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FURTHER CONIFERS OF THE PINACEAE FROM THE WEALDEN FORMATION OF BELGIUM

BY

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(WITH 10 PLATES.)

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INTRODUCTION

Earlier contributions in this series on the Ch. Bommer Collection of plants from the Wealden of Belgium have been concerned with the Taxodiaceous conifers (Harris, 1953) and a number of cones belonging to the Pinaceae (Alvin, 1953 and 1957*b*). The present paper brings to a conclusion the Pinaceous remains (except for isolated woods which have not so far been studied at all) and deals with four further species of cones and some vegetative material also believed to be of Pinaceous affinity.

Methods. — In dealing with the vegetative remains, it has been found useful to employ other techniques besides the standard softening and celloidin embedding procedure. External cuticles are, in general, very poorly preserved in this material, and if the standard maceration treatment in nitric acid + potassium chlorate is employed, nothing usually remains but a few useless shreds of cuticle. Preparations of reasonable quality, however, have been obtained by sticking fragments of leaves, which have first been soaked overnight in hydrofluoric acid to remove fine particles of mineral matter, to thin cellulose acetate film, and then removing the carbonaceous substance by soaking in peroxide + about 2 % sodium carbonate; after an hour or two only the delicate cuticles are left adhering to the film. Another technique that has been of some value in studying leaf anatomy, has been to macerate fragments by first swelling them in potassium hydroxide, and then transferring them to peroxide + soda; here after a few minutes they become macerated in such a manner that when squashed gently under a cover-slip the cells tend to separate in much the same way as in recent material macerated in chromic acid.

Note on dimensions. — Most of the specimens in the collection have been removed from the original matrix, but the small specimen of *Pityostrobus villerotensis* shown in figure 6, plate X, is in situ, and it is striking how much smaller the cone is than the cavity (impression) that it occupies in the now dry matrix. The following are the dimensions (taken in the plane of compression) :

Length of specimen	2,5 cm
Length of impression	3,0 cm
Breadth of specimen	1,2 cm
Breadth of impression	1,5 cm

The linear dimensions of the fossil are thus nearly 20 % less than those of the impression. The fine-grain matrix itself has presumably shrunk to some extent on drying, so that it may well be that the linear dimensions of the specimen are nearly 25 % less than originally. There is no reason to suppose that this one specimen may have shrunk more than any other. Some correction, therefore, should perhaps be applied to the macroscopic dimensions given in the descriptions.

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FURTHER CONIFERS OF THE PINACEAE

FROM

THE WEALDEN FORMATION OF BELGIUM

Order CONIFERALES.

Family PINACEAE (1).

Genus PSEUDOARAUCARIA Fliche.

Pseudoaraucaria gibbosa (Coemans) n. comb.

Pinus gibbosa Coemans, 1866, p. 13, pl. V, fig. 2.

Material assigned to this species consists of a few cones, all somewhat damaged, some scales and an abundance of cone-axes and fragments of axes.

Although all four of the more or less complete cones that I have examined are somewhat larger than Coemans' specimens, I am convinced that they belong to the same species.

The species is clearly classifiable in the organ-genus *Pseudoaraucaria* Fliche which has recently been recognized as a distinctive cone-type in the Pinaceae (Alvin, 1957*a*).

Emended diagnosis. — Cone ellipsoidal or ovoid, (2,5-) 3,6 (-4,4) cm long, (1,4-) 2,1 (-2,5) cm broad; apex truncate or slightly depressed.

Bract obovate, 1,5 mm broad; free part about 2,5 mm long.

Ovuliferous scale typically about 16 mm long, 9 mm broad, bent so that the upper laminate part makes an angle of about 130° with the lower seed-carrying portion; interseminal ridge narrow, scarcely overarching the seeds; apex of scale thin, rounded to sub-acute, with a terminal triangular umbo 2 mm long.

Seed 3-6 mm long, 2 mm broad; wing 11 mm × 4 mm, covering most of the upper surface of the scale.

Vascular system of the axis much dissected; supply to the bract simple, arising from the bottom of the « leaf-gap »; supply to the ovuliferous scale horseshoe-shaped, arising from the sides of the gap. Seed-trace strong, passing into a tube-like basal extension of the sclerotesta.

Tissue on the adaxial side of the lower part of the scale composed of narrow, elongated, thin-walled cells; sclerenchyma in the lower part of the scale confined to the lateral regions and to the top of the interseminal ridge.

(1) Following Engler's « Syllabus der Pflanzenfamilien » (1954) the name *Pinaceae* is used in preference to *Abietaceae* as was used in earlier papers in this series.

Resin canals distributed in a ring of about 21 in the cortex of the axis; adaxially distributed in the basal part of the scale, some canals lying immediately beneath the seeds.

Horizon. — Wealden.

Lectotype. — The one from La Louvière figured by COEMANS.

Localities :

1. Houdeng-Aimeries.
2. Baume, La Louvière.
3. Culot, Villerot.

Detailed description : External form. — The somewhat fragile structure of this cone probably accounts for the fact that it is represented largely by pieces of cone-axis bearing only the extreme basal portions of scales. In fact, I have seen only four specimens which still have most of their scales attached, whereas I have counted over sixty axes or axis-fragments. The axes, a typical example of which is shown in figure 1, plate III, are generally unaccompanied by a débris of scales, so they were probably preserved in their present state; the fact that some clay matrix is present between the remaining scale-bases also suggests this.

Although in size the specimens vary considerably (as judged largely by the isolated axes), the cone is on the whole smaller than *Pseudoaraucaria heeri* (ALVIN, 1957*b*) with which species there is a general resemblance in external form and gross structure.

The scales are compactly arranged in 3 + 5 spiral ranks. The abaxial surface bears fine longitudinal striations, and in well preserved examples there is a prominent, terminal, tooth-like appendage, which, by comparison with the living pines, may be called an umbo. These processes are particularly clear in BOMMER's photograph (Pl. I, fig. 1), although the same cone, the opposite side of which is shown in its present state in figure 4 on the same plate, has since become damaged so that only a few of the umbos remain. In no other specimen are the tips of the scales sufficiently well preserved to show them.

A typical scale from the middle region of the cone, but lying at right-angles to the plane of compression, shows a knee-bend about one-quarter of the way from the base to the apex (Pl. I, fig. 2 and 7). The lower portion is attached to the cone-axis at an angle usually rather less than 90°, but towards the base of the cone this angle is greater and the scales are more sharply bent, and towards the top, the angle is less and the scales are straighter (Pl. I, fig. 2). The scales which happen to lie in the plane of compression are variously distorted so that sometimes they are quite straight and flat, and sometimes (chiefly those from the lower part of the cone) artificially strongly bent with a much shortened basal portion (Pl. I, fig. 8). It was probably scales of this kind that COEMANS examined, so that he overlooked the bend.

At the extreme base and apex of the cone, the scales are small and sterile, as is quite usual in the Pinaceae.

The bract (Pl. I, fig. 9) becomes free from the ovuliferous scale just below the knee-bend. It has a rounded apex.

The seeds are situated in depressions in the basal portion of the scale on either side of the narrow interseminal ridge. Distally the seeds carry large, longitudinally striated wings which together cover the whole of the laminate portion of the scale except a narrow distal border (Pl. I, fig. 7). The body of the seed is usually somewhat curved, especially on the side towards the scale, so that only about the lower two-thirds (containing the kernel) is

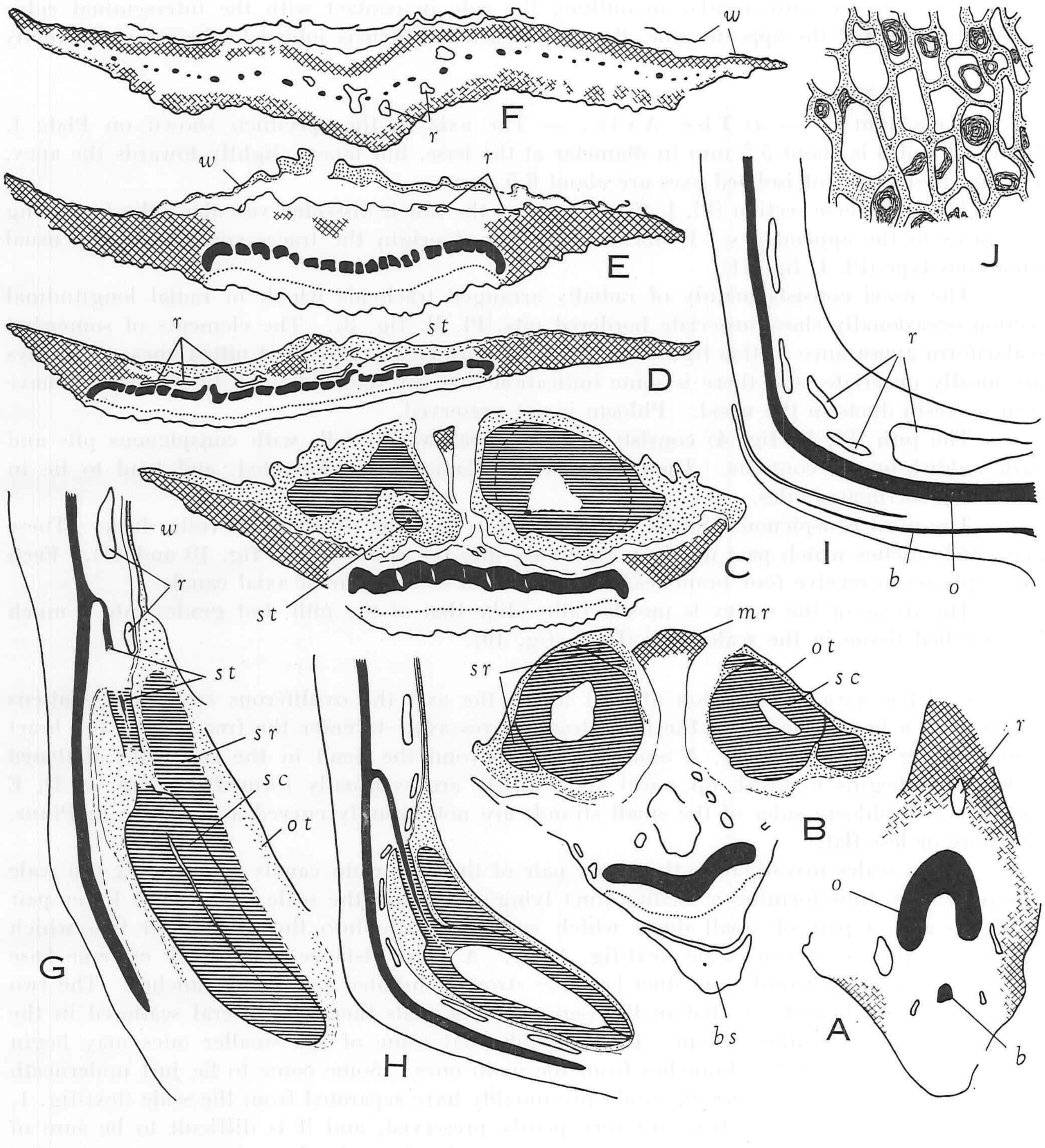

FIG. 1. — *Pseudoaraucaria gibbosa* (COEMANS) n. comb.

A-F : series of transverse sections of the scale; *b*, bract trace; *o*, ovuliferous scale trace; *bs*, bract; *mr*, interseminal ridge; *ot*, outer layer of the testa; *sc*, sclerotesta; *sr*, ribs of the testa; *st*, seed trace; *w*, wing; *r*, resin canals. All except D from series F1; A from section 1/8; B, 4/3; C, 7/13; E, 11/2; F, 18/16; D from F2/7/5. All ×15. — G : longitudinal section through the base of a scale, passing through a seed; labelling as before. F6/2/4. ×15. — H, I : reconstructed longitudinal sections based on series F6; H, passing through a seed; I, in the median plane; labelling as before. — J : cells from the abaxial tissue lying below the dotted line in fig. B-E. F1/3/10. ×400.

orientated parallel to the lower part of the scale (text-fig. 1, H). The exposed face of the seed is convex as seen in cross-section (text-fig. 1, B and C). As seen in surface view (Pl. I, fig. 7) it is almost semi-circular in outline, the side in contact with the interseminal ridge being straight, but the opposite side, the upper part of which is joined to the wing, distinctly curved.

Anatomy. — *a*) The Axis. — The axis in the specimen shown on Plate I, figures 2 and 3 is about 5,5 mm in diameter at the base, but tapers slightly towards the apex. The broadest pieces of isolated axes are about 6,5 mm.

The transverse section (Pl. I, fig. 10) shows the much dissected vascular cylinder giving off traces to the appendages. In form and mode of origin the traces conform to the usual Pinaceous type (Pl. I, fig. 11).

The wood consists mainly of radially arranged tracheids which in radial longitudinal section occasionally show unseriate bordered pits (Pl. II, fig. 3). The elements of somewhat scalariform appearance in this figure are probably only poorly preserved pitted ones. The rays are mostly unseriate, and there is some indication that ray tracheids may be present. I have seen no resin ducts in the wood. Phloem is not preserved.

The pith (Pl. II, fig. 4) consists of fairly thick-walled cells with conspicuous pits and dark reddish-brown contents. These cells are isodiametric to elongated, and tend to lie in somewhat corrugated files.

The most conspicuous feature of the cortex is the ring of about 21 resin ducts. These give off branches which pass nearly horizontally into the scales (Pl. I, fig. 10 and 11). Each scale appears to receive four branches, two from each of one pair of axial canals.

The tissue of the cortex is mostly rather like that of the pith, but grades into a much larger-celled tissue in the scale-bases (Pl. I, fig. 10).

b) The scale. — Soon after it leaves the axis the ovuliferous scale trace flattens out to form a broad band, and the bract trace moves away to enter the free part of the bract before fading out (text-fig. 1, A and B). Just beyond the bend in the scale, the flattened scale strand begins to break up, until about thirty are eventually formed (text-fig. 1, D, E and F). The phloem sides of the small strands are not strongly curved as they are in *Pinus*, but more or less flat.

In the scales investigated, the upper pair of the four resin canals which enter the scale appear to fuse, thus forming a median duct lying just above the scale trace. The lower pair divide to give a pair of small ducts which run eventually into the bract, and two which continue in the ovuliferous scale (text-fig. 1, A). A short distance beyond the extreme base of the scale, the uppermost resin duct becomes strongly inflated and then branches. The two lateral ducts also branch, so that in the region of the seeds there are several scattered in the tissues above the vascular system. It is possible that some of the smaller ones may begin and end blindly, and not as branches from the main ones. Some come to lie just underneath the seeds where these, at dispersal, would presumably have separated from the scale (text-fig. 1, C-E and H); but the tissues here are very poorly preserved, and it is difficult to be sure of the exact distribution. In the upper part of the scale the resin ducts become more or less evenly scattered on both sides of the vascular system (text-fig. 1, F).

The distribution of fibrous tissue of the kind shown in transverse section in text-figure 2, B is confined, in the lower part of the scale, to the cross-hatched areas in drawings A-F in text-figure 1. The abaxial tissue lying below the dotted line in figures C-E is composed of narrow, elongated cells with quite thin walls, and containing a yellowish substance often in the form of a ring or cylinder (text-fig. 1, J). It is possible that this material may represent the shrunken and altered remains of an inner and perhaps thick wall-layer, but I would suppose that the tissue was different in some way from the fibrous tissue present elsewhere, and that it was not merely differently preserved. In *Cedrus* there occurs, in a comparable position in the scale, a fibrous-like tissue in which the cell walls are apparently fatty in nature.

The rest of the ground tissue in the lower part of the scale is composed of a large-celled parenchyma of the kind shown in text-figure 2, A.

A transverse section of the upper part (Pl. II, fig. 2) shows two slightly sunken bands of fibres, one on each side. Figure 1, plate II, shows a section in the intermediate region, just above the seeds.

c) The seeds. — In structure the seed is similar to that of *Pseudoaraucaria loppineti* (ALVIN, 1957*a*). There are well-defined sclerotic ribs running longitudinally down the seed on opposite sides (text-fig. 1, B, *sr*). These should probably be regarded as part of the outer, soft layer of the testa, but they are more or less in contact with the true sclerotesta and appear in places to grade into it. They extend backwards into the chalazal cushion (text-fig. 1, G and H), where they together form a rather diffuse mass of isodiametric sclerenchyma lying above the stalk-like basal extension of the sclerotesta which encloses the vascular supply (Pl. I, fig. 12; text-fig. 1, C). There are histological differences between the sclerenchyma of the ribs and that of the sclerotesta, for whereas the latter consists of angular stone-cells, the ribs are made up of rounded cells of very variable size. A similar difference in cell shape is reported by QUISUMBING (1925) in the seed of *Pinus*.

The sclerotesta seems variable in thickness : in two seeds from the same cone it measured 50 μ and 200 μ.

The rest of the outer layer of the testa and chalazal cushion (shown stippled in text-figure 1, A-E, G and H) is composed of irregular, thin-walled cells. The inner soft layer of the testa which is typically present in gymnosperm seeds, is recognizable in that region where the integument is free from the nucellus; it consists of a thickened epidermis and a partly broken down sub-epidermal layer. Elsewhere, there is only a dark structureless layer between the sclerotesta and the megaspore membrane.

Cutinized membranes removed from the seeds by maceration yield the finely papillate megaspore coat, and a cap-like membrane showing cell-outlines which is believed to be the nucellus cuticle. Part of this is shown in text-figure 2, C.

The vascular supply to the seed is relatively strong. It departs from the scale system some distance above the chalaza (text-fig. 1, D and G) and proceeds downwards to enter the tube-like prolongation of the sclerotesta. I have not been able to find out how far it reaches before fading out.

There are no resin cavities in the seed itself.

I have failed to find pollen in macerated seeds.

Discussion. — The following species are now classified in the genus *Pseudoaraucaria* :

P. loppineti FLICHE	Albian-Cenomanian.	France.
P. major FLICHE	Albian-Cenomanian.	France.
P. benstedi (MANTELL) ALVIN	Lower Greensand (Aptian).	England.
P. heeri (COEMANS) ALVIN	Wealden.	Belgium.
P. gibbosa (COEMANS) n. comb.	Wealden.	Belgium.

The most important characters separating *Pseudoaraucaria gibbosa* from the other species are : 1) the comparatively soft structure of the basal part of the scale; 2) the tube-like basal extension of the sclerotesta; 3) the close association of resin ducts with the seeds.

The first of these characters is of interest since the virtual absence of sclerenchyma from the scale in *Pseudolarix* represented one of the chief points of difference between the cone of this recent genus and the other species of *Pseudoaraucaria* (Alvin, 1957*b*). Thus, in this character, *P. gibbosa* tends to draw the two genera closer together. There are, of course, still important differences, such as the absence of an umbo in *Pseudolarix*.

The third character could be interpreted as a condition intermediate between that in *Pseudoaraucaria bestedi* in which there are resin cavities in the testa, and that in the other species which apparently lack such cavities. It suggests a possible mode of evolutionary origin of seed resin cavities which are characteristically present in *Cedrus, Abies, Tsuga* and *Keteleeria* among the living genera of Pinaceae.

The genus *Pseudoaraucaria,* if in fact it does represent a natural group of species, for only the cones are known, was probably an important one in the Cretaceous period. That it was widespread both geologically and geographically is suggested by the fact that a cone almost certainly belonging to the same assemblage has been figured by Penny (1947) under the name « *Abietites* sp. » from the Upper Cretaceous Magothy flora of North America. It is not unlikely that a critical study of the « *Abietites* » cones in this flora, of which several have been only superficially described, would reveal the genus to be well represented.

Genus PITYOSTROBUS Nathorst.

Pityostrobus hautrageanus n. sp.

This species seems quite distinct from any previously described; I am therefore describing it under a new name derived from the locality.

D i a g n o s i s . — P i n a c e o u s c o n e, cylindrical or elongate-ovoid, more than 6 cm long; breadth, 2,5-3,2 cm (cone open); apex sub-acute.

B r a c t less than 1 mm long.

O v u l i f e r o u s s c a l e typically 2 cm long, 0,9 cm broad at the widest part (i.e. about three-quarters up from the base) where the scale is somewhat thickened; apex sub-acute, not or only slightly reflexed. Umbo small, terminal.

S e e d 4 x 2 mm; wing typically 8 x 3,5 mm, asymmetrical, reaching about two-thirds the length of the scale, becoming very thick where it joins the seed. Sclerotesta about 0,2 mm thick, smooth except on the side in contact with the scale. Outer layer of the testa rather thick, containing more or less loose, dark brown cells suggestive of tannin-filled cells.

V a s c u l a r s y s t e m of the axis only moderately dissected; bract trace simple, arising from the bottom of the « leaf-gap »; scale trace horseshoe-shaped, arising from the sides of the gap. About 12 small strands with curved phloem sides in the upper part of the scale.

R e s i n c a n a l s in the cortex of the axis numbering about 21; distributed abaxially and laterally in the scale base; becoming scattered in the upper part.

F i b r o u s t i s s u e in the basal part of the scale confined to the middle of three layers of tissue lying abaxially to the vascular system. P i t h of thick-walled cells, mainly elongated, but some isodiametric and lying in nests or small horizontal plates.

