

ON THE TWO CONES
PSEUDOARAUCARIA HEERI (COEMANS) NOV. COMB.
AND
PITYOSTROBUS VILLEROTENSIS NOV. SP.
FROM THE WEALDEN OF BELGIUM

Genus PSEUDOARAUCARIA FLICHE.

This genus (written *Pseudo-Araucaria*) was erected by FLICHE (1896) for some fossil cones from the Albien-Cénomaniens of the Argonne which he described under three specific names (*P. loppinetti*, *P. major* and *P. lamberti*). FLICHE, whose descriptions were vague and poorly illustrated, regarded the cones as being closely related to the Araucariaceae, the main difference being that each scale bore two seeds instead of one, and this view has been generally accepted ever since (e.g. SEWARD, 1919, p. 261). By the kind permission of the director of the Ecole nationale supérieure de Géologie appliquée, Nancy, where the type material was deposited, I was able to borrow all that remained of this. The specimens were found to be excellently preserved and worthy of thorough reinvestigation. This has been carried out (ALVIN, 1957) with the result that the cones, which have now been condensed into two species (*P. loppinetti* and *P. major*), have proved to be distinctly Abietaceous but to possess some interesting features not found in the living members of the family.

An emended generic diagnosis has been published (ALVIN, 1957).

Pseudoaraucaria heeri (COEMANS) nov. comb.

Pinus heeri COEMANS, 1866, p. 14, Pl. V, fig. 3.

This species, although presenting the same general form as the French ones, is quite distinct in size and structure and is geologically older. It was first described by COEMANS in 1866 who considered it to belong to *Pinus* to which indeed there is a strong superficial resemblance. As far as I know it has not been reported since.

Emended Diagnosis. — Cone stoutly ellipsoidal, typically 3.5 cm long \times 2.5 cm broad (extremes : length, 2.2 cm-4.5 cm; breadth, 1.7 cm); apex obtuse, sometimes slightly depressed.

Axis 7-8 mm in diameter.

Bract 1 mm broad; free part 4 mm long.

Ovuliferous scale very sharply bent; basal part about 5 mm long, 5-7 mm broad and 4-5 mm high; interseminal ridge somewhat overarching the seeds; upper part of the scale 10-13 mm long, 9-12 mm broad, surmounted by a conspicuous umbo 2-3 mm long.

Seeds about 4.5 \times 2 mm; sclerotesta usually about 0.15-0.2 mm thick, pitted at the chalazal end; seed-wing asymmetrical in shape, usually about 8 mm long, covering most of the surface of the scale.

Vascular system of the axis much dissected; supply to the bract simple, leaving the axial cylinder at the base of the « leaf-gap »; supply to the ovuliferous scale at first of two strands, one from each side of the gap, but fusing and becoming horseshoe-shaped in the cortex; strand flattening in the scale and dividing up just above the seeds into a number of small strands.

Tissue on the abaxial side at and for some distance above the bend in the scale composed of narrow, elongated, relatively thin-walled cells; horizontal part of the scale largely sclerotic.

Horizon. — Wealden.

Localities.

1. Baume, La Louvière; clay workings.
2. Houdeng-Aimeries; Canal du Centre.

Detailed Description. External form. — Unfortunately, all the cones at my disposal were more or less damaged, but with the help of BOUMER's excellent photographs, it was possible to obtain a fairly good conception of the external form of a typical intact cone. The outstandingly fine specimen photographed by BOUMER and shown here in figures 1 and 2, plate II, is one which I have been unable to find, but I have no doubt it belonged to this species.

The specimen in figure 2, plate I appears to be the same as the one figured by COEMANS (Pl. V, fig. 3, middle right); its appearance suggests that it may have been charred before fossilization.

The cone is typically ellipsoidal, although larger specimens tend to be more or less cylindrical (Pl. II, fig. 1), and smaller ones often almost spherical (Pl. I, fig. 2). The apex is always very blunt, usually rounded, but sometimes definitely depressed as in the recent *Cedrus* and species of *Abies*. None of the specimens has a peduncle.

