer of the integument there is a small amount of delicate tissue in which no details were observed.

Inside this there is a suggestion of a distinct continuous layer round the endosperm which is interpreted as the megaspore membrane.

The endosperm is a striking tissue composed of dark angular blocks separated by clear spaces (Pl. VIII, fig. 11). I regard these blocks as representing

the modified oily contents of the endosperm cells and the clear spaces as their walls. In some seeds there are regions of disorganised tissue between these endosperm cells; but if these represent the proembryo there is no evidence !

No seeds were successfully studied by maceration.

Comparison. — Elatides bommeri will be compared first with E. williamsoni (to justify its inclusion in Elatides) and then be compared with other living and fossil conifers.

Elatides bommeri closely resembles E. williamsoni see HARRIS 1943 in the branching and general appearance of the twigs, and in the way the female cones are borne. The twigs agree in their short, spirally arranged, incurved leaves. In both the leaves are rhomboidal in section, in both, the stomata are limited to narrow bands and agree in being rather crowded and transvesely orientated, and in lacking papillae on the subsidiary cells as well as on other epidermal cells. Differences are : the smaller size of the leaf of E. bommeri, the better development of the upper part of the leaf cushion of E. bommeri (so that the leaf arises at its middle instead of near its top); the occurrence of the stomatal bands on the two upper leaf faces of E. bommeri, but on the lower of E. williamsoni, and a difference in the stomata which lack encircling cells in E. bommeri, but possess them in E. williamsoni.

The female cones agree in their spiral construction and persistend scales. In both, the cone scale is flattened and ends in a terminal point. In both it bears a delicate « ligule » on its upper side, immediately below which are the placentae bearing a row of small, flattened orthotropous seeds, with micropyles facing the axis. The seeds apparently agree in possessing an endosperm with an unusually persistend oily reserve in the cells.

Differences are : the cones of E. bommeri are smaller, the cone scales have a better marked stalk and shorter apical point; the ligule is straighter and less lobed, the placentae less prominent and the seeds are three instead of five.

The differences between these two conifers show that they must certainly be distinct species but are not, in my judgement, of generic importance. Their points of agreement however justify their being placed in the same genus. This involves the assumption that the numerous unknown features of the two agree, an assumption that must always be made when incompletely known fossil plants (and indeed living plants) are to be classified together.

Bearing in mind the chance of error from this assumption, we will attribute to the genus *Elatides* all that is known of the two species, and the sum is impressive since our knowledge of the two is partly complementary and this sum can be compared with other conifers.

The organs known are :

1. Lateral shoots. — The form of large specimens is known in E. williamsoni and of small pieces in E. bommeri. The leaf form and cuticle

are known in both species, the internal structure is known in *E. bommeri*. The anatomy of small and fairly large branch stems is known in *E. bommeri*.

Leader shoots are not known in either but it is unlikely that they would differ greatly from the lateral branches, except perhaps in better developed leaves and xylem.

2. Female cones. — The form and position on the shoot is known in both species. The external shape of the cone scale and seeds is known in both; the internal anatomy including vascular bundle course is known in E. bommeri. The anatomy of the seed is known in both though in rather different ways.

3. Male cone. — This organ is known in E. williamsoni alone, knowledge includes its position on the shoot; its form, the form and arrangement of the microsporophylls, the number and shape of the pollen sacs and the shape of the pollen grains.

The unknown but systematically valuable organs are the gametophytes and embryos. It is rare for these to be available in a fossil (a little information is available about the ripe female gametophyte of E. williamsoni).

Comparison of Elatides with recent genera. — It can be stated at the outset that *Elatides* is very much more like certain recent Taxodiaceous genera than any other conifers. Individual features of certain organs can be matched among other families but the resemblance is spoilt by great differences between other features of the same organs. Thus the form of the leafy shoot resembles *Araucaria excelsa* and species of *Dacrydium* but the cuticle and wood anatomy differ. The elongated, fused pollen sacs agree with various *Abietineæ* but they differ in their number and in the wingless pollen grains. The *Cupressaceæ* indeed share several characters with *Elatides* but this family is in any case rather close to the *Taxodiaceæ* and these characters are seen equally in recent *Taxodiaceæ*. It does of course differ from the *Cupressaceæ* in the important characters of its spirally arranged leaves and inverted ovules.