P o l l e n of *Pinus* type.

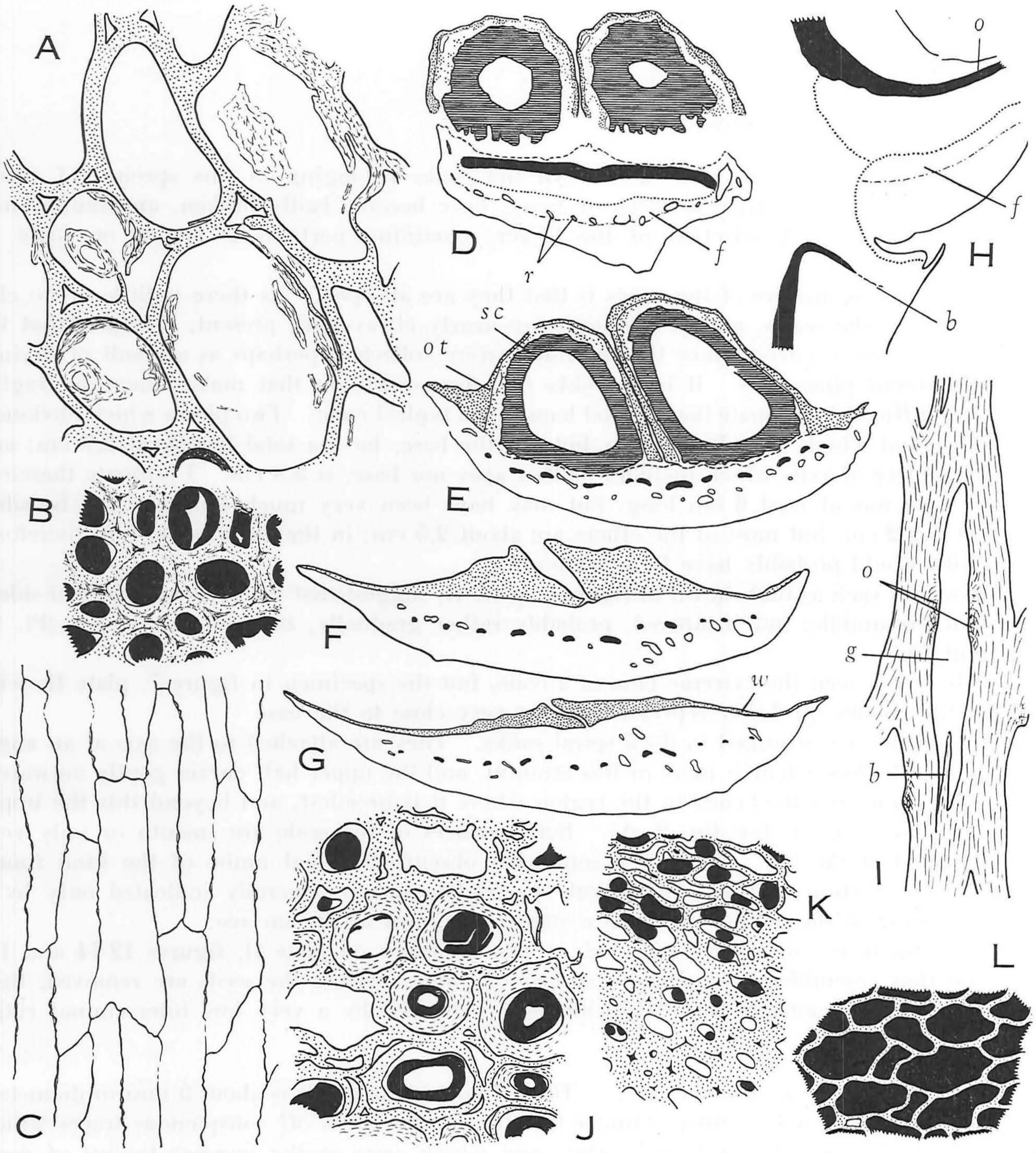

FIG. 2.

A-C. — *Pseudoaraucaria gibbosa* (COEMANS) n. comb.

A : cells of the tissue lying adaxial to the vascular system in the basal part of the scale. Fl/3/11. ×400. — B : cells from the fibrous tissue at the extreme top of the interseminal ridge. Fl/3/10. ×400. — C : cell-outlines from the nucellus cuticle. F7a. ×225. (In B, dark cell contents are shown solid black.)

D-L. — *Pityostrobus hautrageanus* n. sp.

D-G : series of transverse sections of the scale; *r*, resin canals; *w*, seed wing; *f*, abaxial fibrous tissue; *ot*, outer layer of the testa; *sc*, sclerotesta. All from series G1; D from section 2/8; E, 5/4; F, 7/13/ G, 9/4. All ×15. — H : median longitudinal section through the base of the scale; *b*, bract trace; *o*, ovuliferous scale trace. G3/11/3. ×10. — I : tangential longitudinal section through the cone-axis showing part of the vascular system; *o*, *b*, as before; *g*, « leaf-gap ». G3/6/1. ×10. — J : cells of the pith in transverse section. G2/6/4. ×400. — K, part of the abaxial fibrous tissue from the base of the scale in transverse section; at the top the fibrous tissue grades into parenchyma. G1/2/14. ×400. — L : part of the parenchyma lying immediately abaxial to the vascular system at the base of the scale. G1/2/14. ×400. (In J, K and L, dark cell contents are shown solid black.)

Horizon. — Wealden.

Type-Specimen. — Pl. II, fig. 5.

Locality. — Hautrage.

Detailed description. — All the cones belonging to this species, of which there were probably originally a dozen or more, have become badly broken, apparently since they were collected. A selection of the larger remaining portions is shown on plate II, figures 5-11.

One striking feature of the cones is that they are all open. As there is little or no clay matrix between the scales, and as the seeds are nearly always still present, I believe that the opening may have occurred since the specimens were collected, perhaps as a result of drying, just as in recent pine-cones. It is probably the open condition that makes them so fragile.

It is difficult to estimate the original length of a typical cone. Two pieces which obviously fit together and which include the apex but not the base, have a total length of 5,7 cm; and the longest piece of axis, which includes neither apex nor base, is 3,8 cm. I estimate therefore that the cone was at least 6 cm long, but may have been very much longer. The broadest fragment is 3,2 cm, but most of the others are about 2,5 cm; in the closed condition therefore, the breadth would probably have been 2-2,5 cm.

Portions such as that shown in figure 8, plate II, suggest that the cone was parallel sided, at least in the middle; but it tapered, probably rather gradually, to a sub-acute apex (Pl. II, fig. 5 and 10).

I have not seen the extreme base of a cone, but the specimen in figure 7, plate II, with its very short scales, probably represents a part very close to the base.

The scales are arranged in 3 + 5 spiral ranks. They are attached to the axis at an angle of about 20°; the lower half is more or less straight, and the upper half curves gently outwards. The scale is somewhat thickened in the region where it is broadest, and beyond this the upper surface becomes convex (text-fig. 3, A). Both surfaces of the scale are smooth or only very faintly striated at the top. There is a somewhat obscure terminal umbo of the kind found in the *Strobus* section of *Pinus*; it scarcely protrudes, and is generally indicated only by a sudden thinning of the extreme tip, and a slight roughness of the surface.

The appearance of the winged seeds in situ is shown on plate II, figures 12-14 and 16. In general they resemble those of many species of *Pinus*. When the seeds are removed, they leave shallow depressions in the scale which are separated by a very low interseminal ridge (Pl. II, fig. 15 and 17).

Anatomy. — *a*) The axis. — The cylindrical cone-axis is about 5 mm in diameter. The moderately dissected vascular cylinder (Pl. II, fig. 20) gives off conspicuous traces which run almost horizontally through the cortex, and which arise in the manner typical of most of the Pinaceae (text-fig. 2, I). The scale trace which, in the primary condition probably consisted of two separate strands, one from each side of the « leaf-gap », consists in the mature state of a massive horseshoe-shaped strand arising from the sides and top of the gap.

The vascular tissue is represented only by the wood, the position of the phloem being indicated either by a space or by a narrow band of a black substance. The wood, which as usual is mainly secondary, consists of uniseriately pitted tracheids and narrow rays. The cross-field pitting is obscure, but there appear to be two or three small bordered or half-bordered pits as, for example, in the wood of *Pinus cembroides* Zucc. There are no obvious ray-tracheids with dentate walls.

The pith, which is about 2 mm in diameter, consists probably entirely of thick-walled cells. In transverse section (text-fig. 2, J) the cells are roundish and there are many small intercellular spaces. Although most of the cells are seen to have thick walls, some appear at first sight to be thin-walled, and various intermediate conditions are common. I believe these differences are due only to differences in the preservation of the thick, inner layer of wall material. In longitudinal section (Pl. III, fig. 5), although most of the cells appear elongated, there occasionally occur nests or small horizontal plates of short, isodiametric cells.

The cells of the cortex are similar, except that they show a rather greater variation in size and shape, especially as seen in longitudinal section.

b) The scale. — The structure of the scale presents no particularly interesting features, and, in a general way, is similar to that in several species of *Pinus* and several other pine-like fossil cones [e.g. *Pityostrobus andraei* (ALVIN, 1953)]. The series of transverse sections drawn in text-figure 2 (D-G) shows the break-up of the xylem band and the distribution of resin-canals. Only the tissue differentiation in the basal part of the scale is somewhat unusual for a pine-like cone : the fibrous tissue, instead of occupying the extreme abaxial zone, is apparently confined to a rather narrow region mainly towards the inside of the line of resin canals (text-fig. 2, D and H); adaxially this tissue grades into a « secretory » parenchyma, the cells of which are typically thin-walled, several times as long as broad and packed with a dark, reddish-brown deposit (text-fig. 2, K and L). Abaxially the fibres grade into another apparently thin-walled, and often more or less collapsed tissue, of which the cells are similar in their narrow elongated form to the fibres. This differentiation persists throughout the region of the seeds, but as the vascular system breaks up, so also does the continuity of the dark « secretory » tissue.

In the upper part of the scale (Pl. III, fig. 2) the internal tissues consist of a rather irregular parenchyma in which are scattered large, thick-walled cells, but which becomes more regular and smaller-celled around the vascular bundles. Towards the surfaces of the scale, this general tissue gives place to fibres.

The seeds also are pine-like in their gross structure just as much as in their external form. However, there are a few features which are somewhat unusual. Firstly, the surface of the sclerotesta lying adjacent to the scale is curiously pitted, especially towards the micropyle end (text-fig. 2, D; Pl. II, fig. 18). These pits or furrows are usually occupied by a yellowish substance resembling that present in many of the resin canals. However, there is no sign that the cavities were ever lined by a secretory epithelium. A similar yellowish substance occurs in cavities within the outer layer of the testa (Pl. III, fig. 4). I believe these spaces may have been resin-filled, but that they did not constitute well defined secretory cavities such as are found, for example, in *Abies* or *Cedrus*; it is interesting to note however, that the seed coat is said to become resinous in some living species of *Pinus* (QUISUMBING, 1925). Other features worthy of note are : *a*) the rather unusual thickness of the outer layer of the testa : in most pines it is thin and often absent over the body of the seed at maturity so that the sclerotesta is exposed; *b*) the more or less separated, black cells resembling tannin-filled cells, into which the inner part of this layer seems to have become dissolved (Pl. III, fig. 4) : similar cells have been noted in *Pityostrobus villerotensis* (ALVIN, 1957*b*); *c*) the massive pad of large-celled tissue occurring at the base of the seed (Pl. II, fig. 19; Pl. III, fig. 3) : this somewhat resembles the chalazal cushion in *Pseudoaraucaria*.

Macerated seeds have yielded the megaspore membrane and a cuticle which, by comparison with other fossil and living examples, is taken to be the nucellus cuticle (text-fig. 3, B). Pollen of the *Pinus*-type has been found at the tip of the nucellus (text-fig. 3, C).

Discussion. — This species, on the basis of scale and cone form, is apparently related to the *Haploxylon* sub-genus of *Pinus*; only certain structural features separate it. The differentiation of the abaxial tissues in the lower part of the scale is of a kind which, as far as I know, does not occur in *Pinus*; the outermost tissue is like that in *Pseudoaraucaria gibbosa*, and perhaps comparable with the peculiar tissue in the scale of *Cedrus*. The extensive cushion-like thickening at the base of the seed-wing is also somewhat like that in *Pseudoaraucaria*, but it contains no vascular trace and no sclerotic tissue except a few very small thick-walled cells near where it comes into contact with the scale; it may perhaps be compared with the much thickened base of the wing in *Pinus coulteri* D. Don, a species far removed from the *Haploxylon* pines, and quite unlike the fossil it its massive, woody cones.

As far as previously described fossils are concerned, no well known species is comparable. There is a general external resemblance to *Pinus magothensis* Penny (1947) from the Upper Cretaceous of North America, but although few structural details are given in the description of this species, there appear to be certain anatomical differences : thus, for example, it is said that in the American species resin canals are distributed in two rows in the scale.

Pityostrobus soigniesiensis n. sp.

There is only one specimen belonging to this species; it resembles *Pityostrobus andraei* (Coemans) Alvin (1953) externally, but is much smaller, and has certain anatomical differences. The specific name is derived from the locality.

Diagnosis. — Pinaceous cone, cylindrical, about 1,7 cm broad, 5 cm or more long (specimen incomplete).

Bract minute.

Ovuliferous scale typically 13 mm long, 6 mm broad, spirally arranged in 5+8 ranks; exposed part of scale (apophysis) rhomboidal, typically 6 mm wide, 4,5 mm high, bearing an obscure transverse ridge interrupted by a small central rhomboidal area about 2 mm wide, 1 mm high; upper part of apophysis faintly radially striated.

Seed about 3 mm long, 1,5 mm wide; total length of winged seed (developed) about two-thirds the length of the scale. Sclerotesta about 0,15 mm thick.

Vascular system of the axis moderately dissected; bract trace simple arising from the bottom of the « leaf-gap »; scale trace horseshoe-shaped, arising from the sides and top of the gap; about 12 small strands with curved phloem sides in the upper part of the scale.

Resin canals in the cortex of the axis numbering about 21; distributed abaxially in the scale-base, becoming scattered in the upper part.

Fibrous tissue occupying the abaxial side of the scale in the seed-bearing region. Compact sclereidal tissue in thick, horizontal plates in the pith, and in nests in the cortex and upper part of the scale.

Horizon. — Wealden.

Locality. — Soignies, carrière Perlonjour.

Type-specimen. — Pl. III, fig. 6-9; Pl. IV, fig. 1, 2; text-fig. 3, D-N.

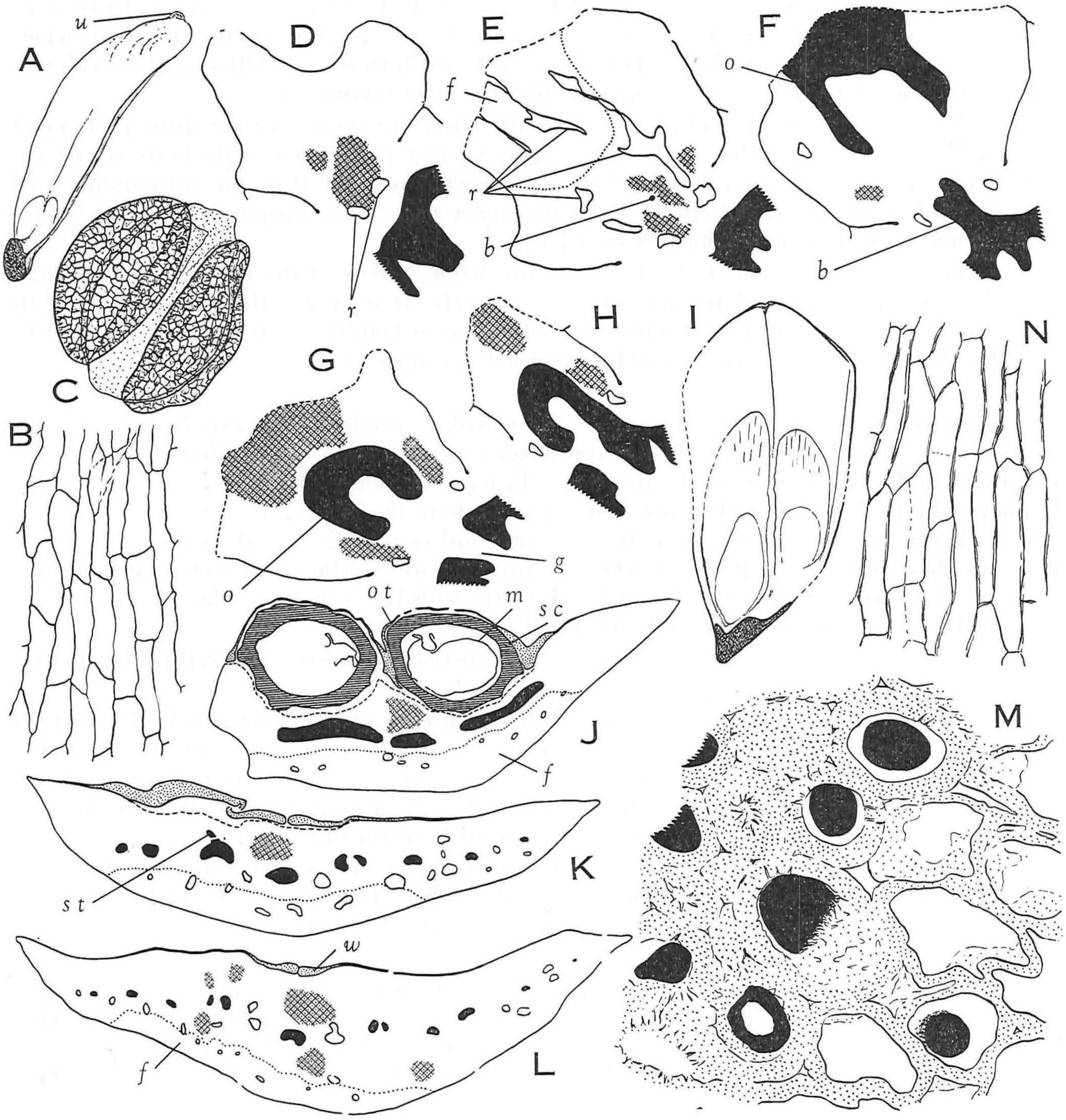

FIG. 3.

A-C. — *Pityostrobus hautrageanus* n. sp.

A : scale with the seeds removed; *u*, umbo. ×2.5. — B : cell outlines from the nucellus cuticle. G4a. ×225. — C : pollen grain from the tip of the nucellus. G4e. ×500.

D-N. — *Pityostrobus soigniesiensis* n. sp.

D-H : series of transverse sections of the cone-axis at the base of an appendage showing the origin of the vascular traces, resin canals (*r*) and the distribution of stony tissue (shaded); *b*, bract trace; *o*, ovuliferous scale trace; *g*, gap in the axial stele (« leaf-gap »); *f*, abaxial fibrous tissue. All drawn from series H3; D from section 1/12; E, 2/14; F, 3/12; G, 4/9; H, 5/2. All ×15. — I : adaxial surface of scale with the seeds in situ. ×6. — J-L : series of transverse sections through the scale; *st*, seed trace; *ot*, outer layer of the testa continuous with the wing (*w*); *sc*, sclerotesta; *m*, megaspore membrane; shading as before. All from series H1; J, from section 2/4; K, 4/4; L, 5/5. ×15. — M : part of a group of sclereids at the junction with parenchyma from the pith. H3/5/10. ×400. — N : cell-outlines from the nucellus cuticle. H5c. ×225.

Detailed description. — The specimen upon which this species is based is not complete, and may represent only the upper portion of a cone. The extreme apex is damaged, and shows an asymmetry which is probably due to malformation. Although the scales are firmly stuck together, the structure suggests that the cone was mature.

The scales are arranged in 5+8 spiral ranks; they are small, but not disproportionately so in relation to the diameter of the cone. The exposed part of the scale bears no distinct umbo, but only a small central area which is somewhat rougher than the surrounding part. The survival of delicate radial striations on the upper part of the apophysis does not suggest that the umbo has become flattened by abrasion.

The adaxial surface of the scale carries two winged seeds of the *Pinus*-type, the length of which (except when they have not developed properly) is about two-thirds the length of the scale (text-fig. 3, I). The fact that quite often either one or both the seeds have failed to develop suggests that the specimen was probably somewhat depauperate.

Anatomy. — *a*) The axis. — The vascular cylinder of the axis is about 3,5 mm in diameter. It gives off traces to the appendages in association with rather small gaps, so that the cylinder is only moderately dissected. In form and mode of origin the traces conform to the usual type found in the Pinaceae, but, at any rate in the lower part of the specimen from where sections were cut, they take a slightly downward course through the cortex (text-fig. 3, D-H); the bract trace (*b*) is therefore seen free from the axial cylinder in sections below those in which it is seen to join it (fig. E and F); similarly with the scale trace (fig. F, G and H, *o*). The bract trace attenuates very rapidly (cf. fig. E and F).

The tracheids are very thick-walled and are uniseriately pitted. Ray cell pitting has not been oberved.