The exposed part of the scale, including the conspicuous terminal umbo, is broader than high, typically about 11 mm by 7 mm. The surface bears faint striations which converge towards the base of the umbo.

A number of specimens in the collection (e.g. Pl. I, figs. 4 and 5) have completely lost the erect portions of their scales, and are left with only the horizontal parts carrying the seeds (a few of which have sometimes dropped out). Although it is possible that this condition

represents a natural stage in seed liberation (see Discussion below) it seems more likely that it is due only to severe abrasion, for less advanced conditions are sometimes found (e.g. the cone in fig. 1, Pl. I) in which only the end of the erect portion of the scale has been eroded, and also more advanced conditions where little remains but the cone-axis. Moreover, the exposed parts of all these specimens are usually pitted with sand particles as were the abraded cones of *Pityostrobus andraei* (see ALVIN, 1953).

The cone-axis is fairly stout, occupying about one-quarter of the diameter of the cone (Pl. I, fig. 1 and Pl. II, fig. 2). It is more or less cylindrical, decreasing abruptly towards the apex. As seen in longitudinal section (Pl. II, fig. 2) the cone-apex is bud-like, consisting of a great many reduced scales.

The scales are densely crowded on the axis. The basal parts are contiguous, so that no area of bare axis occurs between them; this can be seen from the partly dissected cones (Pl. I, figs. 1 and 3) and also from the abraded specimens (Pl. I, figs. 4 and 5). The scales become smaller and sterile towards the extremities of the cone; they are also slightly different in shape from those in the middle region: at the apical end, the lower part of the scale, instead of being at right-angles to the axis, points slightly upwards, and at the base, slightly downwards (Pl. II, fig. 2). The upper laminoid part of the scale is normally set at almost a right-angle to the lower part, but again, towards the apex of the cone, this angle tends to be more obtuse, and towards the base, more acute.

The adaxial surface of the scale with the winged seeds in situ is shown in figure 6, plate I, and in figure 3 on plate II. Between the seeds there is the prominent ridge, which, being broader at its crest, overarches the seeds to some extent (text-fig. 1, H; Pl. I, figs. 10 and 11; Pl. II, fig. 3). The ridge is continued for a distance in a gradually attenuating form up the vertical portion of the scale before it fades out (text-fig. 2, A-C).

The seeds can be described as being wedge-shaped with one face curved, and the other flat or only slightly curved, the strongly curved face being in contact with the scale and ridge, and the other exposed. In transverse section it thus appears almost semi-circular (Pl. I, figs. 10 and 11). The thin, narrow micropylar end lies towards the axis (Pl. I, fig. 6). BOMMER's drawings of isolated seeds (Pl. II, fig. 5) show the shape well. The wing is well developed, strongly asymmetrical in shape, and set nearly at right-angles to the seed itself (Pl. II, fig. 3).

The simple tongue-like bract is moderately well developed (Pl. I, fig. 8; Pl. II, fig. 6). It is free from the ovuliferous scale from about the right-angle bend in the latter.

Anatomy. — The anatomical description is based mainly on a study of the cone in figure 1, plate I. In spite of some abrasion, the specimen was found to be structurally well preserved.

a) **The Axis.** — The axis contains a broad continuous pith about 2 mm in diameter surrounded by a considerably dissected vascular cylinder (text-fig. 1, A) and a narrow cortex. The cortical resin canals are distributed in a single ring; they are fairly small and inconspicuous. The xylem apparently lacks resin ducts; certainly there are no large ones present, but the possibility of small ones occurring here and there cannot be ruled out. I have found that in recent cones the presence of small canals in the xylem is often not obvious until sections have been stained and cleared.

The vascular supply to the bract is in the form of a simple, but fairly strongly developed strand arising from the bottom of a gap in the axial cylinder (text-fig. 1, C, b).