Close camparison wild be confined to the Taxodiaceæ.

Leafy shoot. — Fairly similar foliage is seen in Taiwana cryptomeriodes, Cryptomeria japonica, Sequoia gigantea and Glyptostrobus pensilis. Sequoia gigantea agrees with E. bommeri in the transverse section of the leaf which shows a similar, reather small vascular bundle with two patches of transfusion tissue and a large resin duct. The mesophyll is very similar and there is an almost exactly similar layer of hypodermal fibres. Cryptomeria on the other hand is less similar, fibres are lacking and the mesophyll is different. It is notewortby that Cunninghamia (which as will be seen has similar cone scales) has a rather different mature leaf, being flattened, with a double vascular bundle and fibrous mesophyll. The *Taxodiaceæ* have remarkably varied cuticles but all the individual features of *Elatides* can be matched among recent genera, more closely indeed than with the genera of any other family.

1. Arrangement of stomata. — In *Elatides* as in other conifers with thick needles of diamond shaped cross section, the stomata occur on the flat sides. In *E. williamsoni* they occur on the two abaxial sides, in *E. bommeri* on the two adaxial; in another Yorkshire species (yet to be described) they are chiefly on the abaxial sides but in a few large leaves there are small adaxial bands also. In the above mentioned conifers, *Sequoia gigantea*, *Cryptomeria*, *Glyptostrobus* there are four bands but *Taiwana* has only two very broad abaxial ones.

Irregularly orientated stomata are rather unusual in the conifers; but they are seen in the Araucariacex (which in other respects are different) and in the Taxodiacex for instance in all four conifers mentioned just above, and in Athrotaxis in addition. It is noteworthy that Cunninghamia is very different in its logitudinal stomata.

2. Structure of stomata. — Very similar stomatal structure is seen in *Taxodium distichum* where the rectangular pit formed by the subsidiary cells is almost exactly like that of E. bommeri.

Most Taxodiace have amphicyclic stomata (the subsidiary cells having cut off « encircling » cells in development), and *Elatides* is therefore not quite usual, since *E. williamsoni* has an incomplete ring of encircling cells and *E. bommeri* few or none at all. However in *Taxodium*, *Cryptomeria* and some others the encircling cell ring is often incomplete so that the difference is merely one in the degree of their development. *Athrotaxis* is very different since the adjacent stomata usually share subsidiary cells.

Papillae are absent from the subsidiary cells and other epidermal cells of nearly all *Taxodiaceæ*, just as in *Elatides*. (*Sciadopitys* is exceptional in having them.) The cell walls too are normally straight as in *Elatides*; (*Cunninghamia* with sinuous ones is exceptional).

Stem. — Many Taxodiaceæ, as well as some other conifers have stems showing a general similarity to E. bommeri in transverse section. In the Cupressaceæ for instance there are similar cortical resin canals and a fibrous phloem. The secondary xylem however which is of the Cupressinoxylon type is more limited, being found in some Podocarpaceæ, Taxodiaceæ and Cupressaceæ.

Wood structure. — Although the wood is only known from twigs (which are not to be expected to show the full characters only seen in the later wood of the main trunk) and although the preservation is not perfect, it does show striking features of agreement with the *Taxodiaceæ*. It agrees in the

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uniseriate well spaced tracheid pits; presence of plenty of xylem parenchyma, « Taxodioid » cross field pits, thick horizontal walls of ray cells and in the absence of any resin canals, ray tracheids, or spiral thickennings of the tracheids. These characters taken together are typical of the *Taxodiaceæ*, though not quite exclusive of other genera, e.g., of the *Cupressaceæ*. Sciadopitys is the only genus of the *Taxodiaceæ* with extremely different wood structure.

Male cone. — (This refers to *E. williamsoni* only since the male cone of *E. bommeri* is unknown.)