The most striking anatomical feature is the occurence of isodiametric sclereids in thick horizontal plates in the pith, and also in smaller nests in the cortex and scale (Pl. III, fig. 7 and 8). The individual sclereids are polygonal as seen in transverse section (text-fig. 3, M) and square or rectangular longitudinally (Pl. III, fig. 9); they are arranged compactly without intercellular spaces, and are usually filled with a dark reddish-brown substance.

The rest of the pith is composed of elongated, fairly thin-walled cells, and the cortex of heterogeneous tissue comprising some thick-walled cells. The outer tissues of the decurrent bracts are conspicuous by the small size and dark contents of the cells.

b) The scale. — In general structure the scale and seeds conform to the *Pinus*-type (text-fig. 3, J-L; Pl. IV, fig. 1 and 2). The abaxial fibrous tissue is homogeneous; it is massive in the region of the seeds, but gradually diminishes above. The vascular band formed by the flattening of the scale trace breaks up in the seed-bearing region to form eventually about 12 small strands. Weak seed traces have ocasionally been observed (text-fig. 3, K); they rapidly fade out without entering the seeds.

The ground tissue of the scale is highly heterogeneous. Sclereidal nests occur scattered in the upper part (Pl. IV, fig. 1), but in the seed-bearing region, only one is usually visible lying adaxially between the seeds; this is an upward extension of a sclereidal mass which begins above the scale trace in the cortex of the axis (text-fig. 3, G and H). It persists well above the seeds (text-fig. 3, K and L). The lateral portions of the scale in the seed-bearing region are occupied by a sclerenchyma of large, round cells which are more or less isodiametric (Pl. IV, fig. 2); this tissue becomes more diffuse (by interspersion with parenchyma) and more evenly scattered in the upper region, but tends to be more plentiful on the adaxial side (Pl. IV, fig. 1).

The seed structure presents nothing worthy of special mention. As in many pines, the outer layer of the testa is membranous over the smooth sclerotesta but thickened to form lateral ribs where it joins the scale. Part of a cuticle believed to be from the nucellus is shown in text-figure 3, N. Pollen has not been found.

D i s c u s s i o n . — In coupling the *Diploxylon* type of scale with the cylindrical cone form more typical of *Haploxylon*, this species resembles *Pityostrobus andraei*, an abundant cone in more than one locality in the Wealden of Belgium (ALVIN, 1953). *Pityostrobus soigniesiensis* is, however, clearly distinguishable by its peculiar and striking pith structure and other anatomical features, and also, although perhaps less reliably, by differences in the form of the apophysis and the generally smaller size. As regards external appearance, both fossils are rather like *Pinus montezumae* LAMBERT, in which at least the larger cones tend to be practically cylindrical.

There are several Cretaceous cones of similar general form with which *Pityostrobus soigniesiensis* might be compared. Few of these however have been described beyond gross external features, and little is to be gained from an extensive comparison. It appears that the cylindrical cone with a regular phyllotaxy, and more or less thickened, reflexed scales was a common type in the Cretaceous, but it is not known how these are related to the two sub-genera into which the living species of *Pinus* fall; nor is it known indeed that they were even borne on trees that would have been recognizable on vegetative characters as belonging to this genus.

Genus PINUS LINNAEUS.

Pinus belgica n. sp.

I am classifying this cone in the genus *Pinus* on account of its close agreement in shape and structure with the cones of typical species belonging to the *Diploxylon* sub-genus.

D i a g n o s i s . — C o n e ovoid-conic, about 4,5 cm long, 3 cm broad.

B r a c t minute, triangular.

S c a l e from middle region of the cone about 2 cm long, 0,9 cm wide; thick; exposed part (apophysis) rhomb-shaped, 7-10 mm wide, 5-8 mm high, with a prominent central umbo typically 5 mm wide, 2 mm high; abaxial surface of the scale below the apophysis with a median longitudinal ridge.

S e e d 9 mm long, 4 mm wide, covered by the membraneous outer layer of the testa; wing somewhat acute, two-thirds to three-quarters the length of the scale. Sclerotesta 0,1-0,5 mm thick.

V a s c u l a r s y s t e m of the axis massive, little dissected; trace to the ovuliferous scale horseshoe-shaped, but tending to form a cylinder with the bract trace at departure from the axial cylinder. About 18 small strands with strongly curved phloem sides in the upper part of the scale.

R e s i n c a n a l s in a ring in the axial cortex; in a single row in the abaxial fibrous tissue in the base of the scale; becoming abundant and scattered, some markedly inflated, in the distal part. Small resin canals occasional in the wood, especially near the pith.

P i t h composed mainly of large, elongated cells with conspicuously pitted walls, but with scattered, narrow, resin- or tannin-filled cells, and occasional groups of thick-walled cells.

H o r i z o n . — Wealden.

Locality unknown.

Type-specimen. — Pl. IV, fig. 3-13; Pl. V, fig. 1-8; text-fig. 4.

Detailed description. — Unfortunately, the one specimen upon which this species is based is unlocalized. However, in its practically uncompressed, lignitic state, it resembles most of the other plant remains from the Belgian Wealden, and the adhering particles of fine-grained, grey matrix are similar to the usual kind of matrix; there is thus no good reason to doubt that it comes from the same formation.

The specimen (Pl. IV, fig. 3) which I imagine was probably entire when collected, has suffered dismemberment, so that no intact scale remains in position : it in fact consists of the stout axis carrying irregularly broken off scale-bases and a few seeds (*s*); an accompanying débris includes scales and seeds that obviously belong to the cone. The specimen has now been further broken to provide pieces for sectioning.

The scales are attached at a very acute angle to the axis and are subtended by quite broad but very short, triangular bracts. The scale arrangement, as judged by the shape of the cone, is probably an indefinite spiral as is typical in the *Diploxylon* sub-genus.

The form of the scale is shown in figures 5-11, plate IV. The strongly asymmetrical scale in figure 11 apparently carried only one developed seed, the second having aborted. Judging from the occurrence of seeds and of cavities left by seeds in the cone specimen, I would say that this one-seeded state was common. In a number of scales (e.g. Pl. IV, fig. 7 and 10) both seeds are abortive. The high proportion of abortive seeds is probably due only to unfavourable conditions of development or imperfect pollination, and cannot be taken as having any taxonomic significance.

The umbo is conspicuous; it is borne in the middle of the rhomb-shaped apophysis, and stands out considerably beyond its general surface (Pl. IV, fig. 4); it extends laterally into a low ridge which ends in opposite corners of the rhombus. The apophysis shows no other distinctive characters.

The abaxial surface of the scale below the apophysis characteristically bears a single median ridge (Pl. IV, fig. 9); the adaxial surface usually also bears a similar ridge at the distal end only (Pl. IV, fig. 7 and 11). These ridges are probably related to the way in which the scales were packed together in the cone.

I have seen no scale with fully developed seeds in situ, nor, in fact, any loose seeds with wings attached. The form of the winged seed may, however, be deduced from the nut (text-fig. 4, L) and from scales carrying abortive seeds (Pl. IV, fig. 6 and 10). The seed was probably very similar to that of *Pinus sylvestris* LINNAEUS and many other species.

Anatomy. — *a*) The axis. — About a third of the way up from the base (where the specimen was sectioned) the axis is about 12 mm in diameter; it contains a pith about 5 mm wide and a massive, little dissected, woody cylinder nearly 2 mm thick (Pl. V, fig. 1 and 2). The vascular traces to the bracts and scales depart in the usual manner (text-fig. 4, A-E), but the associated « leaf-gaps » are small, and there is a general tendency for the horseshoe-shaped scale trace to be at first united below with the bract trace so as to form, for a short distance, a continuous cylinder (tex-fig. 4, B; Pl. V, fig. 3, bottom). The bract trace, however, soon becomes free from the scale trace (Pl. V, fig. 3, upper part) and takes a downward course through the cortex before turning up into the bract (text-fig. 4, A and B). The massive scale trace soon flattens on entry into the somewhat decurrent scale base, and begins to break up into smaller strands (text-fig. 4, D and E).

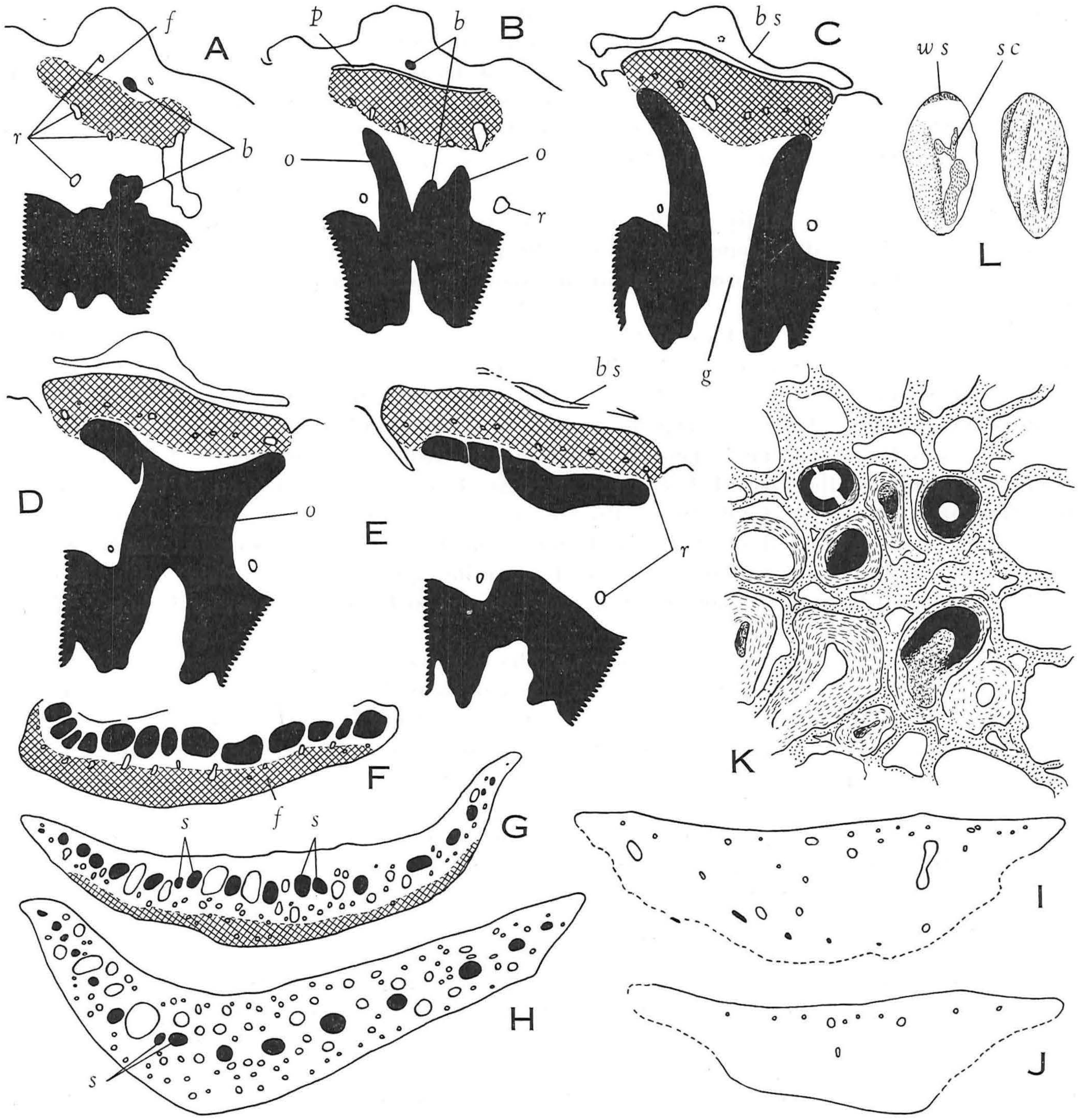

FIG. 4. — *Pinus belgica* n. sp.

A-E : series of transverse sections of the cone-axis at the base of a scale showing the origin of vascular traces, resin canals and the distribution of fibrous tissue (*f*); *b*, bract trace; *bs*, bract; *o*, ovuliferous scale trace; *p*, pocket between bract and ovuliferous scale; *g*, « leaf-gap ». All drawn from series J2; A, from section 2/1; B, 2/4; C, 3/5; D, 4/5; E, 5/5. ×10. — F-J : series of transverse sections through the scale; *f*, abaxial fibrous tissue; *s*, sub-ovular strands. All from series J1; F, from section 1/5; G, 3/14; H, 5/6; I, 7/3; J, 7/8. ×10. — K : part of a nest of thick-walled cells from the pith seen in transverse section; dark cell contents shown solid black. J2/2/3. ×240. — L : seed : the upper surface on the left, the lower surface on the right; *ws*, scar where the wing was attached; *sc*, patches where the membranous outer layer of the testa has disappeared exposing the sclerotesta beneath. ×3.5.

Resin canals occur in the cortex. The resin system of the scale and bract appears to arise from branches given off from a pair of axial canals; two small canals accompany the bract trace, but fade out before the free portion of the bract is reached (text-fig. 4, A and B).

The pith and cortex is composed mainly of large, relatively thin-walled cells, often somewhat irregular in shape, amongst which are frequent narrow cells often with dark, reddish-brown contents; also in the pith occur occasionally small groups of narrow, thick-walled cells (Pl. V, fig. 4; text-fig. 4, K). The basic parenchyma shows striking pitting in longitudinal section (Pl. V, fig. 5).

The wood shows hardly any details of structure : the tracheids are narrow and appear to have very thick walls; some of the ray cells may have sculptured walls (Pl. V, fig. 8). Occasional small resin ducts are present in the wood, especially near the pith.

b) The scale. — The structure of the scale is remarkably similar to that in *Pinus sylvestris* L. At the base, the abaxial fibrous tissue is prominent (text-fig. 4, F. *f*), and the resin canals occur either within this tissue or at its junction with the parenchyma in which the vascular bundles lie. Above this region (text-fig. 4, G and H; pl. IV, fig. 12 and 13) the fibres diminish, and the resin canals become more evenly distributed and more abundant, some enlarging greatly as they pass between the vascular strands. In the region of the apophysis, the attenuated strands eventually turn outwards and converge towards the umbo (text-fig. 4, I; Pl. IV, fig. 4); above the umbo no vascular strands occur (text-fig. 4, J). No seed trace is present, but pairs of strands which sometimes eventually re-unite, appear to be associated with the seeds (text-fig. 4, G and H, *s*); a similar condition was reported in *Pityostrobus andraei* (Alvin, 1953).

c) The seed. — Nothing is known of the seed contents : macerations of a number of seeds yielded no recognizable parts. The somewhat tissue-like material visible in figure 7, plate V (on the right) does not represent the seed contents, for it is continuous through a hole in the testa into the cone-axis, and is visible again on the lower, left-hand side in figure 2. The material, the nature of which is a mystery, is very localized; it may possibly be occupying a bore-hole.

The three layers of the testa are visible in figure 7, plate V, the outermost (left) consisting of about two rows of thin-walled, elongated cells, and the innermost represented by a thin, black structureless substance; the sclerotesta (Pl. V, fig. 6) is thick, consisting of 6-8 layers of stone-cells.

Discussion. — There is no important character to separate this cone from the *Diploxylon* sub-genus of *Pinus* : I imagine it to be quite closely related to such species as *Pinus pinaster* Aiton, *P. sylvestris* L. or *P. nigra* Arnold. Although the vascular supply to the scale and bract is not strongly combined into a cylinder as it is in *P. sylvestris*, there is obviously some tendency for this to occur; but in any case, the *Diploxylon* group shows considerable variation in this character, and in fact *P. nigra*, for example, presents a condition rather close to that in the fossil.

If *Pinus belgica* is accepted as a Wealden member of the *Diploxylon* sub-genus, it becomes one of the earliest known members of the group. Cones of conical form having scales of the thick type with a distinct dorsal umbo are much rarer in the Cretaceous than those of cylindrical form with thin, straight scales (*Haploxylon* type). The cone called *Pinus wohlgemuthi* Fliche (1896) from the Albian-Cenomanian of France appears, on the strength of its external characters, to belong to *Diploxylon*. Further evidence that this group existed in at least the early part of the Upper Cretaceous comes from American remains of pollen, leaves and a cone, all of which have been compared with the living North American species *Pinus resinosa* AITON (PIERCE, 1957). As far as the Wealden in concerned, it is not unlikely that the isolated scales described under the name *Pinus feronensis* CARPENTIER (1927) which are very similar in form to the scales of *Pinus belgica* but rather smaller, may represent a closely related species.

Genus PREPINUS JEFFREY.

The leafy shoots described here as a new species belonging to JEFFREY'S (1908) genus necessitates some amendment to the generic diagnosis suggested by STOPES and KERSHAW (1910).

Emended generic diagnosis. — Coniferous shoot segments, simple or occasionaly with 2-3 branches in a whorl at the distal end; segments bearing proximally, cataphylls and distally, needle-leaves, all in close spiral arrangement.

Cataphylls simple, flattened, imbricated, largely fibrous in structure.

Leaf parallel-sided, drawn out to a finely pointed apex; in transverse section polygonal, with 4-6 often unequal flat sides; two lateral resin ducts present; a large zone of non-photosynthetic tissue round the bundle; bundle single or divided; hypodermal fibrous tissue strongly developed; amphistomatic. Stomata orientated longitudinally, rather evenly spaced in rows alternating with the hypodermal fibrous strands.

Prepinus sclerophylla n. sp.

Diagnosis. — Shoot segments usually 0,5-1,0 cm in diameter (including cataphylls and leaf-bases, but excluding the spreading portions of the leaves), 2,5-5,0 cm in length, simple or sometimes with 2-3 branches in a whorl at the distal end.

Cataphylls with margins beset with unicellular hairs; some at least with long slender points resembling reduced needle-leaves.

Leaf about 1 mm in diameter, more than 6 cm long; somewhat flattened at the base but soon becoming polygonal in section; angles minutely serrated. Hypodermal fibrous tissue in massive longitudinal strands dividing the mesophyll into more or less discrete columns.

Stomata deeply sunken, the pits usually separated by 2-3 cells. Epidermal cells between the stomatal rows usually 2-4 times as long as broad; anticlinal walls as seen in cuticle straight, sparsely pitted, thicker and clearer than the walls of the cells in the stomatal rows; epidermal cells at angles of leaf slightly longer and narrower. Stomata monocyclic, with 6-8 subsidiary cells, the two polar usually elongated, the 4-6 lateral usually smaller and short; subsidiary cells (as seen in section) with very thick outer walls; slightly overarching stomatal pit.

Woody cylinder of stem up to 1 cm in diameter, enclosing a pith up to 4 mm broad; in slender shoots, cylinder thin and greatly distorted by emission of leaf-traces, or sometimes unrecognizable. Trace large, band-shaped; xylem differentiated tangentially into two portions. Wood tracheids uniseriately pitted; rays uniseriate, 1-13 cells high (mostly 1-4).

Horizon. — Wealden.

Locality. — Bernissart. (Fragments also from Houdeng-Aimeries.)

Type-specimen. — Plate VI, fig. 15; text-fig. 5, H.

Detailed description. — Morphology. — The material consists of some one hundred portions of leafy shoots and an abundance of leaf fragments. Most of the larger shoot portions are segments 2-5 cm in length, and, excluding the spread of the leaves, typically 1 cm wide. The base of a typical segment does not normally show a clean break; instead, the cortex is often somewhat constricted, with the woody cylinder sometimes protruding (Pl. VI, fig. 2, 5, 11 and 15). Although this may be due only to differential shrinkage of wood and cortex as the specimens dried, the appearance suggests that each segment represents some genuine unit such as a dwarf shoot or one season's increment of the long shoot of a tree having an annual season of growth. A few specimens (Pl. VI, fig. 12 and 14) are obviously merely the broken off upper portions of true segments.

The shoots show considerable variation in the way in which they terminate apically. A few end in a cluster of broken needles (Pl. VI, fig. 8 and 9), which are long enough to conceal any terminal bud which may be present in the centre. In most of the specimens the leaves are broken off lower down, and the stem is seen to end in one or a few club-shaped or rosette-like masses of broken scales (Pl. VI, fig. 2-4, 6 and 11-15). These scales are always imperfectly preserved, but appear to be similar to, although often smaller than, the cataphylls borne on the lower part of a typical shoot segment. I interpret these terminal masses of scales, a section through one of which is shown in figure 4, plate VIII, as remains of buds, or, if they are rosette-like, the scars of broken off or decayed buds or branches. A few specimens carry distally a decorticated continuation of the main stem (text-fig. 5, A), and sometimes also two or three decorticated stumps of lateral branches (Pl. VI, fig. 1, 5 and 10).

The appearance of the specimen in text-fig. 5, A strongly suggests that the continuation represents a portion younger than the main part of the stem below, for apart from being less well preserved, the woody cylinder appears genuinely thinner, and the marks on the surface, which I take to be the scars of vascular traces, are finer and more closely arranged than those on the lower part; perhaps the smaller scars belong to traces to cataphylls borne on an upper shoot segment of which only the basal stump of its vascular cylinder remains. It seems reasonable to suppose that the upper segment grew from a bud situated at the end of the older, lower part. The decorticated fragment in text-figure 5, B (which is the woody cylinder from the specimen in figure 2, plate VII) shows a swelling which may well represent the position of a terminal bud. A transverse section below the swelling shows considerably more wood than one taken above (Pl. VII, fig. 4 and 5), and there is also some indication that the wood contains two growth rings below and only one above.