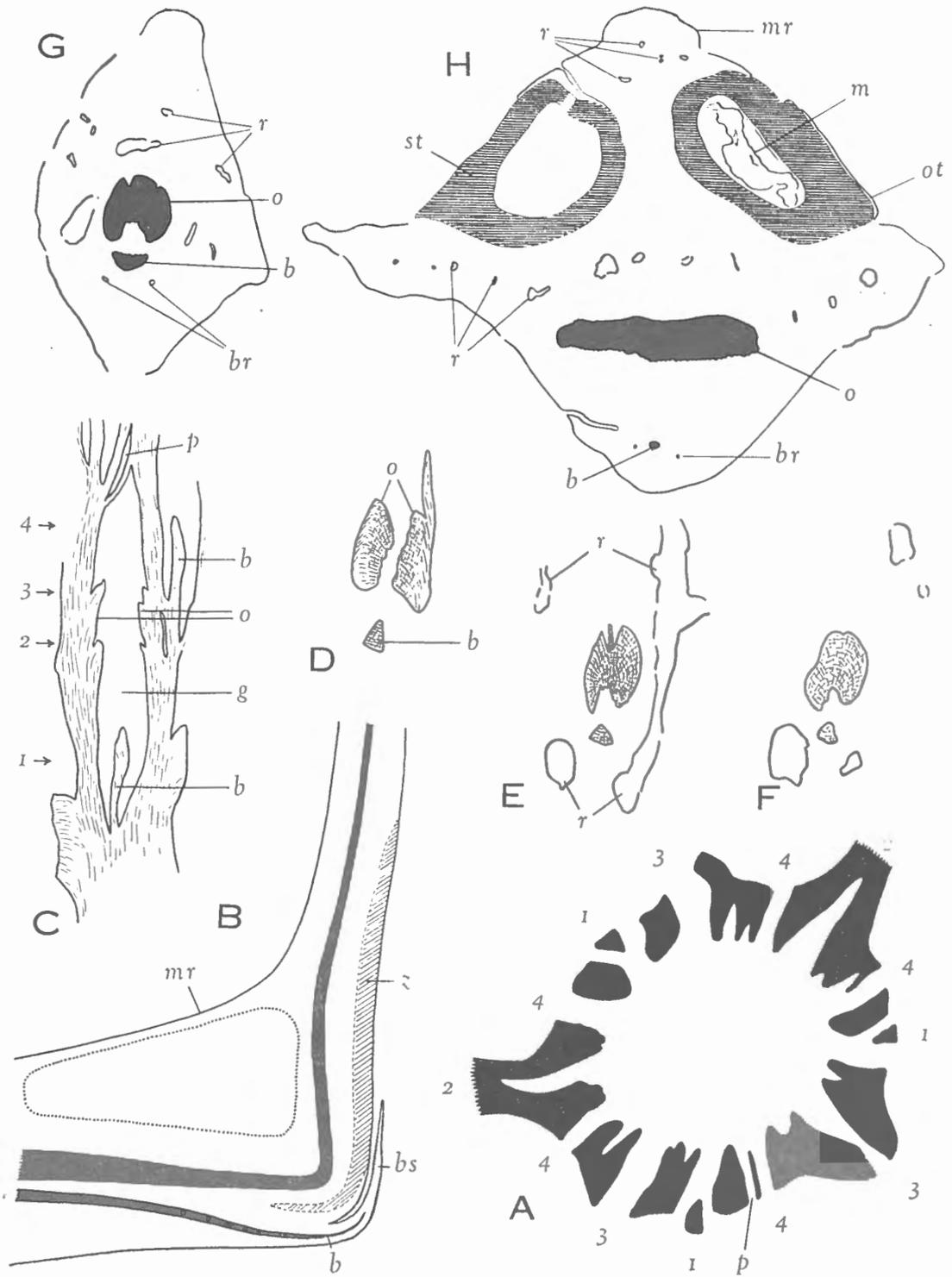


FIG. 1.