The position of the small male cones, borne in a cluster at the end of a shoot is one seen in many conifers besides genera of the Taxodiaceæ. The shape of the microsporophyll, which has a rather long and slender stalk suddenly expanding distally into an upturned scale is not specially a Taxodiaceous character (where the stalk is usually very short) but much more like an Abietinean male cone. The number of pollen sacs is however typical of the Taxodiaceæ where there may be more than two sacs (Cunninghamia and Sequoia agree in having three). The sacs in Sciadopitys which has only two are similar to *Elatides* in being elongated and partly united to one another and to the stalk but those of Cunninghamia are separate and those of Sequoia are both separate and quite short. No other Taxodiaceous genera shows this form of fused pollen sacs, but it is seen in various Abietineæ and Podocarpaceæ. It is a rather surprising character for *Elatides* shows no other approach to *Sciadopitys* and such adnation or fusion is in general regarded as an advanced character.

In their thin walls the pollen sacs of *Elatides* agree with nearly all conifers except the Araucarians where they are several cells thick.

Pollen. — (Elatides williamsoni). The round-oval pollen grains with a single shallow furrow agree with those of the Taxodiaceæ and many other conifers; but differing from the winged grains of Abietineæ and Podocarpaceæ.

Female cone. — In the size and general development of the female cone and its position on the shoot *Elatides* agrees with various *Taxodiaceæ* and also with the *Abietineæ* and *Araucariaceæ*; in fact with all but the genera with feebly developed cones or none. Its spirally arranged scales differentiates it from the *Cupressaceæ* and the numerous ovules (five in *E. williamsoni*, three in *E. bommeri*) differentiate it from all but the Taxodiaceae and among this family it is closest to *Cunninghamia*.

In the Taxodiaceæ there is very great variety of cone scale form and structure. In Elatides the bract scale is considerably larger than the seed-scalecomplex of FLORIN (ovuliferous scale) and forms the exposed surface of the cone as in Cunninghamia and Taiwana; in Athrotaxis only a little of the seed-scalecomplex is visible on the outside but in the other genera the seed-scale-complex is better developed and thickened to form a large part of the exposed surface. The isolated cone scale agrees very closely indeed with *Cunninghamia*. The « ovuliferous scale » is here a small and almost completely adnate structure with only a slight membranous free extension or ligule beyond the ovules and the ovules are borne on rather prominent and separate placentae with the micropyle facing the cone axis. *Taiwana* is similar but with only two ovules.

The vascular supply of the cone scale has a single vascular strand which gradually widens and becomes partly broken (by ray-like tissue) into a single row of vascular bundles of normal orientation. There are in addition some very minute strands (presumed to be of inverted orientation) which pass up towards the placentae but end without entering either placentae or ligule.

This vascular supply is closely similar to that of *Cunninghamia* (see AASE, 1915).

The small flat seeds which are attached by their bases only with the micropyle pointing inwards and agree with the *Taxodiaceæ* (and *Cupressaceæ*) but with no other family. No survey of conifer seed structure is known to me, but I have made a comparison with the seed of *Cunninghamia sinensis* which, seems to agree with *Elatides* rather closely. Significant facts in *Elatides* are the possession of a rather thin but fibrous integument, the apical micropyle, the short micropylar canal (blocked after pollination in *E. williamsoni*). The nucellus is cutinised and seems to be free over most of the seed and there is no definite pollen chamber, but grains are found (in *E. williamsoni*) around its apex).

The megaspore membrane is well developed but with no special peculiarities. It encloses a certain amount of cellular tissue which seems to be the altered contents of the outer cells of the endosperm, and there is an apical group of archegonia.

It can be stated that *Cunninghamia* appears to share every one of these characters, but I cannot say what other genera of the *Taxodiaceæ* and *Cupressaceæ* share them also, except that some of them certainly occur in other genera..