Most specimens bear appendages of two kinds : firstly, on the lower part of the segment there are scale-leaves or cataphylls, and secondly, on the more distal part, needle-leaves. Both are borne in one close spiral and may intergrade.

The typical appearance of the cataphylls is shown in text-figure 5, H; they are flat, adpressed to the cataphylls or leaf-bases immediately above, and taper gradually to bluntly pointed apices. The apex almost always shows an abraded spot, as if some terminal appendage may have fallen off or decayed. In a few, the apex does run out into a slender, awn-like projection about 3 mm long (Pl. VII, fig. 3, *c*); I do not know, however, whether these examples are typical, or whether they are organs intermediate in nature between cataphylls and leaves : I have only seen them in the upper part of the cataphyll region where one might expect to find intermediate organs. It is possible that the cataphylls typically carried delicate terminal processes which easily got broken off, or which perhaps were naturally caducous as are the scale leaves on the long shoot in *Pinus*.

The cataphylls are further distinguished from the leaves or leaf-bases in possessing a fringe of unicellular hairs marginally or sub-marginally on the abaxial surface, and also by their different anatomy (text-fig. 5, I and 6, M).

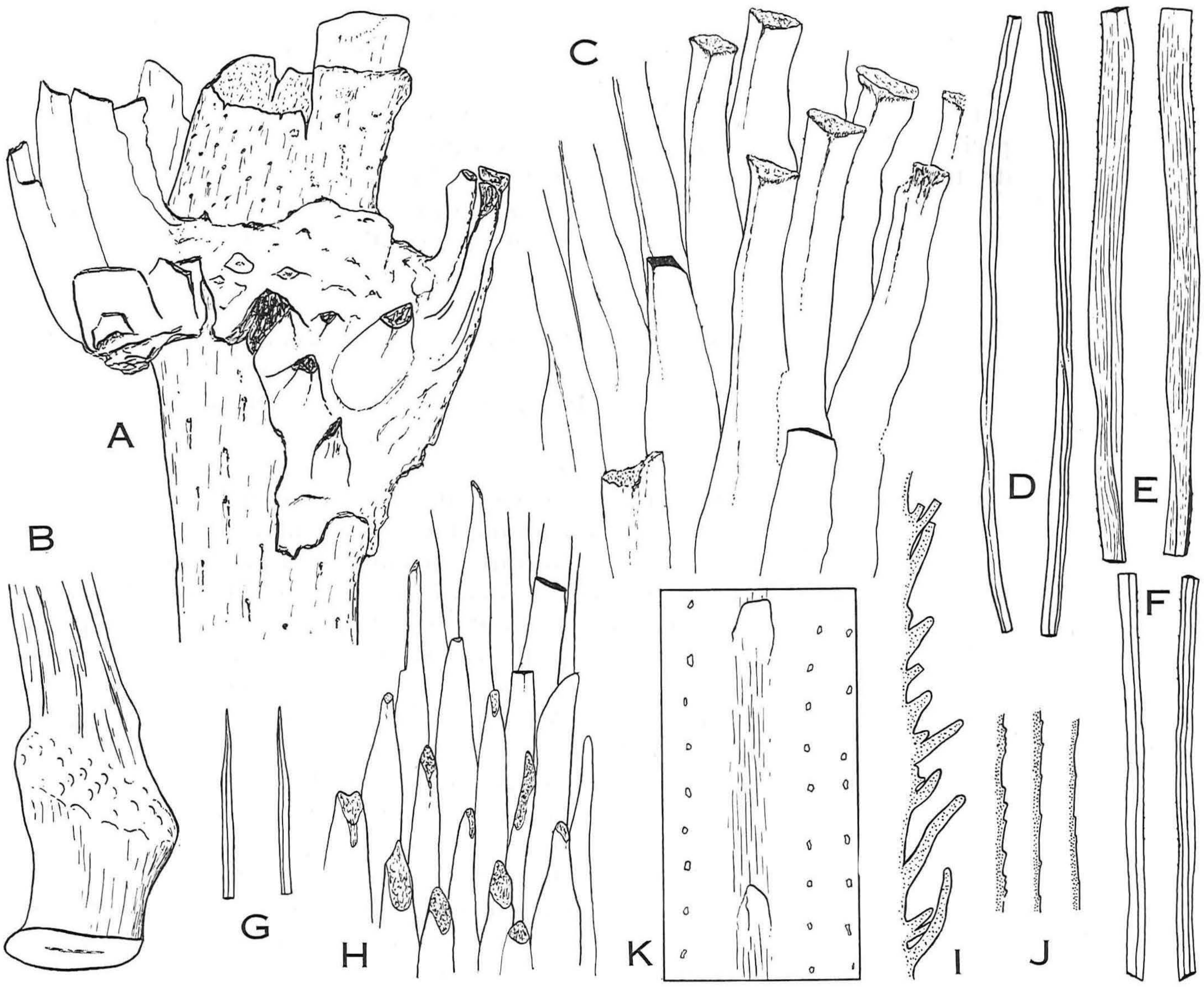

FIG. 5. — *Prepinus sclerophylla* n. sp.

A : the reverse side of the specimen in fig. 1, Pl. VII, showing evidence of a bud scar. ×6. — B : part of the woody cylinder from the specimen in fig. 2, Pl. VII, showing a swelling which may represent the position of a bud. ×6. — C : part of the specimen in fig. 12, Pl. VI, showing a number of leaf-bases. ×6. — D-G : four leaf fragments each drawn from two opposite sides; the specimen in fig. G represents the end of a leaf. ×2½. — H : cataphylls, probably grading into leaves above, from the type-specimen (Pl. VI, fig. 15). ×6. — I : edge of cataphyll. ×100. — J : leaf-edges showing variation in serration. ×12. — K : part of the leaf surface (including an edge) from a cuticle preparation, showing distribution of stomata and two serrations. Slide L 10a. ×100.

The needles are at first somewhat flattened and appressed, but soon become rhomboidal (text-fig. 5, C and 6, L) and eventually irregularly polygonal in transverse section (Pl. VII, fig. 9). They average about 1 mm in breadth. I have seen no complete leaf, but isolated fragments occur up to 6 cm long. A selection of fragments, including one terminal portion, is shown in text-figure 5. The angles are minutely serrated (text-fig. 5, J).

There is some evidence that leaf abscission occurred, for in a number of specimens the remaining leaf portions are almost equal in length (Pl. VI, fig. 11-14). The ends of such leaf-bases are often expanded (Pl. VII, fig. 3; text-fig. 5. C), but this is probably due only to a slight infilling of matrix which has prevented the extreme tip from shrinking as much as the rest. The larger attached portions of leaves (supposedly younger leaves) such a those in figures 7-9, plate VI, are quite parallel sided, and show no sign of an abscission point.

Anatomy. — The preservation has unfortunately proved to be comparatively poor, and in many specimens the soft tissues are riddled with fungal hyphae. Although compression is only moderate, the tissues are often so compact that it is difficult to see the outlines of cells in thin sections. I have not succeeded in obtaining any satisfactory sections of the cortex of the thicker axes, and the wood has yielded only scanty information. Most is known about the leaves.

a) The leaf. — A transverse section of the needle has a striking appearance due to the massive development of hypodermal fibres, the wedge-shaped areas of which divide the mesophyll into separate islets (text-fig. 6, L; Pl. VII, fig. 9). The centre of the leaf is occupied by an elliptical area containing the vascular system, and on either side of this area, which I have called the bundle sheath, run two resin canals.

A section of the leaf-base (Pl. VIII, fig. 3) shows a thick and continuous fibrous zone round the outside and a curved, band-shaped xylem strand towards the adaxial side of a dark, presumably parenchymatous ground tissue. This structure is maintained throughout the length of the persisting leaf-bases in such specimens as those shown in figures 11-14, plate VI; only above this level (5-8 mm from the extreme base) does the leaf begin to achieve its typical structure by acquisition of a vascular sheath and break-up of the fibrous tissue to give pockets of mesophyll, the latter process occurring first on the outer (abaxial) side (text-fig. 6, J-L).

The epidermis is composed of very thick-walled cells, the appearance of which in transverse section is similar to that of the fibres. Whereas, however, the epidermal cells are seldom as much as four times as long as broad, the fibres are greatly elongated.

Cuticle preparations show that the epidermal cells have straight or only very slightly irregular walls; the walls tend to be thicker, and the cells more even in shape, in the bands alternating with the stomatal rows (text-fig. 6, A). The cuticle on the leaf-angles (text-fig. 6, B) shows rather narrower cells, each bearing a longitudinal stripe which is probably a fold due to the flattening of what was originally a strongly curved surface. Serrations are visible at intervals along the edge (text-fig. 5, K).

Cuticles show nothing of the stomata except the pits surrounded by the rather obscurely delimited subsidiary cells. Sections and macerated leaves show that the guard cells are deeply sunken and almost completely covered by the subsidiary cells (text-fig. 6, D-I). The walls of the subsidiary cells seen in section are enormously thick towards the exterior, but are thin where they abut on to the guard cells. The upper ends of the subsidiary cells tend to arch over the stomatal pit somewhat (text-fig. 6, G and H).

Sections usually reveal nothing of the structure of the mesophyll; but macerated leaves, provided that the soft tissues have not been destroyed by a fungus, as they quite often have, show a sponge-like series of cells much swollen by the treatment (Pl. VII, fig. 11; text-fig. 6, N); their appearance suggests that the walls may have had infoldings like those in *Pinus, Cedrus, Pseudolarix* and *Cathaya.*

The vascular system in the main part of the leaf is recognizable only as a somewhat denser area edged on one side by a dark line within the bundle sheath (text-fig. 6, J-L). The dark line (*p*), which I take to represent the crushed phloem, usually appears divided in the middle; the bundle itself was therefore probably divided, except near the base of the leaf (fig. J).

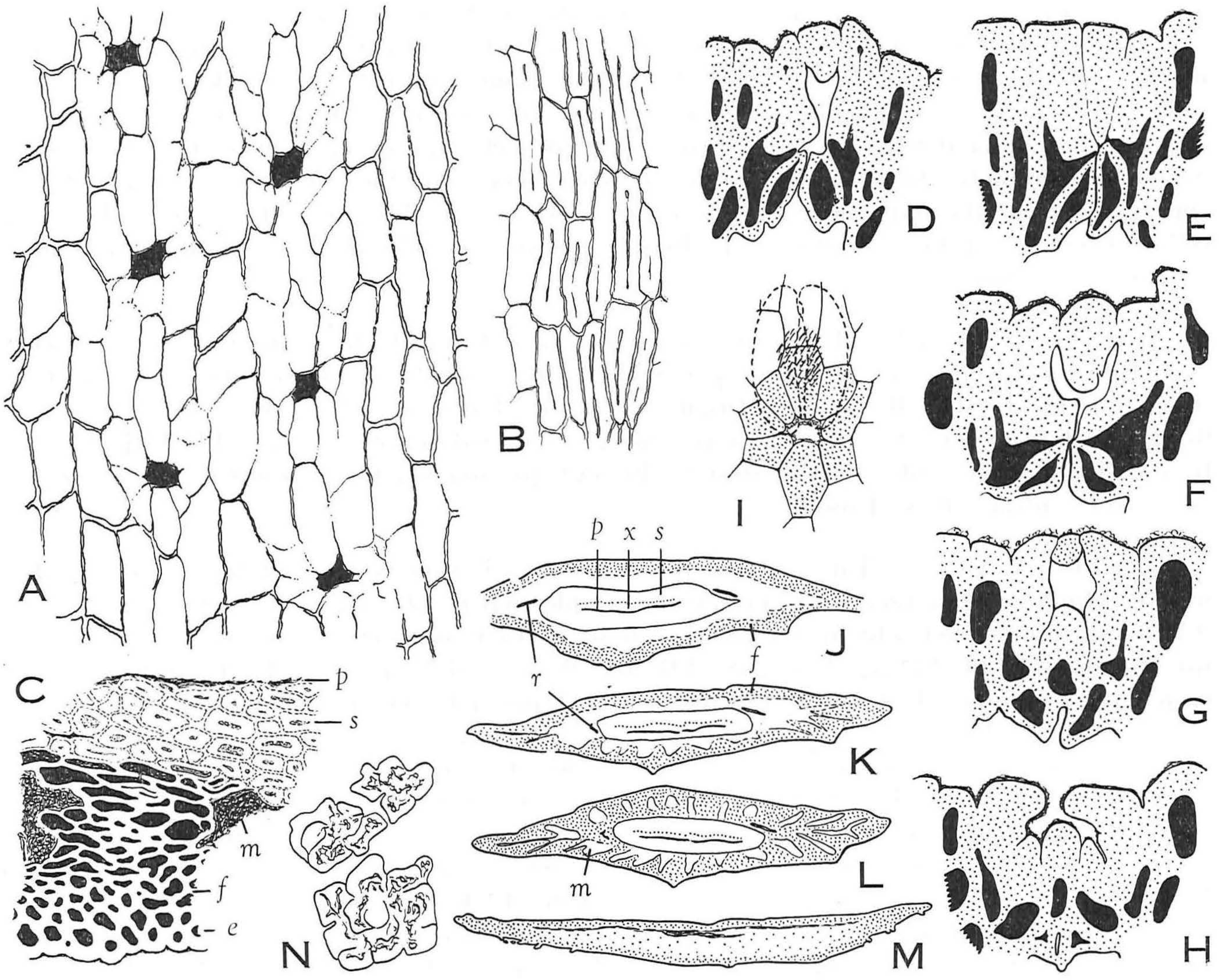

FIG. 6. — *Prepinus sclerophylla* n. sp.

A : portion of leaf cuticle from a flat surface; stomatal pits are shown black. Slide L 10b. ×375. — B : portion of cuticle from the edge of a leaf. Slide L 10a. ×375. — C : part of a transverse section of a leaf; *e*, epidermis; *f*, fibrous tissue; *m*, remains of mesophyll; *s*, vascular sheath; *p*, dark line probably representing position of phloem. Section L 1/5/3. ×375. — D-H : transverse sections of stomata; in D, the plane of section is more or less median through the guard cells; in E and F it is sub-median; in G and H it goes through the guard cells near their ends, and through the lumen of one of the polar subsidiary cells. All from series L 1; D from section 5/5; E, 5/7; F, 5/1; G, 5/4; H, 3/2. All ×440. — I : surface view of stoma showing subsidiary cells (stippled) surrounding the stomatal pit, and, at a lower focus, the outlines of the guard cells. Draw from a macerated leaf fragment. Slide L 11a. ×375. — J-L : acropetal series of transverse sections of a leaf near the base; *x*, region of xylem; *r*, resin canal; other labelling as in fig. C. Drawn from series L1; J, from section 1/3; K, 3/5; L, 6/7. All ×44. — M : transverse section of a cataphyll; stippling here, as in J-L, represents fibrous tissue. Section L 7/3/11. ×44. — N : mesophyll cells from macerated leaf. Slide L 11d. ×375.

The xylem strand in the basal part of the leaf is much more conspicuous, and is unusual for a conifer not only in its ribbon-like form, but also in being apparently differentiated tangentially into two parts, a smaller adaxial part more or less separated from the main part by a narrow dark region presumably representing parenchyma (Pl. VIII, fig. 3). JEFFREY (1908) emphasized that in *Prepinus* centripetal xylem was present. Although his figures (of transverse sections) are not entirely convincing on this point, they do show a tangential differentiation in the xylem.

The tissue of the bundle sheath, like the xylem itself, often shows no clear cellular structure, but in a few specimens a pattern of cells is discernible in thin sections by differences of colour in the almost homogeneous substance. The cells (text-fig 6, C, *s*) are marked by a network (shown by broken lines) of a dark reddish colour, and a thick wall-like layer which is rather lighter in colour surrounds a dark central area (shaded). They have the appearance of sclereids, except that no pits are visible; it is unlikely, however, that the vascular system would be surrounded by a sheath of sclerenchyma; moreover, the cells have a very different appearance from the hypodermal fibres which were presumably truly thick-walled lignified cells. There is nothing except their position to suggest that the sheath cells might represent transfusion tracheids.

b) The cataphyll. — Except for a narrow band of black material in the middle which probably represents collapsed parenchyma, the cataphyll consists entirely of fibrous tissue (text-fig. 6, M). It can be distinguished from a leaf-base in transverse section in being thinner, relatively broader and in having marginal or sub-marginal hairs (Pl. VIII, fig. 4). It contains no discernible vascular strand, although presumably there may have been a small one in the central collapsed zone.

c) The axis. — The cortex of the larger axes is usually more or less loose from the woody cylinder and is very badly preserved; samples when softened tend to disintegrate, and it has been impossible to obtain any useful sections. The woody cylinder in two such specimens investigated (i.e. Pl. VI, fig. 3 and Pl. VII, fig. 2) was fairly massive (1-2 mm thick). The large pith is composed of moderately thick-walled parenchyma, and in one specimen there were marks round the outside of the pith suggesting a ring of resin canals.

In transverse section the wood shows either a highly compact structure where the individual tracheids have collapsed (Pl. VII, fig. 6), or else a more open structure as in parts of the specimen in figures 4 and 5, plate VII. In this specimen there is a tendency for compacted and open wood to lie in alternating bands reminiscent of growth rings. The way in which these bands follow the contour of small extensions of the pith (which I take to be associated with the departure of leaf-traces) suggests that they reflect some genuine differences in structure. Moreover, in the regions where the wood is compacted throughout, such as at the top in figure 4, plate VII, the rings are still marked by slight differences in colour. I believe therefore that growth rings (presumably annual) were present.

Longitudinal sections of the wood are even more disappointing than transverse. Occasionally the radial section shows uniseriate rows of bordered pits, although the limits of individual tracheids cannot be clearly distinguished (Pl. VII, fig. 7). Cross-field pitting is not visible, nor is it clear whether or not the rays are homogeneous. It is possible to count the cells in the rays in tangential sections (Pl. VII, fig. 8) by the dark spots which presumably represent the cell lumina. One hundred rays counted at random had the following cell numbers :

Number of cells high	1	2	3	4	5	6	7	8	9	12	13
Number of rays (out of 100)	33	21	16	12	5	3	3	3	1	1	2

Transverse sections of one of the more slender and presumably younger shoots (similar to that in figure 7, plate VI), show a very irregular outline due to the closely arranged leaf-bases, and inside, a bewildering maze of vascular strands which can only be interpreted as an anastomosing system of irregular, band-shaped leaf-traces (Pl. VIII, fig. 1 and 2). The section in figure 2, which is cut nearer to the apex than that in figure 1, shows, in the centre, a continuous cylinder which looks like an axial system; however, examination of the series of sections (of which only these two are figured) makes it clear that this central cylinder rapidly attenuates downwards until it disappears in the dark, ill-preserved ground tissue : it is represented in figure 1 by the small central dumb-bell-shaped area. Above the level of figure 2, the cylinder breaks up and fuses with the loops and small cylinders outside it. Towards the edge of the section, the picture is further confused by the thick layer of fibrous tissue on the outside of the decurrent leaf-bases which resembles the xylem in appearance except that its cells are not radially seriated (cf. Pl. VIII, fig. 3). The shoot from which these sections were cut ended in a bud-like mass of small cataphylls (Pl. VIII, fig. 4).

The specimen in figure 6, plate VI was also sectioned, and found to contain a conventional, though irregular, axial cylinder : its leaf-traces were again long, snake-like strands.

I know of no modern conifer which approaches this in the vascular anatomy.

D i s c u s s i o n . — The genus *Prepinus* was erected by JEFFREY for some coniferous shoot fragments and needles that he named *P. statensis* from the Raritan formation (Upper Cretaceous) of New York. It was STOPES and KERSHAW (1910), however, who gave the first generic diagnosis when they described an isolated needle from the Upper Cretaceous of Japan under the name *P. japonicus*. JEFFREY, also in 1910, described another species (*P. viticetensis*) based on two very imperfect fragments from the Magothy (Upper Cretaceous) of Massachusetts, and more recently, PENNY (1947) has named some specimens, also from the Magothy Flora, as *P. delawarensis*.

It is possible that the Belgian species which differs from those previously described not only by being considerably larger with more massive wood and in showing evidence of branching, but also in being geologically older, may not really belong to the same natural genus. However, I am provisionally classifying it here on account of the following characters which it shares with *Prepinus statensis* :

1. The general morphology of the shoot segment (as it is here called) or dwarf-shoot (according to JEFFREY) which consists of a stem bearing scales (cataphylls) proximally and needle-leaves distally, and often terminating in small scales which, as is suggested here, may represent one or more buds;
2. The general anatomy of the leaf-base and of the needle itself;
3. The almost wholly fibrous structure of the cataphylls;
4. The tangential differentiation of the xylem of the leaf trace (i.e. centripetal and centrifugal metaxylem according to JEFFREY).

The Belgian species, represented as it is by a comparative wealth of specimens, provides certain new information, chiefly about the shoot organization, but also about the leaf epidermis.

It seems unlikely that what is here called the « shoot segment » essentially represents a dwarf-shoot in the usual sense as JEFFREY envisaged; for although some of the smaller specimens may possibly have been dwarf-shoots, some at least, on the evidence of their branching and massive secondary wood, must have persisted and grown for several years, and if, as is suggested, the « segment » itself represents one annual increment of growth, extension growth was vigorous as compared with that of the dwarf-shoots in *Cedrus*, *Larix* and *Pseudolarix*, all of which, of course, have dwarf-shoots of prolonged growth and duration.

There is no evidence that branching occurred in the shoot system elsewhere than at the end of the segment, so that, as is suggested by the restoration shown in text-figure 7, the branching was probably similar to that in *Abies* or *Araucaria*. But whether this shoot system was a long-shoot comparable to that in such genera as these, or whether it was a lateral appendage of essentially limited, if rather prolonged and extensive growth, is a question which, for the present, must remain unanswered.

Another question that arises is — Why did the shoot systems break up so regularly into segments ? Again no satisfactory answer can be given, but it has been noticed that if partly decayed twigs of *Pinus* are bent, they do tend to break just above a terminal bud scar rather than elsewhere.

Jeffrey emphasized the similarity in leaf anatomy between *Prepinus* and *Pinus*; this is now further borne out by the epidermal organization by which the fossil differs from *Pinus* only in having straight instead of undulating anticlinal walls. In *Pinus*, however, juvenile leaves have only weakly undulating epidermal cell walls, and sometimes they are straight (Florin, 1931). The massive hypodermal fibrous tissue is particularly striking in the Belgian fossil, but hardly more so than in certain living pines with very long leaves, such as *Pinus oocarpa* Schiede where the fibrous strands often reach to the endodermis. The mesophyll apparently agrees with that in *Pinus, Cedrus* and certain other Pinaceae. The absence of an endodermis represents a difference from *Pinus*. The nature of the bundle sheath in the Belgian species is uncertain, but in *Prepinus statensis* it consisted, according to Jeffrey, of two zones of transfusion tissue : such a structure is unique.

Nothing is known of the cone borne by *Prepinus*. Many isolated Pinaceous cones are now known from the Belgian Wealden, of which all but *Pseudoaraucaria* and *Pityostrobus corneti* are broadly pine-like. I have seen no specimen of either *Pseudoaraucaria* or *Pityostrobus corneti* from the Bernissart locality; indeed, the only cone at Bernissart seems to be *Pityostrobus bommeri* Alvin (1953). This cone has distinctive columns of sclereids in the pith of the axis, and no such cells have been seen in *Prepinus sclerophylla*. It is noteworthy, however, that the leafy remains called *Abietites longifolius* (Fontaine) Berry from the Cretaceous of Maryland, which appear to be similar to *Prepinus*, and the cone called *Abietites macrocarpus* Fontaine which may well be rather like *Pityostrobus bommeri* were both reported to be « common » in one locality by Berry (1911).

Jeffrey compared *Prepinus* with Seward's (1895) *Pinites solmsi* from the English Wealden, the material of which consists of compressed leafy shoots with cones attached, and Andrews' (1947) restoration of *Prepinus* is in fact based on this fossil. But until this material is critically reinvestigated it cannot be supposed to be generically identical to *Prepinus*.

Family ? PINACEAE.

Genus ABIOCAULIS Suzuki.

This name was established for a petrified stem which, on the basis of its structural features, was judged to have affinity with Jeffrey's *Abieteae* group of the Pinaceae. It does not appear to have been used since the type-species was described from the Upper Cretaceous of Japan (i.e. *Abiocaulis yezoensis* Suzuki, 1910). I am employing this designation here for a well preserved stem of basically similar structure in preference to Nathorst's (1897) form-genus *Pityocladus* which has often been used for ill preserved or inadequately described material of leafy twigs showing the sort of dimorphism characteristic of *Larix, Pseudolarix* and *Cedrus*.

SUZUKI gave no generic diagnosis. I therefore suggest the following :

Woody coniferous long-shoots with spirally arranged, decurrent leaf-bases. Annual extension growth by terminal buds with well defined bud-scales; occasional axillary lateral buds or branches also present. Cortex in at least two-year old twigs with periderm. Two resin canals in each leaf-base. Wood of the *Cedroxylon* type.

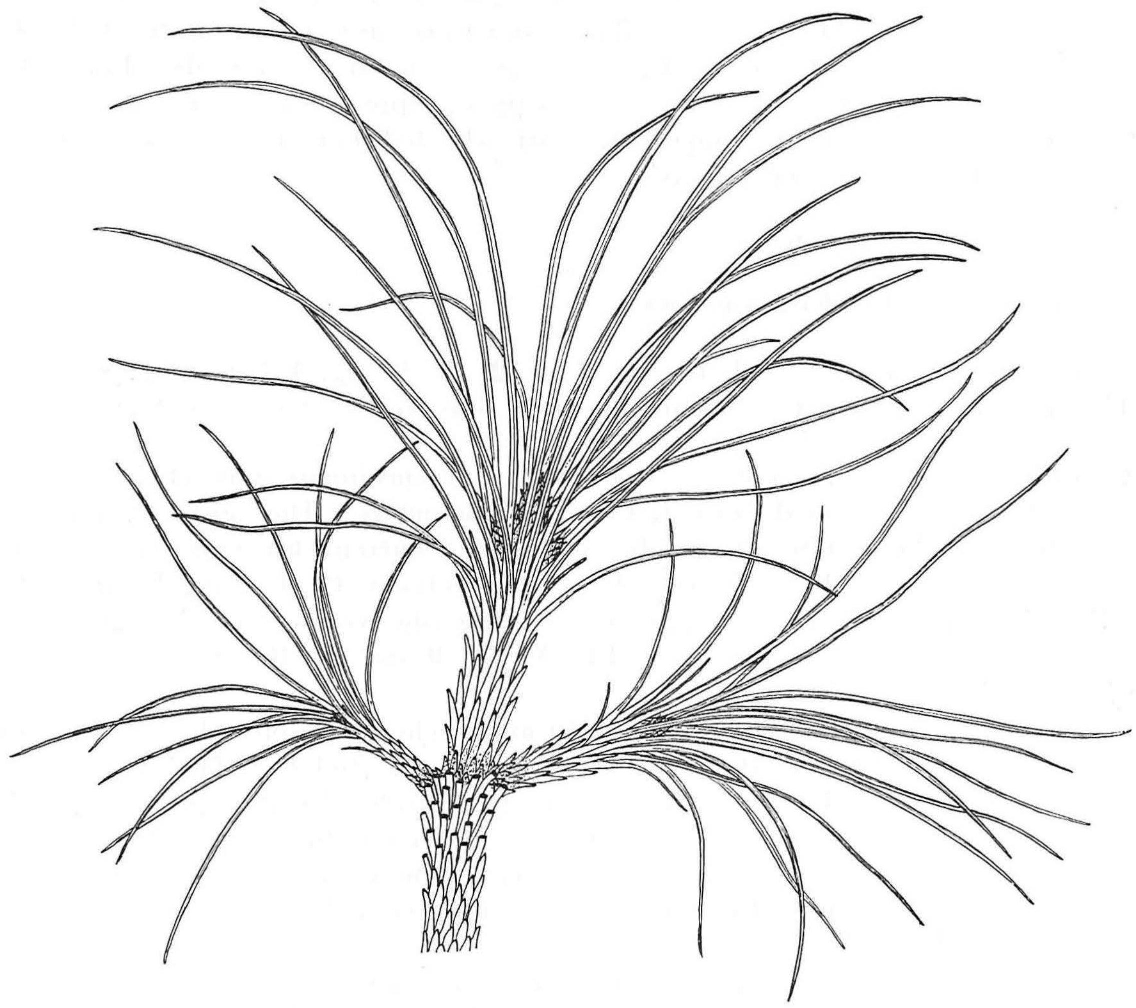

FIG. 7. — A suggested restoration of the shoot of *Prepinus sclerophylla*.

Abiocaulis verticillatus n. sp.

Diagnosis. — Stems (up to three years old) 1,5-6,0 mm in diameter. Annual increments of extension growth well marked by persistent terminal bud-scales which form whorl-like masses; lateral winter buds with persistent scales also occasionally present; axillary lateral branchlets probably also growing out directly without first forming winter buds. Bud-scales triangular to rounded, about 1,5 mm in both breadth and length. Cataphylls rather similar to bud-scales at the base of the annual extension shoot.

Cortex of two-year old twig with well marked periderm following the outline of the leaf-bases, and composed mainly of cells with dark contents; in three-year old twig periderm much more extensive, and leaf-bases less conspicuous. Nests of roundish or irregular sclereids present in the inner part of the cortex, probably mostly adjacent to, if not sometimes within, the secondary phloem. Leaf-bases with hypodermal fibrous tissue. Leaf-trace divided by parenchyma into two strands.

Pith 1,0-2,5 mm in diameter, homogeneous, composed of rather thick-walled, conspicuously pitted cells about 2-4 times as long as broad.

Wood with growth rings, but late tracheids not markedly different from early. Tracheids typically 15-20 μ in diameter; bordered pits on radial walls uniseriate and spaced, mostly near the ends of the tracheids. Rays numerous, uniseriate, mostly 1-3 cells high, homogeneous; ray cells with even or slightly irregular, fairly thick walls, abundantly pitted especially on the tangential walls which in consequence appear « nodular ». Cross-field with (1-)2-3(-5) elliptical pits, usually appearing narrowly half-bordered (« taxodioid »). Wood parenchyma absent. Resin canals absent.

Horizon. — Wealden.

Locality. — Houdeng-Aimeries.

Type-specimen. — Pl. IX, fig. 1, 9-12; Pl. X, fig. 1-3; text-fig. 8.
The specific name is derived from the whorl-like girdles of persistent bud-scales.

Further description. — The selection of specimens illustrated on plate IX and in text-figure 8, A and B, show the essential external characters. The most conspicuous feature, apart from the general armour of spirally arranged decurrent leaf-bases, is the whorl-like masses of persistent terminal bud-scales. The type-specimen (Pl. IX, fig. 1) shows two such girdles, the distance between them thus representing one year's extension growth; on the evidence of the annual rings in the wood (Pl. IX, fig. 9 and 10) this portion proves to have been in its second year.

All the specimens appear at first sight to be unbranched, but some show remains of lateral axillary buds or branch-bases (text-fig. 8, B; Pl. IX, fig. 5 and 6). That winter buds with persistent scales were sometimes formed laterally is indicated by the specimen in figure 7, plate IX. There is a definite branch-base immediately below the lower girdle of bud-scales in the type-specimen. The small scars such as those shown in text-figure 8, B, show no persistent scales, and were probably formed by branchlets which grew out directly without first forming buds.

No leaves are attached, even on slender portions estimated to be in their first year. This does not imply that the tree was deciduous, for in many conifers the leaves soon fall off when shoots are cut. The leaves could equally well have been disposed either radially or, by twisting of the bases, in one plane.

Anatomy. — The lower portion of the type-specimen was used for the anatomical investigation. The general structure is shown in text-figure 8, C, which is from a section through the second-year portion. The most striking feature is the dark reddish-brown periderm which follows the outline of the leaf-bases. At this stage there is clearly only one phellogen; in the third-year portion, however, at least in places, a second phellogen has been established (Pl. X, fig. 3), and at the same time the leaf-bases are only vaguely discernible, so presumably by this stage the leaves might have been shed.

The parenchyma of the primary cortex is ill preserved, but there are striking nests of sclereids usually situated either a little way out in the cortex or at least separated from the outermost wood by a dark brown substance which presumably represents phloem; sometimes,

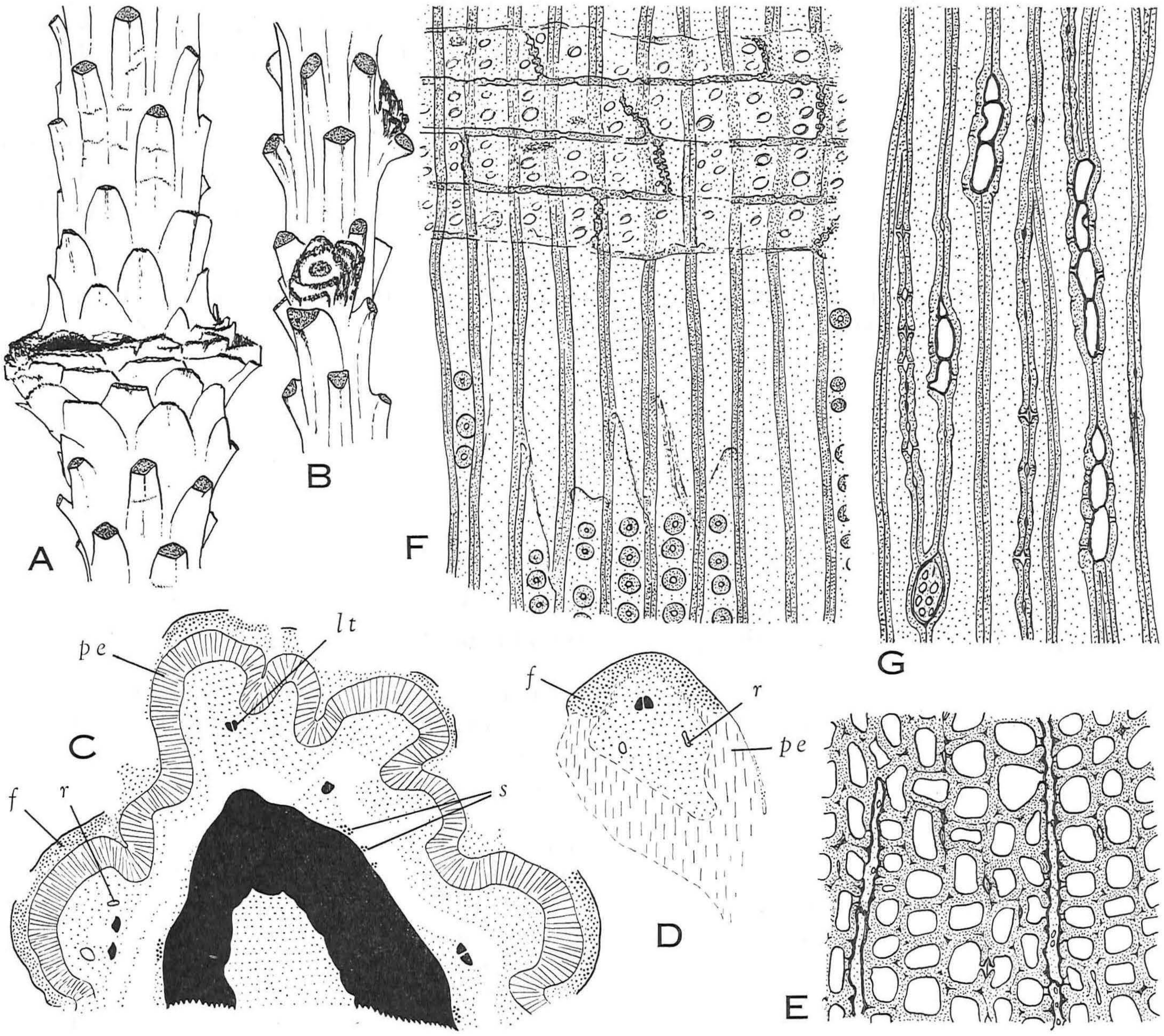

FIG. 8. — *Abiocaulis verticillatus* n. sp.

A : part of a specimen showing a girdle of broken bud scales from a terminal bud. ×6. — B : specimen showing two latral axillary buds or branchlet scars. ×6. — C : transverse section of the stem in its second year; *pe*, periderm; *f*, fibrous tissue; *r*, resin canal; *lt*, leaf-trace; *s*, sclereids. Section K1/6/1. ×20. — D : leaf-base from a tangential longitudinal section of the stem; labelling as before. K 5/2/2. ×20. — E-G : transverse and longitudinal sections of the wood from a twig in its third year. E, from K3/4/3; F, K4/3/1; G, K5/3/3. All ×375.

however, they are more or less embedded in this substance, and are so close to the wood that they could hardly have been elsewhere than in the phloem. The individual cells of the nests are roundish or irregular and have abundantly pitted walls.

The only resin canals I have seen have been pairs in the leaf-bases; they are always visible in tangential longitudinal sections (text-fig. 8, D), and I am sure that they were a regular feature. The cortical parenchyma is too poorly preserved, however, to enable one to be sure that these canals began blindly and not as branches from a cortical system.

The pith is quite homogeneous (Pl. X, fig. 1 and 2).

The wood (text-fig. 8, E-G; Pl. IX, fig. 11 and 12) has a structure which puts it clearly into *Cedroxylon* KRAUS as defined by KRÄUSEL (1949). A striking feature of many of the tracheids in the specimen investigated is the spiral checking shown in the photographs : it has been omitted in the drawings. This could at first sight be mistaken for tertiary thickening, but careful observation makes its true nature quite clear. I do not know whether this was an original and general character of the wood. Another feature not mentioned in the diagnosis is the presence in many of the ray cells of small granular masses, one per cell, resembling nuclei : two are visible in figure 11, plate IX, and some are shown in the drawing (text-fig. 8, F). They do not look like resin bodies.

The following table gives the percentages of rays of different numbers of cells high, based on a count of 200 rays :

Number of cells high	1	2	3	4	5-8
Percentage of rays	46	32	15	4	3

The bud-scales in transverse section show a thick hypodermal zone of fibres on the outside, and large-celled, thin-walled parenchyma on the inside; no vascular trace is descernible.

D i s c u s s i o n . — Clearly this twig could not be classified in any living genus of conifers, although all its features taken separately are more or less parallelled amongst living types. It seems to have most in common with the Pinaceae.

The wood does not differ appreciably from that of *Abies* spp. or *Keteleeria*, except that in the latter resin canals may be present. It differs from *Tsuga* and *Cedrus* in lacking ray tracheids, and from *Pinus*, *Picea*, *Larix*, *Pseudotsuga* and *Cathaya* by lacking both ray tracheids and resin canals, and also by other features. It differs from most Cupressaceae and Taxodiaceae by lacking vertical parenchyma.

Persistent bud-scales are found widely in the Pinaceae; they are especially conspicuous in *Abies* spp., *Keteleeria*, *Picea* spp., *Larix*, *Cedrus* and *Pseudolarix*, although in some of these, only the outer scales are horny and persistent, the inner being papery and more or less caducous. In *Sequoia* and *Cephalotaxus* the scales are green and soft but turn brown and persist at the base of the extension shoot; in the latter genus they are rather thin and easily rubbed off.

In *Abies*, lateral buds are practically confined to the end of the annual extension growth, where from 4-5 typically occur on the leaders, and 2 on the branches; this is clearly unlike the fossil. More scattered lateral buds occur in most of the other Pinaceae, and a particularly scattered arrangement is found in *Tsuga*; here too, lateral branchlets frequently grow out from the current extension shoot without first forming buds.

Leaf-bases exactly of the kind in the fossil are not known in any living member of the Pinaceae, although those in *Cathaya* and on the long-shoots in *Pseudolarix* are quite closely similar; in *Cathaya* the scar itself is rather more rounded, and in *Pseudolarix* both base and scar are usually rather less prominent. Most other members of the family present what may probably be regarded as more specialized conditions. Thus, in *Abies* and *Keteleeria* there is virtually no decurrent portion, the leaf-base being sucker-like and falling with the leaf. In *Picea* there are raised leaf-cushions separated by deep furrows, and the narrow persistent petiole arises below the upper limit of the cushion. *Pseudotsuga* and *Tsuga* are rather less unlike the fossil, but the scar itself is round and in *Tsuga*, much constricted. The long-shoot leaf-bases in *Larix* are also rather similar, but again the scar is constricted.

The presence of two resin canals in the leaf-base is a common feature of the Pinaceae, and occurs rarely outside the family, similarly with the divided trace. *Tsuga* is exceptional in having both a single resin canal and an undivided trace.

The periderm tends to follow the contour of the leaf-bases in a number of conifers that I have examined [e.g. *Picea abies* (LINN.) KARST, *Tsuga canadensis* (LINN.) CARRIÈRE and *Pseudotsuga taxifolia* (POIRET) BRITTON] although in the last named it is different in being immediately beneath the epidermis; in both the last two the outer periderm cells contain a dark substance, but then this is also true of *Taxus baccata* LINN.

Scattered stone cells occur in the phloem in a number of Pinaceae.

Few fossils have been described which it is at all useful to compare with *Abiocaulis verticillatus*. SUZUKI's (1910) type-species was based on a portion of an older stem and nothing was discovered about the leaf-bases. The wood was similar except that there was a sparse amount of vertical parenchyma, and that usually there were only 1-2 pits in the cross-field. SUZUKI described very similar sclereidal nests in the cortex and secondary phloem.

The species of *Cedroxylon* which seems most like the twig-wood described here is *C. shimakurai* KRÄUSEL which was described by SHIMAKURA (1937) as « *Cedroxylon* sp. » from the Cretaceous of Hokkaido; it differs in having rays often biseriate and up to 20 cells high.

Many compressed leafy twigs of the general conifer-taxad type have been described, usually under the name *Elatocladus*, from Mesozoic rocks in many parts of the world. There would be little value, however, in an attempted comparison with this isolated stem.