Summary. — The male cone is nearest Cunninghamia (but with one feature of Sciadopitys); the female cone is much nearer Cunninghamia than any other recent genus in both form and structure of the cone scale. The seed agrees with Cunninghamia but very likely with other genera also. The foliage is however not at all like that of Cunninghamia but agrees quite well with several other genera; the wood is typically Taxodiaceous. The inference is that Elatides is to be classified as a typical member of the Taxodiaceæ and perhaps closer to Cunninghamia than to any other genera.

Comparison with fossil conifers. — Elatides is close to Sphenolepis as interpreted in this paper. The foliage is better developed in Elatides but

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similar in the position of the resin duct and in the extremely important epidermal characters. The wood anatomy is very similar indeed. The female cone is a smaller in *Sphenolepis* but very similarly constructed from spirally arranged scales composed of a stalk gradually enlarging into a simple wedge shaped mass. Differences are that in *Elatides* the outer part of the scale continues into a little point but in *Sphenolepis* it is truncate, and that in *Elatides* there are distinct « ligular » upgrowths which are missing in *Sphenolepis*. *Sphenolepis* has more seeds which are attached in two rows instead of in one. The seeds themselves are very similar. The vascular anatomy shows essential similarity consisting almost entirely of the lower, normally orientated system with only a vestige of the upper, inverted system, and the bundles of the upper system appear to die away without supplying any definite structure.

Cunninghamiostrobus Stopes and FUJII 1910, OGURA 1930 is an upper Cretaceous cone known from its internal anatomy and therefore strictly comparable with *Elatides bommeri*; its shoot is however unknown. The scales are of fairly similar shape and bear three bulges which are thought to represent placentae. No attached seeds are known but illpreserved bodies between the scales are no doubt seeds and are of very similar appearance. The vascular supply of the scales is very similar indeed; there is a main normally orientated system formed by the splitting of a single large bundle and some minute inverted bundles above just as in E. bommeri. A difference (but not perhaps of great importance) is that in *Cunninghamiostrobus* the main vascular trace running to the « cone scale » is at first concentric. Another difference is in the absence (so far as we know) of any ligule-like appendages on the upper surface beyond the seeds. It would appear that Cunninghamiostrobus is almost as much like Elatides as it is like Cunninghamia and its classification must await knowledge of other organs.

There are several Mesozoic cones which agree with *Elatides* in size and in the somewhat spinous cone scales, but which are not fully enough known for close comparison. Some of these may ultimately prove to be very similar indeed.

These include :

Ceratostrobus VELENOVSKI (1887), two species from the Upper Cretaceous of Bohemia. It is interesting that BOMMER in his early notes included E. bommeri in the genus Ceratostrobus.

Echinostrobus SCHIMPER. This is the cone of Brachyphyllum expansum (Middle Jurassic) which has been redescribed by KENDALL (1949). The cone scales are more peltate and nothing is known about the seeds. It is unlikely to be related as the cuticles of the leaves are very different.

Athrotaxites UNGER (Upper Jurassic). For A. lycopodioides see SCHIMPER 1870-1942, Pl. 75, fig. 21, SAPORTA 1891, Pl. 199; for A. ungeri see HALLE 1913. The general aspect of these cones is notably similar to Elatides but the leaves are rather thicker and more as in Brachyphyllum.

Athrotaxopsis FONTAINE (1889) from the Middle Cretaceous is a rather confused group of cones which as has been pointed out (see SEWARD 1919) is close to Sphenolepis in general aspect.

The Voltziales of the Older Mesozoic (see FLORIN 1944). It seems to me that *Elatides* has little resemblance to these interesting and primitive conifers, apart from features shared by other *Taxodiaceæ*. It is for instance much less close than is the living *Cryptomeria*. FLORIN however makes the point that the prominence of the placentæ of *E. williamsoni* is a point of approach to the *Voltziales* and of difference from *Cunninghamia*. In *E. bommeri* the placentæ vary being flat or raised, but less raised than in *E. williamsoni*. It is to be noted that in *Cunninghamiostrobus* the placentæ are distinctly raised. This feature is one which had not been considered until FLORIN's work was published; however in view of the fact that in *E. bommeri* the placenta is not vascular it seems to me that it is unwise to press this minute point very far.