Genus ELATOCLADUS HALLE emend. HARRIS.

Elatocladus simplex n. sp.

This leaf may well belong to *Abiocaulis verticillatus*, but proof is lacking.

As it has become customary (e.g. HARRIS, 1935; FLORIN, 1958) to use HALLE's (1913) form-genus for shoots and isolated needle-leaves of the general conifer-taxad type that cannot be more precisely classified, I am following this practice for these isolated leaf fragments. In due course it might become useful to institute a genus for leaves believed to be of Pinaceous affinity but not belonging to any recent genus. Unfortunately, *Pityophyllum* NATHORST (1897) has been used for needle-leaves of various kinds and elucidation of its true status must await reinvestigation of *P. lindstromi* NATHORST.

Diagnosis. — Leaves acicular, straight, tapering rather gradually to acute apices, bifacial, 0,8-1,4 mm broad, slightly contracted at the base, keeled on the lower surface, hypostomatic; margins microscopically even.

Upper epidermis of fairly uniform, rectangular cells in longitudinal rows; midrib not marked in the epidermis; cells typically 5-8 times as long as broad with clearly marked, straight, virtually unpitted anticlinal walls (seen from cuticle).

Lower epidermis with two unsunken stomatal bands 0,1-0,3 mm wide, containing 2-5 closely arranged rows of stomata; cells of non-stomatal regions similar to those of the upper epidermis. Stomata haplocheilic, monocyclic or occasionally incompletely dicyclic, orientated longitudinally, more or less equidistant within the rows; each stoma usually separated from the next by only one square or hexagonal, shared subsidiary cell, but sometimes by two or even three short cells. Guard cells only slightly sunken; stomatal pit rectangular, rather wide. Subsidiary cells 4(-6), two polar, the rest lateral; occasionally a lateral encircling cell present. Lateral subsidiary cells sometimes shared with an adjacent stoma in the row and usually abutting on but not shared with stomata in adjacent rows. Very few non-stomatal cells within the stomatal bands.

Leaf sections showing hypodermal fibrous tissue 1-3 cells deep interrupted only by the stomatal bands. Two sub-marginal resin canals adjacent to the hypodermal fibrous tissue on the lower side. Mesophyll, except near the apex, with well defined palisade on the upper side. Vascular strand double, enclosed within a sheath including some fibres and separated from the mesophyll by a large-celled endodermis.

Horizon. — Wealden.

Locality. — Houdeng-Aimeries.

Type-specimen. — Text-figure 9, A.

The specific name was chosen because of the absence of any specially unusual feature.

Further description. — Fragments of these leaves are common in two small samples of matrix from Houdeng. One of the largest pieces is that chosen as the Type (text-fig. 9, A) which is 12,5 mm long; it is thicker and slightly narrower at one end which is taken to be the base.

The preservation is generally poor : out of six fragments only one was found to have a reasonably well preserved cuticle; it is therefore upon this one that the description of the epidermis is largely based; similarly, out of nine fragments sectioned, only two showed any details of structure; these are figured in text-figure 9, D and E, and that in figure D again on plate X, figures 4 and 5. One macerated leaf showed the upper epidermis very well (text-fig. 9, I).

The transverse section is typically broadly triangular in outline, but near the apex it becomes more terete, and its structure more radially organized, so that the palisade becomes ill defined and the stomatal bands tend to disappear (text-fig. 9, E).

In longitudinal section the endodermis is particularly conspicuous (Pl. X, fig. 4); the cells are 100-140 μ long.

The nature of the sheath cells inside the endodermis, except for a few fibres between and near the vascular strands, is unknown. They appear thin-walled and irregular in shape, and may have been parenchyma or transfusion cells.

A feature of the cuticle which I have not mentioned in the diagnosis because it is indefinite due to the rather poor preservation is that the lateral subsidiary cells tend to look finely punctate and yellower than the ordinary epidermal cells and the polar subsidiary cells; they are probably more heavily cutinized.

Discussion. — The size and shape of the slightly constricted base of this leaf are such that it could have been carried by *Abiocaulis verticillatus*. Further, the two resin canals, the double vascular trace and the hypodermal fibrous tissue are features of agreement. These are the only isolated leaves and stems, apart from fragments of *Prepinus*, that I have seen from Houdeng-Aimeries, but I have no idea how closely associated the remains were, as the stem specimens are entirely devoid of matrix. It seems to me quite probable that they belong together, but as proof is lacking, they must be regarded as separate species.

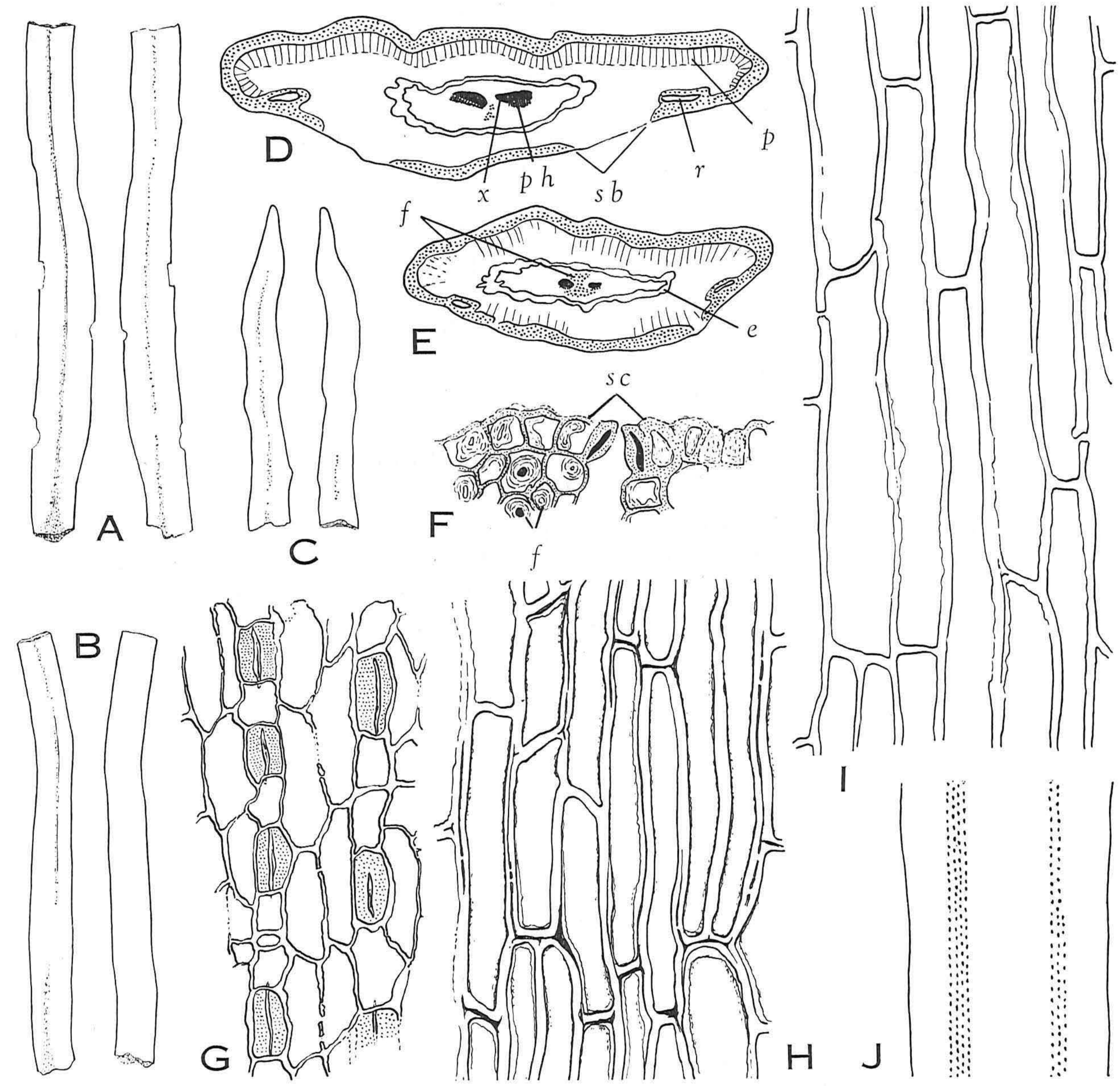

FIG. 9. — *Elatocladus simplex* n. sp.

A-C : specimens, each showing the two surfaces, the lower on the left, the upper on the right. A is chosen as the type-specimen and shows a slight thickening and narrowing at the lower end which is believed to be the base. C shows an apex. All ×6. — D, E : transverse sections of leaves : D, in the middle region; E, upper region; *f*, fibres (hypodermal and perivascular); *e*, endodermis; *p*, palisade; *ph*, phloem; *x*, xylem; *r*, resin canal; *sb*, stomatal band. Both from K'2/3/5. ×64. — F : stoma in median longitudinal section and, on the right, probably another sectioned through the ends of the guard cells; *sc*, subsidiary cells; *f*, hypodermal fibres. K'2/1/2. ×375. — G : part of the cuticle from the stomatal band; exposed parts of the guard cells are shown stippled. K'5a. ×375. — H : cells from the median non-stomatal region of the lower cuticle. K'5a. ×375. — I : cells from the upper epidermis drawn from a macerated leaf. (The cells probably swollen by the treatment.) K'6. ×375. — J : lower cuticle showing distribution of stomata. K'5a. ×22.

The epidermal structure is nearest to that of *Tsuga* (*Eutsuga*) and *Pseudotsuga* (FLORIN, 1931). The only differences from *Eutsuga* are that the subsidiary cells are unstriated (although they may perhaps be finely punctate) and that the stomata of adjacent rows do not, in the specimen investigated, share lateral subsidiary cells. *Pseudotsuga* usually has more rows of stomata in the band, and again lateral subsidiary cells are often shared with stomata in adjacent rows. There is much less resemblance to the other genera of Pinaceae. Outside the family, the fossil appears to be most like *Cephalotaxus*, but in this genus the stomatal rows are more numerous and more spaced, and the stomata are amphicyclic.

The internal anatomy agrees fairly closely with a number of genera of Pinaceae. The double vascular strand surrounded by a sheath and endodermis and the two marginal resin canals are features which occur together, as far as I know, only in that family : species of *Abies* have leaves almost precisely similar.

As far as other fossil types are concerned, again little is to be gained from comparisons with species based only on external morphology. There is some resemblance to certain Jurassic forms of which the cuticles are known. *Bilsdalea* HARRIS has certain resemblances, particularly perhaps *B. angustifolia* FLORIN (1958), but in this genus the stomata are usually partly dicyclic, less evenly spaced in the rows and their lateral subsidiary cells have an outer surface (often reduced to a narrow strip) where the cuticle is very thin. *Elatocladus parvifolius* FLORIN (1958) is also rather similar, differing chiefly in having stomata less evenly spaced in the rows, and in having more non-stomatal epidermal cells in the stomatal bands. *E. kilburnensis* FLORIN (1958) from the Jurassic of Yorkshire also shows resemblances, but differs in having epidermal cells with undulating anticlinal walls provided with jagged thickenings. The older *E. patens* HARRIS (1935) from the Lower Jurassic of East Greenland agrees in its general cuticle organization, but the cell outlines are thinner, the stomata less crowded and always completely monocyclic, and the leaves are petiolate.

GENERAL DISCUSSION AND CONCLUSION

The Pinaceae is richly represented in the Wealden flora of Belgium. The following nine species of cones are now well known :

Pinus belgica n. sp.
Pityostrobus andraei (COEMANS).
P. bommeri ALVIN (=*P. bernissartensis* ALVIN).
P. villerotensis ALVIN.
P. hautrageanus n. sp.
P. soigniesiensis n. sp.
P. corneti (COEMANS).
Pseudoaraucaria heeri (COEMANS).
Ps. gibbosa (COEMANS).

In addition, there are four species described by COEMANS (1866) of which the status is somewhat uncertain; these are :

« *Pinus* » *toillezi*. — A labelled specimen of this in the Natural History Museum, London, seems to me to be like *Pseudoaraucaria gibbosa*.

« *P.* » *depressa*. — This may only be a vertically compressed specimen of *Pseudoaraucaria heeri*.

« *P.* » *omalii*.
« *P.* » *briarti*. } These are based on small, severely compressed cones which may be immature.

Neglecting the wood, which has not yet been investigated, we find only three species of vegetative remains, of which two may in fact represent only one natural species :

Prepinus sclerophylla n. sp.
Abiocaulis verticillatus n. sp.
Elatocladus simplex n. sp.

The cones fall into three groups : 1) those that are broadly pine-like in form and structure; 2) *Pseudoaraucaria* spp.; 3) *Pityostrobus corneti* which seems to have affinity with the *Keteleeria-Abies-Cedrus* group of Pinaceae. Members of the first group outnumber all others by about two to one. Of the vegetative species, *Prepinus*, on the basis of its leaf appears to be related to *Pinus*, but its shoot morphology, which is still to some extent problematic, is obviously quite different from *Pinus*. *Abiocaulis* and *Elatocladus simplex* are not at all like *Pinus*, but may be related to *Abies*, *Tsuga* or *Pseudotsuga*.

The classification of the pine-like cones presents a problem. Of the species that I have studied, only one, namely, *Pinus belgica*, on the basis of its external form and internal anatomy, has seemed to me quite unequivocally a member of the recent genus; the rest have all differed from *Pinus* by some character, sometimes admittedly quite small, which is not encountered amongst the living species. This system may seem rather arbitrary, and it could be argued that it might be better to put all these cones either into *Pinus* or else into a non-committal form-genus. In recent years it has become customary to classify all cones of a pine-like aspect from the Tertiary in the recent genus, but with similar cones from older rocks there has been no generally accepted practice. Boundaries between related taxa, especially if one is considering fossils, obviously cannot always be sharp, and it may well be that in the early Cretaceous, a large group of conifers, the survivors and descendants of which we recognize to-day as the genus *Pinus*, were in an active state of evolution, and included members which retained now unfamiliar ancestral characters, or developed new characters which, owing to early extinction, have not survived amongst living species.

It is perhaps surprising that the vegetative remains do not include any that are classifiable in the genus *Pinus*; but until it becomes possible to collect further material from the same deposits, nothing can be adduced from this seeming discrepancy between the cones and the vegetative remains. It may simply be that owing to preferential collecting of cones and neglect of vegetative material, the two or three leaves and twigs that are at present known are quite unrepresentative of the flora.

Judging from the cones alone, we may confidently say that the Pinaceae was an important and varied family in the early Cretaceous, and it is surprising that only a few, mostly rather doubtful records occur in the Jurassic. In the Lower and Middle Jurassic there are no macrofossils from amongst several floras of north-western Europe and east Greenland which are classifiable in the Pinaceae (Florin, 1958), although pollen types resembling those of *Pinus* and *Tsuga* (*Eutsuga*) have been reported from the Middle Jurassic (Couper, 1958). In the Jurassic floras, however, there are many isolated shoots and leaves which do not fall into any known family, and amongst these there are several which, in their leaf cuticles, have a good deal in common with certain living members of the Pinaceae. The Cretaceous leaf described here has an epidermal organization different, at least in detail, from that of any living genus, but an internal anatomy which strongly suggests a Pinaceous affinity. As has been pointed out, its epidermis has similarities with a number of earlier fossil leaves, and it seems to me very possible that at least some of these may have been either early members of the family or else members of a group of conifers from which the Pinaceae, as we know it, evolved.

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PLATE I

EXPLANATION OF PLATE I.

Pseudoaraucaria gibbosa (COEMANS) n. comb.

FIG. 1. — Almost intact come showing the terminal tooth-like umbos. After BOMMER. ×2 (approx.).

FIG. 2. — Cone with some of the scales removed. ×2.

FIG. 3-6. — Cones. ×1. (Fig. 4 and 3 show the reverse sides of the specimens in fig. 1 and 2, respectively.) All specimens from Houdeng-Aimeries.

FIG. 7. — Scale somewhat laterally compressed with the seeds in situ. ×2 ¼.

FIG. 8. — Scale with the seeds removed; (incomplete distally). ×2 ¼.

FIG. 9. — Abaxial side of the lower part of a scale showing the bract. ×6.

FIG. 10. — Part of the axis in transverse section, showing the pith, vascular system, cortex with resin canals and three scale-bases. F3/4/10. ×12.

FIG. 11. — Part of a tangential longitudinal section through the axis, showing the horseshoe-shaped scale traces and associated bract traces below. F5/3/8. ×12.

FIG. 12. — Transverse section of a scale passing through the chalazal cushions of the seeds. F1/8/14. ×12.

FIG. 13. — Transverse section of another scale (more compressed) passing through the middle of the seeds. F2/5/5. ×18.

FIG. 14. — Part of a seed and the interseminal ridge in transverse section. F1/4/4. ×50. *ri*, one of the two sclerotic ribs of the integument.

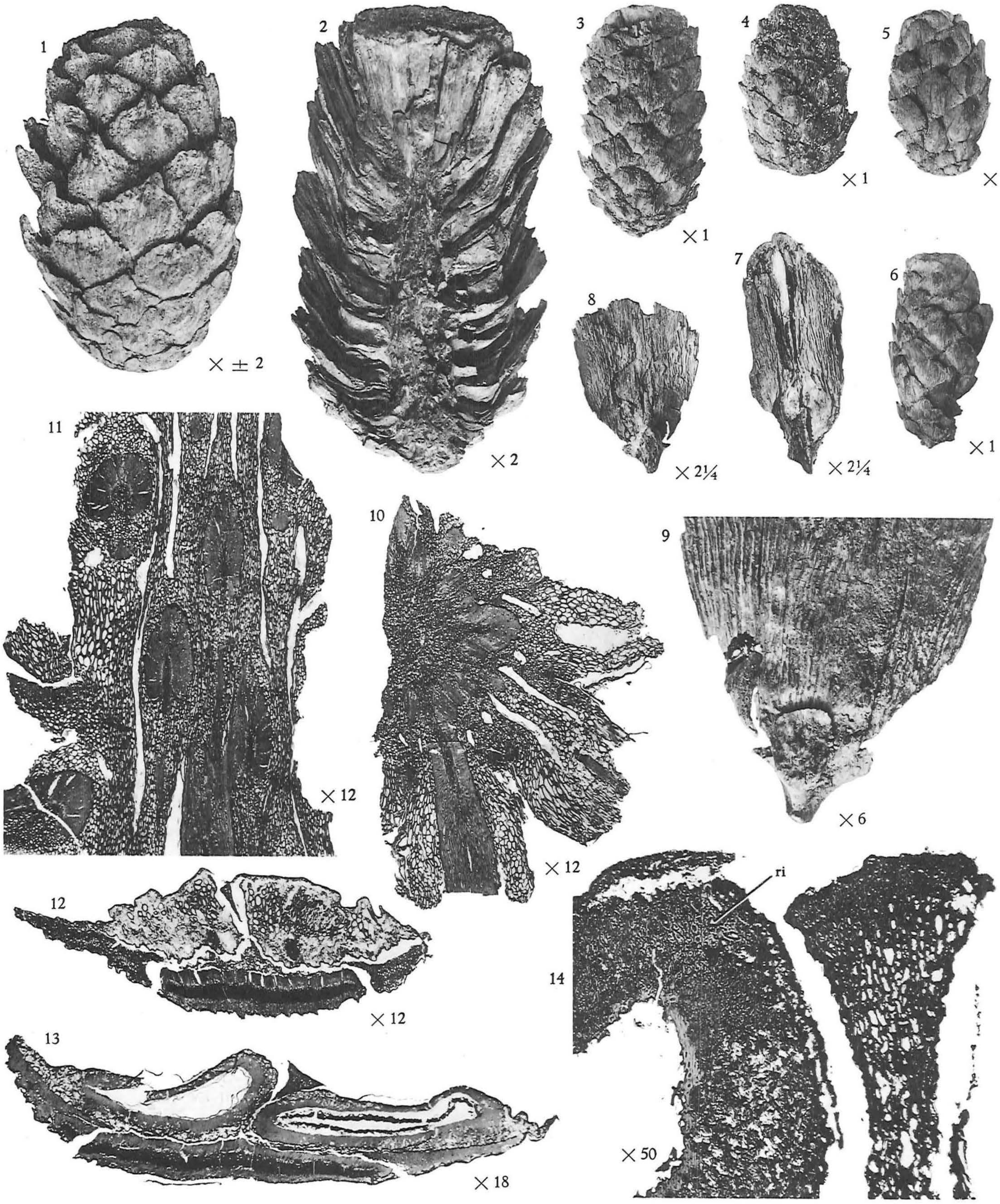

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PLATE II

EXPLANATION OF PLATE II.

Pseudoaraucaria gibbosa (COEMANS) n. comb.

FIG. 1. — Part of a transverse section of the scale just above the seeds showing the seed-wing and the lateral sclerotic tissue of the scale. F1/12/5. ×30.

FIG. 2. — Similar section at a higher level showing two continuous bands of sclerenchyma. F1/17/6. ×30.

FIG. 3. — Small part of the wood in radial L.S., showing a uniseriately pitted tracheid. F4/5/8. ×400.

FIG. 4. — Raadial L.S. of cone-axis showing uniform pith. F4/5/4. ×30.

Pityostrobus hautrageanus n. sp.

FIG. 5-11. — Selection of cone fragments. All ×1. (Fig. 5 shows the Type-Specimen.)

FIG. 12-17. — Scales. All ×2½. (In fig. 15 and 17, the seeds are not present.)

FIG. 18. — Transverse section of a scale passing through the seeds. G1/3/13. ×22.

FIG. 19. — A more distal section passing through the chalazal cushions of the seeds. G1/6/14. ×22.

FIG. 20. — Transverse section of the cone-axis. G2/9/10. ×15.

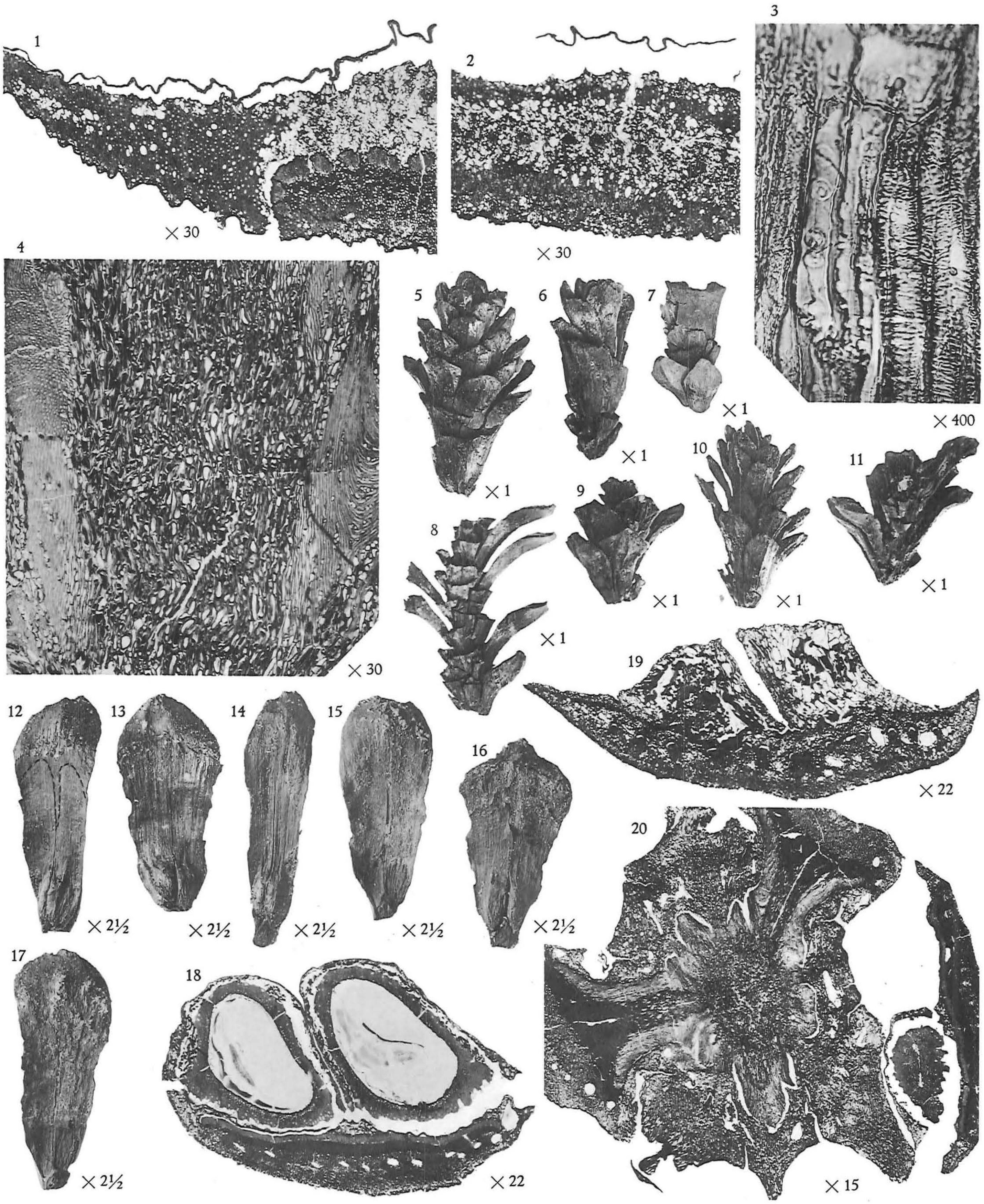

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PLATE III

EXPLANATION OF PLATE III.

Pseudoaraucaria gibbosa (COEMANS) n. comb.

FIG. 1. — A typical isolated cone-axis, completely decorticated at the top, elsewhere with somewhat abraded scale bases. ×2 ½.

Pityostrobus hautrageanus n. sp.

FIG. 2. — Part of a transverse section of a scale in the distal region showing the small, rounded vascular strands and the seed-wing in close contact with the adaxial fibrous tissue. G1/13/9. ×70.

FIG. 3. — Part of the chalazal tissue of the seed in transverse section. G1/7/7. ×78.

FIG. 4. — Part of the testa in transverse section. G1/3/12. ×108.

FIG. 5. — Pith in longitudinal section. G3/10/3. ×78.

Pityostrobus soigniesiensis n. sp.

FIG. 6. — Cone. (Type-Specimen.) ×2.

FIG. 7. — Longitudinal section of the axis. H2/5/4. ×10.

FIG. 8. — Transverse section of the axis. H3/5/9. ×10.

FIG. 9. — Pith in longitudinal section. H2/5/5. ×10.

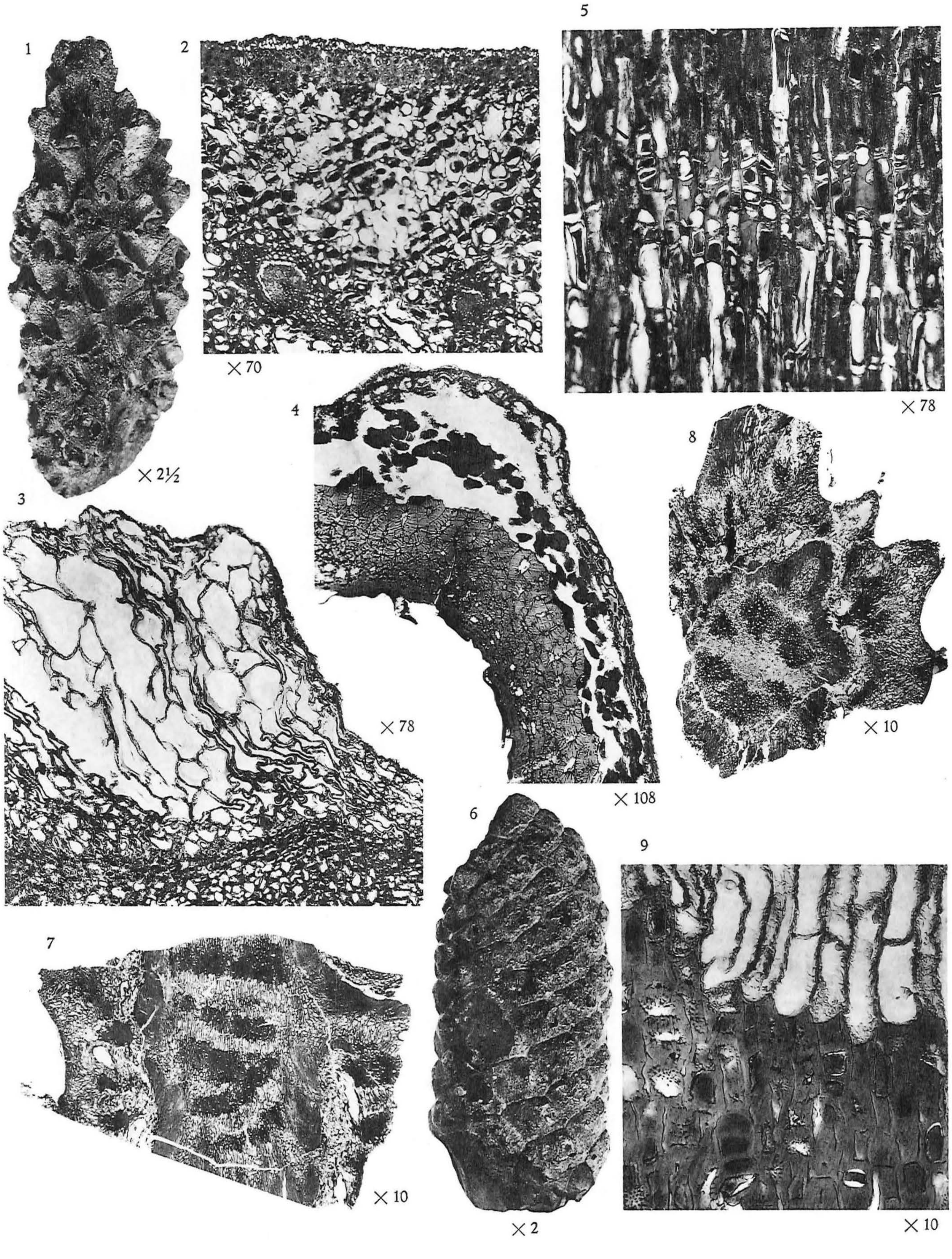

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PLATE IV

EXPLANATION OF PLATE IV.

Pityostrobus soigniesiensis n. sp.

FIG. 1. — Part of a transverse section of the cone showing scales cut at various levels. H1/5/13. ×20.

FIG. 2. — Oblique transverse section through the base of a scale with only one of the seeds cut; the section goes through the wing of the other seed. H1/3/4. ×25.

Pinus belgica n. sp.

FIG. 3. — Cone. The upper parts of the scales are broken off, but a few seeds are still in situ (*s*). ×2. (Type-Specimen)

FIG. 4. — Median longitudinal section through the upper part of a scale. J5/3/4. ×10.

FIG. 5-11. — Scales; some seen abaxially, others adaxially. Fig. 7 and 8, 6 and 9 represent the two sides of the same specimens.

FIG. 12. — Transverse section of the scale shown in fig. 11, passing through the upper region. J1/5/10. ×10.

FIG. 13. — Similar section through the middle region. J/3/12. ×10.

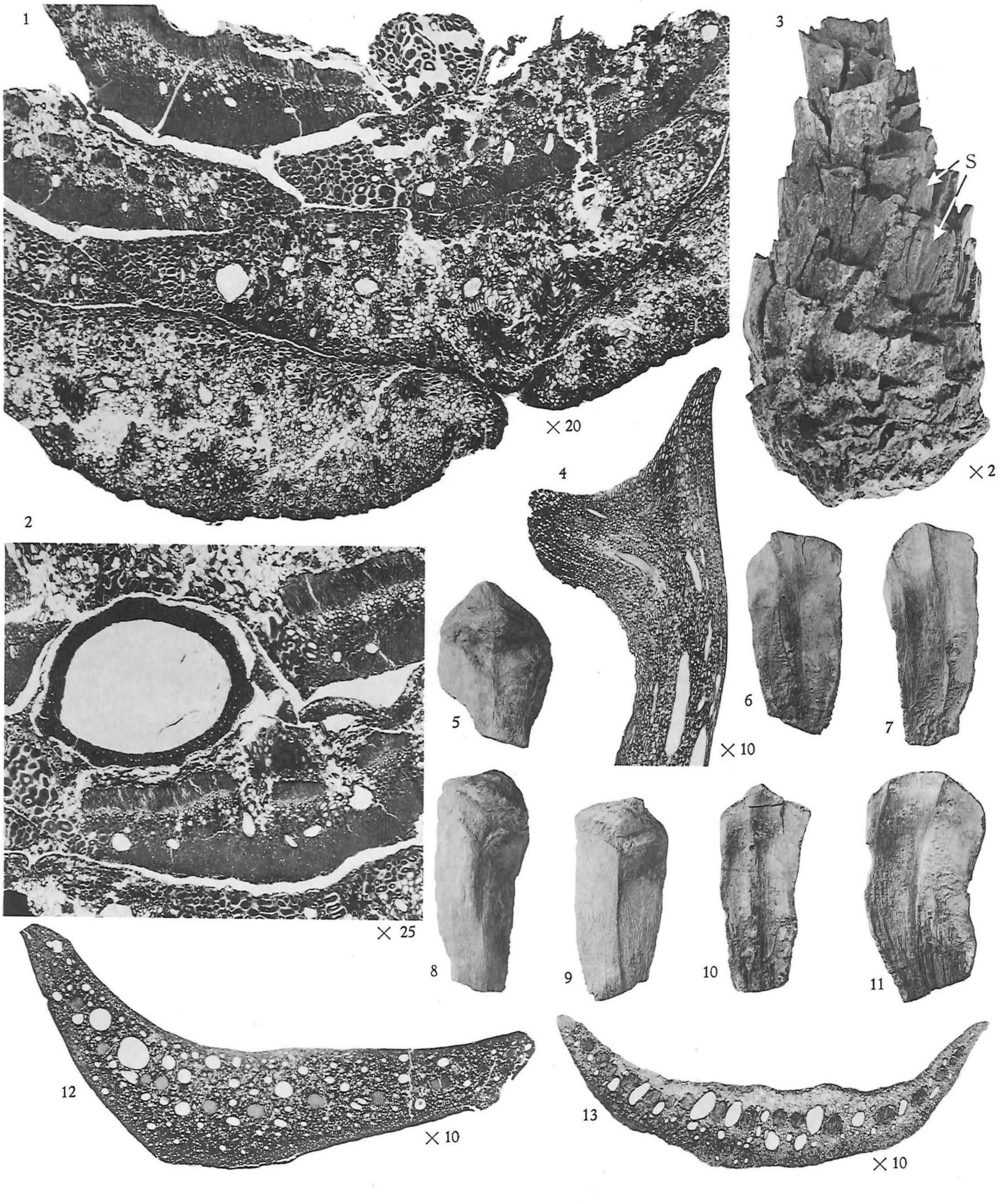

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PLATE V

EXPLANATION OF PLATE V.

Pinus belgica n. sp.

FIG. 1. — Transverse section of the axis. J2/5/1. ×6.

FIG. 2. — Transverse section of the axis. J2/10/1. ×6.

FIG. 3. — Tangential longitudinal section through the cortex showing the scale and bract traces. J4/4/2. ×6.

FIG. 4. — Transverse section of the pith showing a nest of thick-walled cells. J2/4/4. ×150.

FIG. 5. — Longitudinal section of the pith. J4/1/3. ×150.

FIG. 6. — Transverse section of the sclerotesta. J6/2/6. ×220.

FIG. 7. — Longitudinal section of the testa. J3/4/3. ×150.

FIG. 8. — Part of the wood of the axis in radial longitudinal section. ×250.

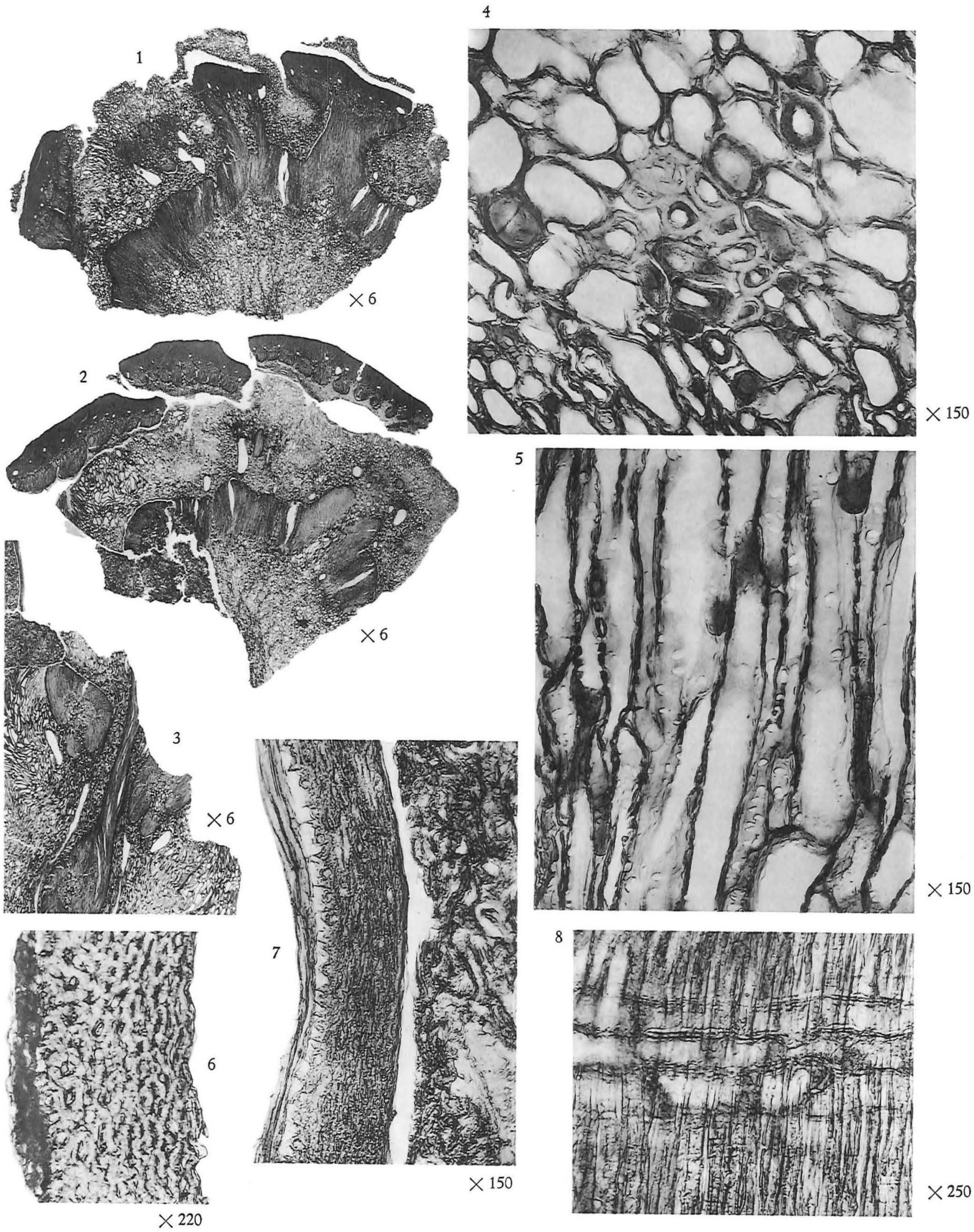

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PLATE VI

EXPLANATION OF PLATE VI.

Prepinus sclerophylla n. sp.

A selection of specimens. The one in figure 15 is chosen as the Type-Specimen. All ×2. All from Bernissart.

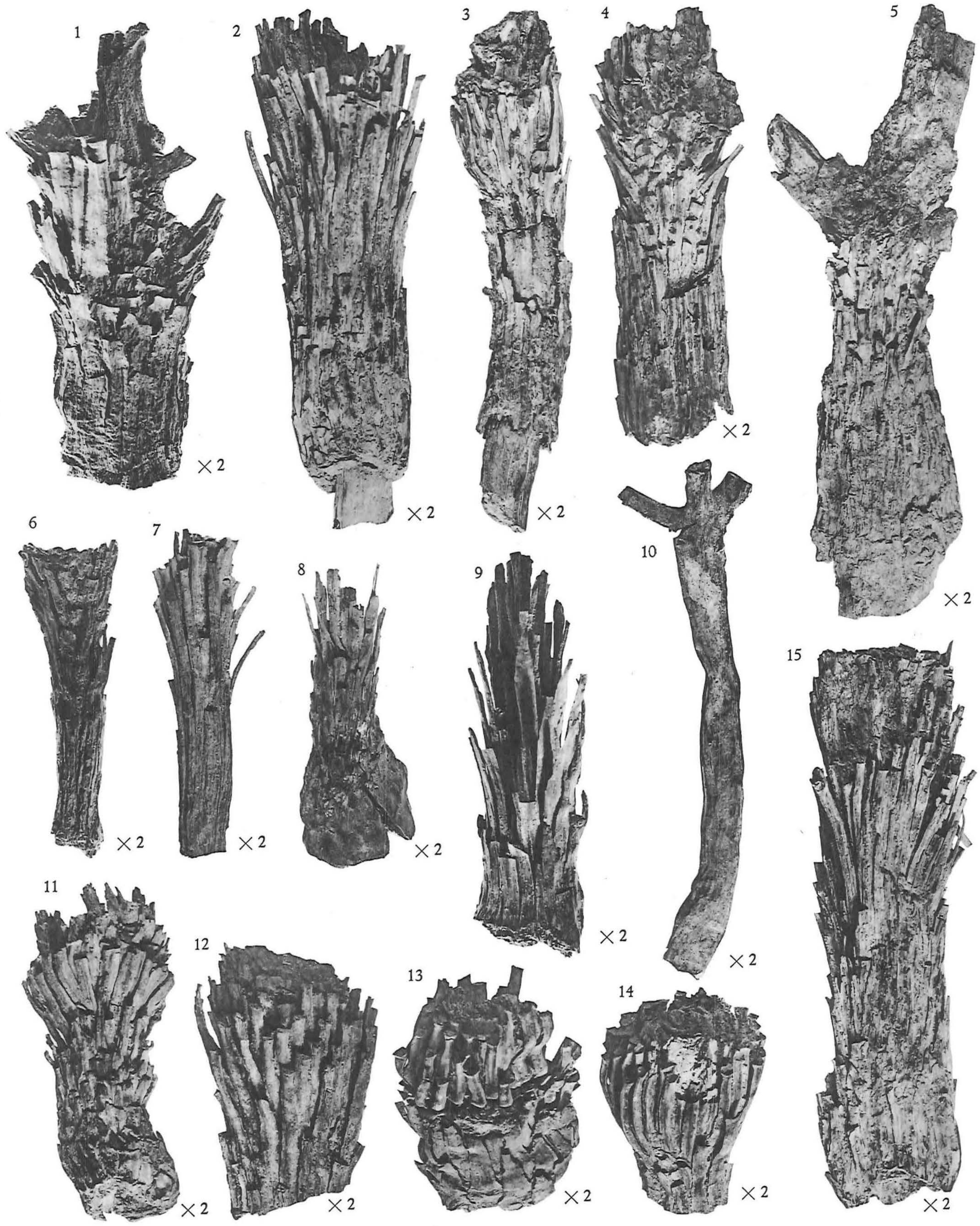

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PLATE VII

EXPLANATION OF PLATE VII.