WORKS QUOTED

- AASE, H. C., 1915, Vascular anatomy of megasporophylls of conifers. (Bot. Gaz., LX, n° 4, pp. 277-313.)
- CARPENTIER, A., 1927, La flore wealdienne de Féron-Glageon (Nord). (Mém. Soc. géol. du Nord, t. X, 1.)
- 1939, Les cuticules des Gymnospermes wealdiennes du Nord de la France. (Ann. paléont., t. XXVII, fasc. 4 (1938), pp. 155-179, pl. XI-XXII.)
- DUNKER, W., 1846, Monographie der Norddeutschen Wealdenbildung. (Braunschweig.)
- FLORIN, R., 1944, Die Koniferen des Oberkarbons und des Unteren Perms. (Palæontegr., Bd. LXXXV, Abt. B.)
- FONTAINE, W., 1889, The Potomac or younger Mesozoic Flora. (Mon. U. S. Geol. Sur., 15.)
- HALLE, T. G., 1913, Some Mesozoic plant-bearing deposits in Patagonia and Terra del Fuego and their Floras. (K. Svensk. Vetenskapsakad. Hand., Bd. LI, n° 3.)
- HARRIS, T. M., 1943, *The Fossil Conifer* Elatides williamsoni. (Ann. Bot. N. S., vol. VII, n° 28, pp. 325-339, pl. VIII.)
- HEER, O., 1876, Beiträge zur Jura-Flora östsibiriens und des Amurlandes. (Mém. Acad. Imp. Sci. Saint-Pétersbourg (7), XXII, n° 12.) (Flora Foss. Arctic., IV, n° 2, 1877.)
- 1881, Contributions à la Flore fossile du Portugal. (Secc. Trab. Géol. Portugal.)
- KENDALL, M. W., 1949, Brachyphyllum expansum (Sternberg) Seward, and its cone. (Ann. Mag. Nat. Hist., Ser. 12, vol. II, p. 308.)
- MICHAEL, F., 1936, Pälaobotanische und Kohlenpetrographische Studien in der nordwestdeutschen Wealdenformation. (Abh. d. Preuss. Geol. Landes. N. F., Heft 166, pp. 6-79, pl. I-IV.)
- NATHORST, A. G., 1897, Zur Mesozoischen Flora Spitzbergens. Zur fossilen Flora der Polarländer, 1.2. (Kungl. Sv. Vet.-Akad. Handl., Bd. 30, n° 1.)
- OGURA, K., 1930, On the Structure and affinities of some Cretaceous Plants from Hokkaido. (Journ. Fac. Sci., Imp. Univ. Tokyo III Botany, vol. II, Part 5, pp. 381-412, pl. XVIII-XXI.)
- SAPORTA, G. DE, 1891, Paléontologie française, vol. IV.
- 1894, Flore fossile du Portugal. (Trav. Géol. du Portugal.)
- SCHENK, A., 1871, Berträge zur Flora der Vorwelt. Die Flora der Nordwestdeutschen Wealdenformation. (Palæontographica, XIX.)
- SCHIMPER, W. P., 1870-1872, Traité de Paléontologie Végétale. (Atlas.)
- SEWARD, A. C., 1895, The Wealden Flora, Part II. (British Museum Catalogue.)
- 1919, Fossil Plants, vol. IV. (Cambridge.)
- STOPES, M. C. and FUJII, K., 1910, Studies on the Structure and affinities of Cretaceous Plants. (Phil. Trans. R. Soc. B., vol. 201.)
- VELENOVSKI, J., 1887, Neue Beiträge zur Kenntniss der Pflanzen der böhmischen Cenomaniens. (Sitzber. k. böhm. Gess. Wiss. (1886).

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PLATES I-VIII.

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EXPLANATION OF PLATE I.

Sphenolepis kurriana.

- FIGS. 1-9. Typical twigs, all \times 2.3. In the specimen shown in fig. 9 two leaves are abnormal in diverging from the stem. Photos by BOMMER.
- FIG. 10. Part of the twig shown in fig. 9, \times 8, reduced from a drawing by Ch. BOMMER.
- FIG. 11. Part of the twig shown in 3, \times 8, reduced from a drawing by Ch. BOMMER.
- FIGS. 12, 13. Two sections through cone scale, « A ». In fig. 12 (below the seeds) the bundle is dividing into three; in 13, (at or above the seed level) it is divided into four strands of which the midrib is clearly distinguished, × 20.
 12 is between B and C in Text-fig. 3, 13 is between E and F in Text-fig. 3.
- FIG. 14. Transverse section through a leaf base, just below the free part of the leaf, showing the palisade. Stem, A, \times 100.
- FIG. 15. Tangential section of the secondary wood of a twig showing the small area disturbed by a leaf trace. Stem series B, Slide 6, \times 100.
- FIG. 16. Transverse section through cone scale « A » showing one of the minute upper bundles. The large strand to the right is the midrib, × 100. Between C and D in Text-fig. 3.
- FIG. 17. Transverse section of cone scale « A » slightly below fig. 16, obscurely showing the origin of the minute bundle (marked by an arrow in 16 and 17), \times 100. Between B and C in Text-fig. 3.

Inst. Roy. Sc. Nat. Belg. — Mém. Nº 126, 1953. Kon. Belg. Inst. Natuurw. — Verh. N^r 126, 1953.



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Phototypie A. Dohmen, Bruxelles

EXPLANATION OF PLATE II.

Sphenolepis kurriana.

FIG. 1. — Cone with part of its pedicel, untouched photo, \times 5.

- FIG. 2. Woody axis of cone after the cone scales have been stripped off. Reduced from Ch. BOMMER's drawing, \times 5.
- FIGS. 3, 4. Two views of a partly dissected nearly mature cone, reduced from Ch. BOMMER's drawings, seeds are still present, \times 5.
- FIG. 5. Cone scale dissected from a cone which has shed its seeds, showing six small placentae, retouched photo, \times 10.
- FIG. 6. Another scale from the same cone as in fig. 5, \times 10.
- FIGS. 7-12. Views from different aspects of a single cone-scale; fig. 7, 8, reduced from Ch. BOMMER's drawings, 9-12 Ch. BOMMER's original drawings, all × 12 approx. A small amount of the epidermis of the scales above seems to be adherent to the distal part. The upper surface is strongly grooved and the placentae are not shown.
- FIGS. 13, 14, 15. Three views of a seed taken from the specimen shown in figs. 3, 4; Ch. BOMMER's drawing, × 18.
- FIG. 16. Base of a cone, shown upside down. There are some transitional scale leaves one or two of which subtend separate axillary bodies, untouched photo, \times 10.
- FIG. 17. Dissected immature cone. The cone axis is on the left, and the upper surface of a cone scale showing five immature ovules, three above, two below, \times 10.
- FIG. 18. Surface of abraded cone showing the resin cavities in the scales. Drawing by Ch. BOMMER, \times 10.



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EXPLANATION OF PLATE III.

Sphenolepis kurriana.

- FIG. 1. Transverse section showing numerous annual rings, same simple others complex, \times 30 approx.
- FIG. 2. Part of the section shown in fig. 1, \times 150 approx. showing scattered resincontaining parenchyma cells.
- FIG. 3. Radial section. The annual growth ring ends at the right side of the figure. There is a resin-containing cell 5 cm from the left side, \times 150 approx.
- FIG. 4. Tangential section; a resin-containing cell is situated at 1 cm from the right side, \times 150 approx.

Photographs by CH. BOMMER of the wood of a branch nearly 1 cm thick.



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EXPLANATION OF PLATE IV.

Elatides bommeri.

FIG. 1. — Group of leafy twigs, $\times 2$.

FIG. 2. — Fragments of larger twigs, \times 2.

FIG. 3. — Cone attached to leafy shoot, Type Specimen, \times 2.

FIG. 4. — Collection of cones (uppermost seen also in fig. 3), all \times 1.3.