Prepinus sclerophylla n. sp.

FIG. 1 and 2. — Partly decorticated specimens. ×2. Bernissart.

FIG. 3. — Specimen showing attenuated tips of two cataphylls (*c*). ×6. Bernissart.

FIG. 4. — Transverse section of the woody cylinder shown in text-figure 5, B (from specimen in figure 2 on this plate) taken below the swelling. L6a/2. ×24.

FIG. 5. — Transverse section of the same from above the swelling showing considerably less wood. L6b/1/3. ×24.

FIG. 6. — Wood in transverse section. L4/1/5. ×200.

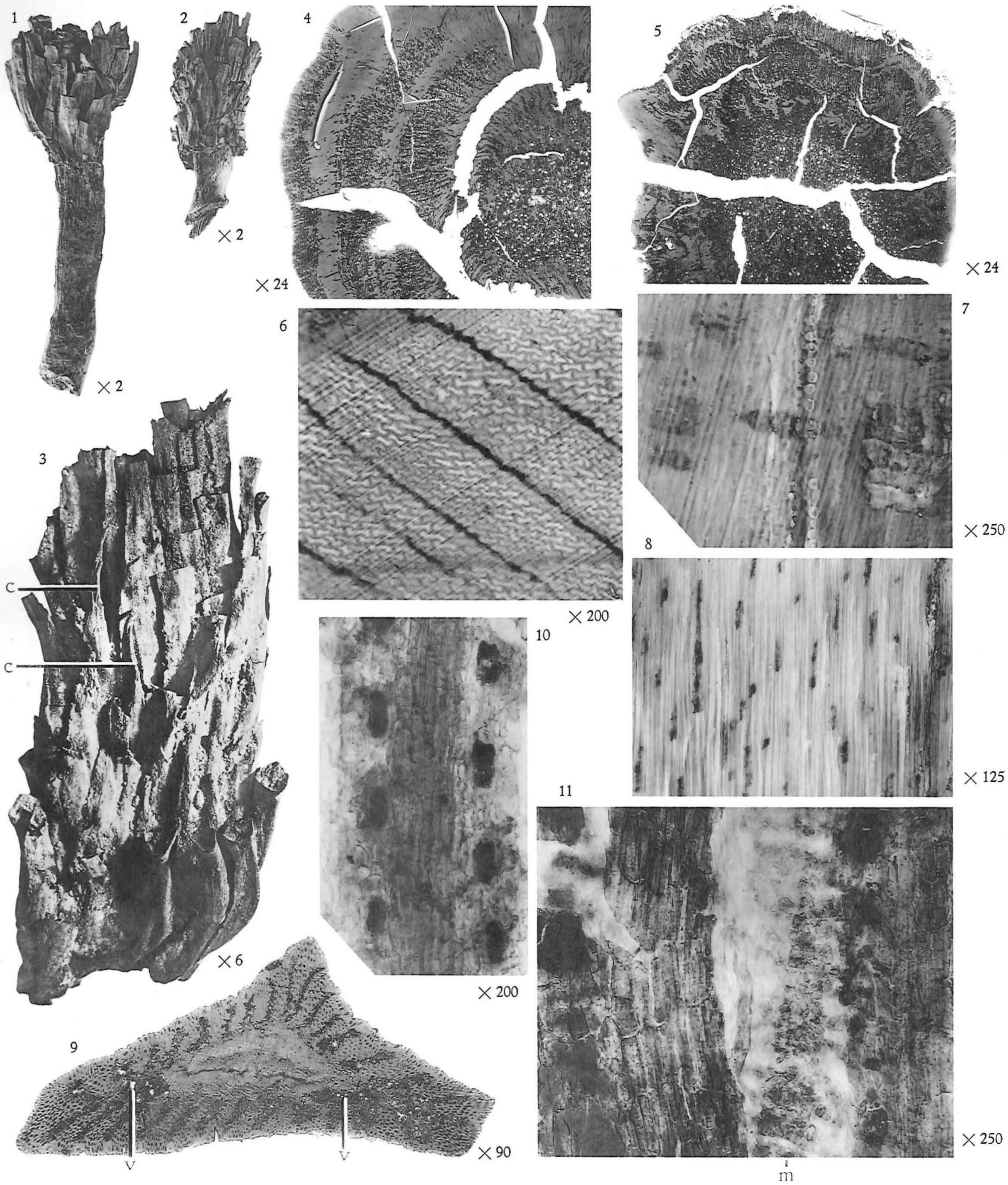
FIG. 7. — Wood in radial longitudinal section. L5/2/5. ×250.

FIG. 8. — Wood in tangential longitudinal section. L5/1/4. ×125.

FIG. 9. — Transverse section of a leaf. *v*, resin canals. L1/6/7. ×90.

FIG. 10. — Part of the leaf epidermis showing stomata. The dark band between the stomatal rows represents a bundle of hypodermal fibres. From a macerated specimen. L11b. ×200.

FIG. 11. — Portion of a macerated leaf showing, through a rupture in the epidermis, part of the mesophyll (*m*). L11c. ×250.



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EXPLANATION OF PLATE VIII.

Prepinus sclerophylla n. sp.

FIG. 1 and 2. — Transverse sections (nearly 1 mm apart) of a slender shoot similar to that shown in figure 7, plate VI, showing leaf-bases and the elaborate system of vascular strands. The higher section (fig. 2) shows a continuous central cylinder, but this fades out downwards and is represented in figure 1 by the small dumb-bell-shaped patch slightly above the centre. L13/3/12 and L13/4/3. × 18.

FIG. 3. — Transverse section of a leaf just above the base showing the thick sheath of fibrous tissue (*f*) and the broad xylem band apparently divided tangentially into two portions (x and x'). L13/4/5. × 120.

FIG. 4. — Transverse section through the apex of the same shoot as in figures 1 and 2, showing a mass of spirally arranged cataphylls (probably bud scales) surrounded by a few of the uppermost needle-leaves. L14/5/4. × 10.

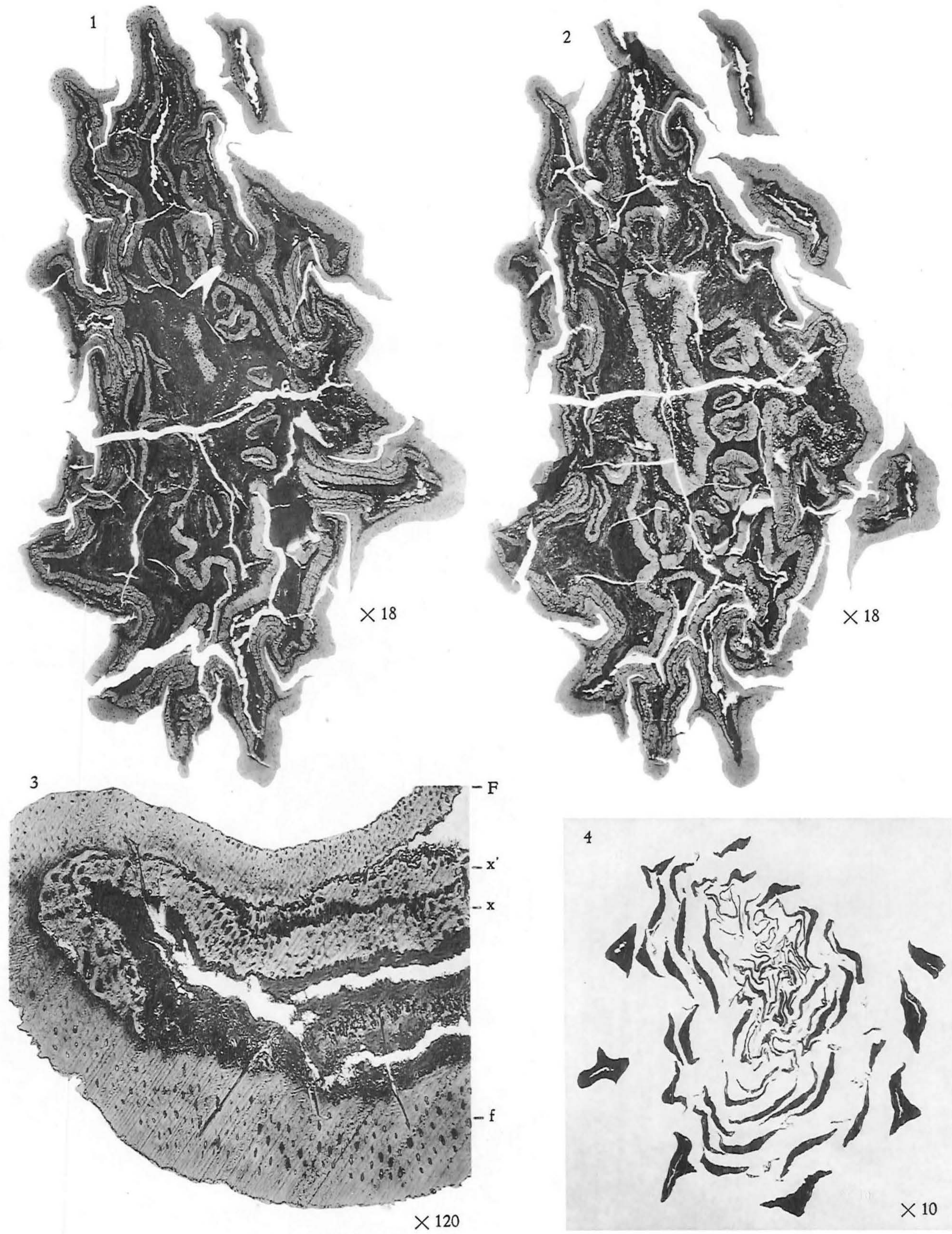

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PLATE IX

EXPLANATION OF PLATE IX.

Abiocaulis verticillatus n. sp.

FIG. 1. — The type-specimen. ×1.

FIG. 2-6. — Other specimens. ×2.

FIG. 7. — Short portion of an axis with the persistent scales of a lateral bud. ×2.

FIG. 8. — A terminal bud. ×2.

FIG. 9. — Transverse section of the type-specimen taken a short distance above the lower terminal bud scar; this portion of the twig is shown to be in its second year. K1/6/9. ×15.

FIG. 10. — Similar section taken below the lower terminal bud scar (i.e. in the third-year portion). *s*, sclereids. K3/4/1. ×15.

FIG. 11. — Radial longitudinal section of the wood. K4a/1. ×430.

FIG. 12. — Tangential longitudinal section of the wood. K2/2/12. ×430.
(Figures 1-8 are from photographs by CH. BOMMER.)

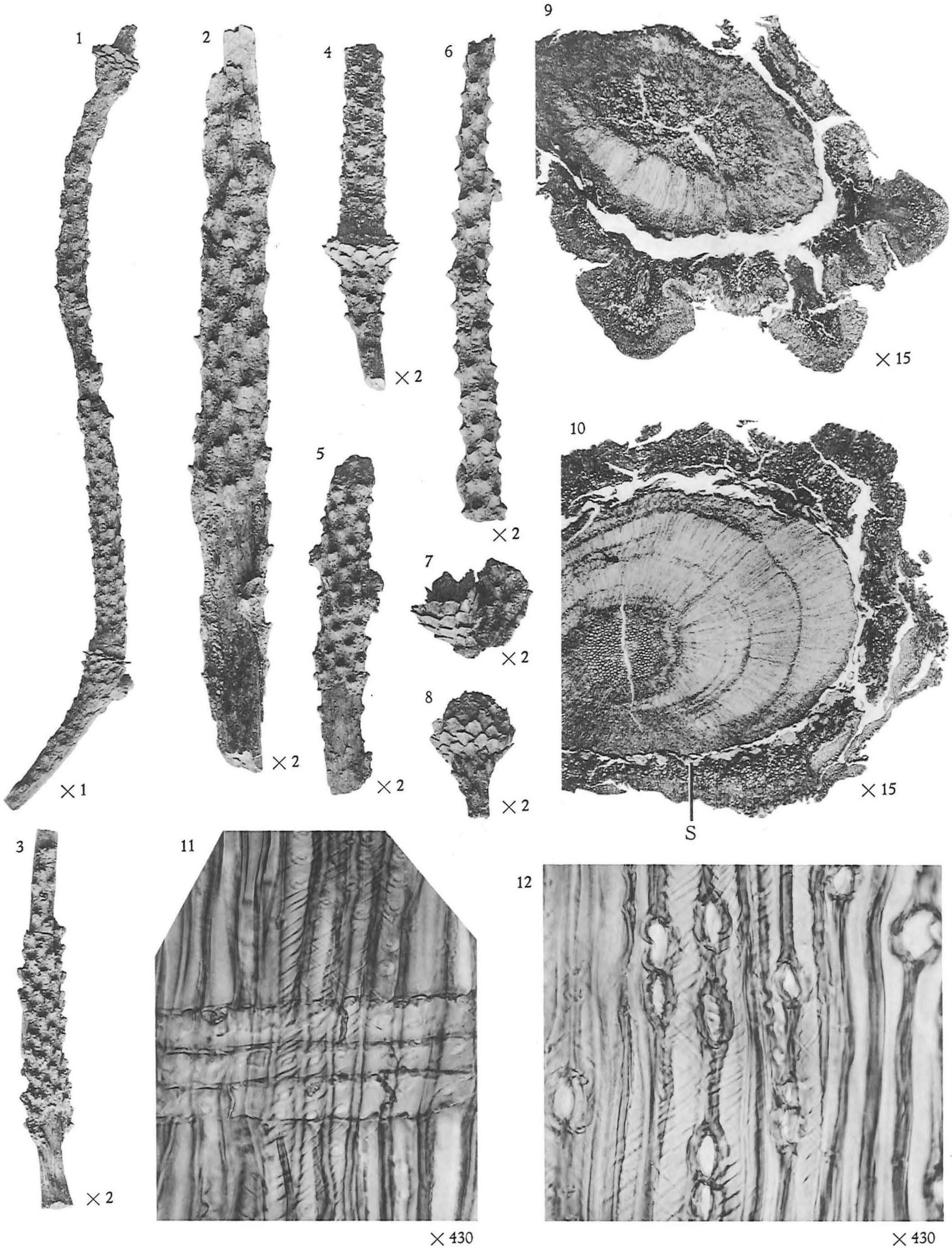

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PLATE X

EXPLANATION OF PLATE X.

Abiocaulis verticillatus n. sp.

FIG. 1. — Pith in transverse section. (Fungal hyphae are visible in some of the cells.) K3/1/6. ×165.

FIG. 2. — Pith in longitudinal section. K5/7/4. ×165.

FIG. 3. — Part of the cortex from the third-year portion of the type-specimen showing the dark periderm cells; p_1 and p_2 are the first and second phellogens. K3/4/6. ×120.

Elatocladus simplex n. sp.

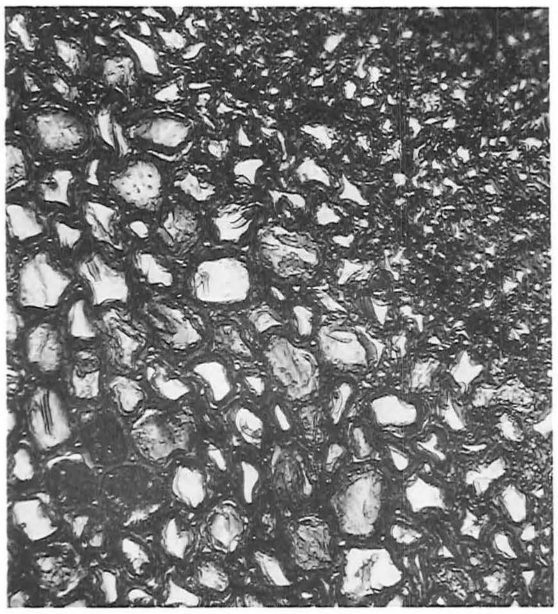
FIG. 4. — Median longitudinal section showing the large-celled endodermis, the mesophyll (palisade on the left) and the hypodermal fibrous tissue. K'4/1/14. ×145.

FIG. 5. — Transverse section (middle region). K'2/2/12. ×145.

Pityostrobus villerotensis ALVIN.

FIG. 6. — Specimen in situ in dry clay matrix : the specimen has shrunk considerably more than the matrix. ×1.

1

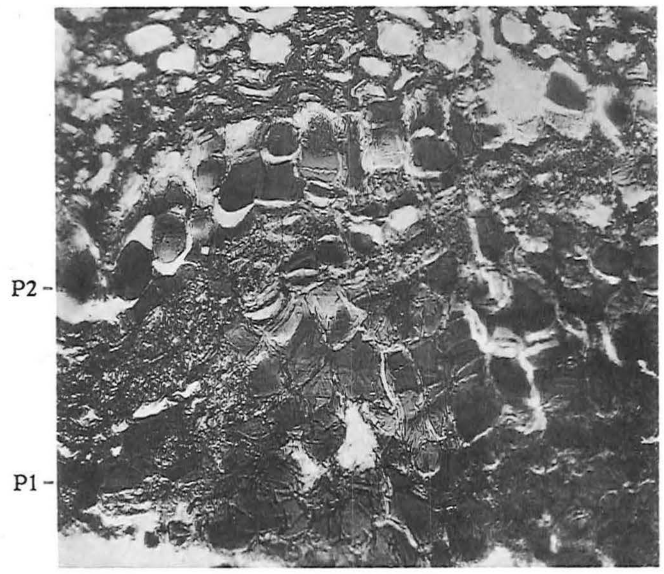


× 165

2

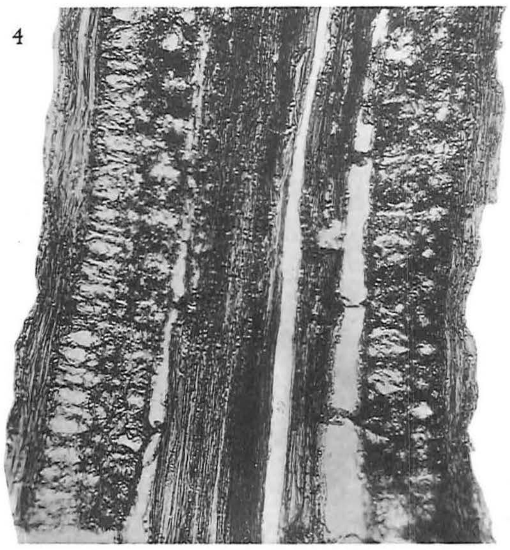
× 165

3



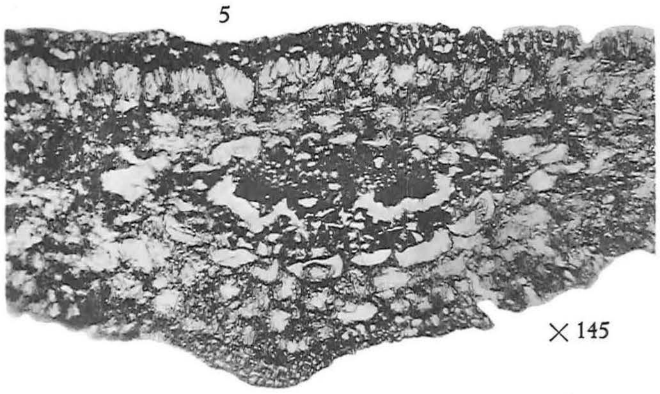
× 120

4



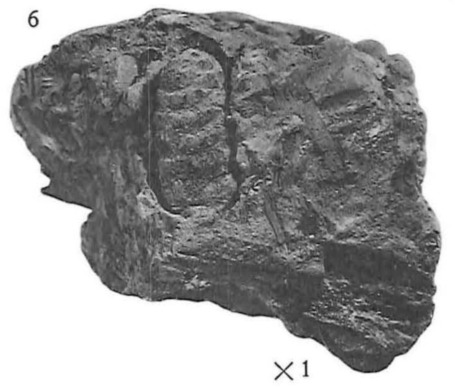
× 145

5



× 145

6



× 1

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