FIGS. 5, 6. — The same cone illuminated from two different angles, \times 4.

All the figures are photographs by CH. BOMMER



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EXPLANATION OF PLATE V.

Elatides bommeri.

- FIG. 1. Woody axis of a cone stripped of its cone scales, \times 4,5.
- FIG. 2. Partly dissected cone, \times 4,5.
- FIG. 3. Ripe cone scale from which the seeds have fallen, \times 6,75.
- FIG. 4. Ripe cone scale which still retains two of its seeds, \times 6,75.
- FIG. 5. Dissected cone axis on which a single cone scale remains, \times 6,75.
- FIG. 6. Same specimen as in fig. 5 from a different aspect, \times 6,75.
- FIG. 7. Partly dissected cone showing three cone scales, \times 4,5.
- FIG. 8. Under side of cone scale (the same as in fig. 14), \times 6,75.

FIGS. 9, 10, 11. — Seed from above, below and the side \times 9.

- FIG. 12. Broken stump of a cone scale showing the vascular strand (seen also in fig. 5), \times 22,5.
- FIG. 13. Cone scale from immature cone (same as in 15, 16, 18, probably from the cone shown in fig. 17), \times 13,5.
- FIG. 14. Ripe cone scale from above, showing all three seeds (as in fig. 8), \times 6,75.
- FIG. 15. Young cone scale from above, \times 13,5.
- FIG. 16. Young cone scale from the side, \times 13,5.
- FIG. 17. Young cone, dissected to show central axis and one remaining cone scale, \times 18.
- FIG. 18. Young cone scale from below, \times 13,5.
- FIG. 19. Young cone scale from within the cone (probably from the cone shown in fig. 17), \times 13,5.

All the figures are drawings by CH. BOMMER.



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Elatides bommeri.

- FIG. 1. Cone-scale, upper surface, stalk missing. The « ligule » has been largely broken away exposing two of the placentae which are prominent. Slide $E_{,\times}$ 8,6.
- FIG. 2. Complete cone-scale, upper surface. Slide $E_1 \times 8,6$.
- FIG. 3. Same cone-scale as in fig. 2, but with the ligule dissected away. In this specimen the placentae are not prominent. Slide E, × 8,6.
- FIG. 4. Transverse section of cone-scale, series C, section 75, \times 17,2. The section is at the base of the ligule.
- FIG. 5. Transverse section of cone-scale, series C, section 92, \times 17,2. The section is near the middle of the ligule.
- FIG. 6. Cone apex viewed from above showing the sharp edge of the cone-scales and their thickened upper surface. Slide F, \times 4,3.
- FIG. 7. Transverse section of upper surface of the cone-scale and ligule, near its top. A hypodermal layer of fibres has appeared in the ligule. Series C, section 101, \times 86.
- FIG. 8. Transverse section of a cone-scale through one of the lateral placentae, (overhung by ligule tissue). The dark cells in the placenta are possibly fibres. Series C, section 69, \times 86.
- FIG. 9. Transverse section through cone-scale showing the vascular bundles at the level of the ligule. The small arched bundle in the centre (cracked vertically) is the midrib, the oblique cavity below is the cavity left by the contraction of the resin (to a small mass above and on the right). Series C, section 82. × 43.
- FIG. 10. Transverse section of a cone-scale showing a lateral placenta overhung by ligule tissue. The large dark mass below is one of the main lateral bundles passing the placenta. Series A, section 117. \times 86.
- FIG. 11. Transverse section of a cone-scale, near its apex. The vascular tissue is largely represented by a band of secondary parenchyma with occasional rows of tracheids. Large fibres are seen above. Series C, section 140, × 86.

Inst. Roy. Sc. Nat. Belg. — Mém. Nº 126, 1953. Kon. Belg. Inst. Natuurw. — Verh. N^r 126, 1953.



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EXPLANATION OF PLATE VII.

Sphenolepis kurriana, Elatides bommeri.

- FIG. 1. Sphenolepis kurriana (DUNKER) SCHENK, Radial longitudinal section of medulla (xylem on left). Stem C, Slide 6, × 83.
- FIG. 2. S. kurriana (DUNKER) SCHENK, Tangential longitudinal section of secondary wood showing a branch trace. Stem C, Slide 2, \times 83.
- FIG. 3. S. kurriana (DUNKER) SCHENK, Transverse section of medulla. Stem C, TS. 1, × 83.
- FIG. 4. *Elatides bommeri* nov sp., Radial longitudinal section of medulla showing the rather spongy tissue. Stem C, Slide 4, × 83.
- FIG. 5. E. bommeri nov. sp., Tangential longitudinal section of secondary wood showing a leaf trace. Stem C, Slide 2, \times 83.
- FIG. 6. *E. bommeri* nov. sp., Transverse section of stem (part of the same section as in fig. 8). Inn the centre is a resin duct, above it some cork and then the tissue of the leaf bases. Inside the resin duct is a detached segment of the xylem ring and then the medulla. Stem A, \times 83.
- FIG. 7. E. bommeri nov. sp., Shoot showing leaf bases. All the leaves have broken off since the specimen was collected. Specimen B, \times 8,3.
- FIG. 8. E. bommeri nov. sp., Transverse section through shoot passing through two leaves. (Fig. 6 is part of this, rotated through 90°). Stem A, \times 16,6.
- FIG. 9. *E. bommeri* nov. sp., Oblique section through the lower part of a leaf showing the resin duct, vascular bundle immediately above it (cracked in the middle) with transfusion tissue at its sides. The obliquity exaggerates the vertical axis of the leaf section. Leaf A, \times 16,6.
- FIG. 10. E. bommeri nov. sp., Transverse section of a leaf, (upper part). There is a central resin duct, the vascular bundle has almost disappeared. Leaf $B_{, \times}$ 16,6.
- FIG. 11. E. bommeri nov. sp., Shoot bearing a bud-like lateral branch with short, flat leaves. Most of the leaf bases of the main shoot have broken away from the xylem. Slide C, \times 8,3.
- FIG. 12. E. bommeri nov sp., Shoot with normally developed leaves. Xylem core is exposed below. Slide D, \times 8,3.
- FIG. 13. *E. bommeri* nov. sp., Shoot with well developed leaf bases, but the free parts of the leaves have been broken off since collecting. The xylem core is exposed above. Slide A, \times 8,3.

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EXPLANATION OF PLATE VIII.

Elatides bommeri.

- FIG. 1. Transverse section near base of cone scale showing the large bundle. A minute group of tracheids has separated from the main mass and lies just above it. The phloem is partly preserved below. Series C, Section 41, × 86.
- FIG. 2. Transverse section of seed, taken near chalazal end, showing chalazal cells, \times 43.
- FIG. 3. Transverse section near base of cone scale showing a resin cavity below the bundle. Series C, Section 52, \times 43.
- FIG. 4. Transverse section through bundle of cone scale, near the top of the stalk. The crack in the main bundle is accidental but a small group of tracheids is separating on the right and upper side. Series B, Slide 6, × 86.
- FIG. 5. Cork tissue near the placenta, (the bundle here appears black). Series C, Slide 2, \times 86.
- FIG. 6. Section a little above 4; two small bundles are seen above the main mass, the right hand one being the reduced remnant of that in Series B, Slide 7, \times 86.
- FIG. 7. Transverse section through the flattened micropyle of the seed, the integument has cracked accidentally, \times 43.
- FIG. 8. Transverse section through the middle of a seed after rather considerable clearing with sodium hypochlorite. The hard outer tissue of the integument encloses some softer inner tissue and resistant cells in the endosperm, \times 86.
- FIG. 9. Section rather higher than that in 6 showing the cork below the placentae. Series B, Slide 10, \times 86.
- FIG. 10. Glancing section of cone scale showing epidermal cells and stomata near its apex. Series C, Section 150, × 172.
- FIG. 11. Transverse section through the middle of the seed showing the integument and endosperm tissue, \times 43.



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