The supply to the scale consists of a pair of strands arising from the sides of the gap (text-fig. 1, C and D, *o*). The two strands very soon fuse in the cortex giving rise to the usual inverted U-shaped or horseshoe-shaped strand (fig. E and F). The « leaf-gap », as will be seen from figures A and C, is continued for a long distance above the point where the scale strands are inserted; (this part of the gap is indicated in these figures by the number « 4 »). In addition to the gaps in the vascular cylinder associated with the departure of traces, there are a few small perforations (*p*).

As regards the finer structure of the axis, there are no features of especial interest. The tissues are however well preserved. The pith (Pl. III, fig. 1) consists of more or less uniform parenchyma, the cells of which have fairly thick, distinctly pitted walls. Most of the cells have a roundish outline in transverse section with small intercellular spaces, and in longitudinal section they are rectangular. Towards the periphery opposite the xylem masses the cells become narrower and more elongated, but opposite the gaps they remain more or less isodiametric. The cells in the gaps are large and elongated radially.

The cells of the cortex are mainly similar to those of the pith, but become slightly smaller, thicker-walled and more elongated towards the outside.

b) The Scale. — The lower, horizontal portion of the scale is rhomb-shaped in vertical section; at first (text-fig. 1, G) it is slightly elongated longitudinally, and then, in the region of the seeds (fig. H and Pl. I, figs. 10 and 11), almost square.

The vascular strand of the ovuliferous portion quite soon loses its horseshoe-shape and becomes flattened out (text-fig. 1, H). The bract trace diminishes as it moves away from the scale strand (fig. B, G and H), and just enters the free part before fading out.

The resin canals appear to have their origin in branches from two of the cortical canals (text-fig. 1, E). With the exception only of two small ones associated with the bract, all lie adaxial to the vascular strand (G and H, *r*; Pl. I, figs. 10 and 11). They ramify and spread out, extending right up into the interseminal ridge. Their distribution in the upper laminoid region is less clear. They are very small and are at first probably confined to the sclerenchyma on the adaxial side (text-fig. 2, A and B, *r*), but at higher levels they probably spread to the other side together with the sclerenchyma.

As the bend in the scale is approached the wing-like lateral flanges become larger and the bract begins to separate from the ovuliferous scale. The vascular strand gradually becomes broader and turns very sharply up into the vertical portion of the scale (text-fig. 1, B; Pl. I, fig. 9). It remains undivided until two temporary gaps arise. These probably lie beneath the chalazae of the seeds (text-fig. 2, A, *g*), but owing to the distortion that occurred in softening, involving the backward displacement of the upper part of the scale and its

EXPLANATION OF FIGURE 1.

FIG. 1. — *Pseudoaraucaria heeri* (COEMANS) NOV. COMB.

A, vascular system of the axis as seen in transverse section. The numbers represent the approximate levels at which the gaps associated with the departure of traces are sectioned (cf. fig. C). *p*, perforation. D2/9/1. — **B**, median longitudinal section through the base of the scale. *b*, bract trace; *bs*, bract scale; *mr*, interseminal ridge; *z*, zone of thin-walled elongated cells. The dotted line indicates the position of the seeds on either side of the ridge. Reconstructed from series D6. — **C-F**, series of tangential longitudinal sections through the axis showing the departure of traces to a single appendage. *o*, ovuliferous scale trace; *g*, « leaf-gap »; *r*, resin canals; other labelling as before. From series D3; C from section 6/3; D, 3/1; E, 1/3; F, 1/1. — **G** and **H**, vertical sections through the base of a scale; *st*, sclerotesta; *ot*, outer layer of the integument; *br*, bracteal resin canals; other labelling as before. From series D4; G from section 2/9; H, 12/5. All $\times 15$. (In C-F the xylem is indicated by line shading, in others it is solid black.)

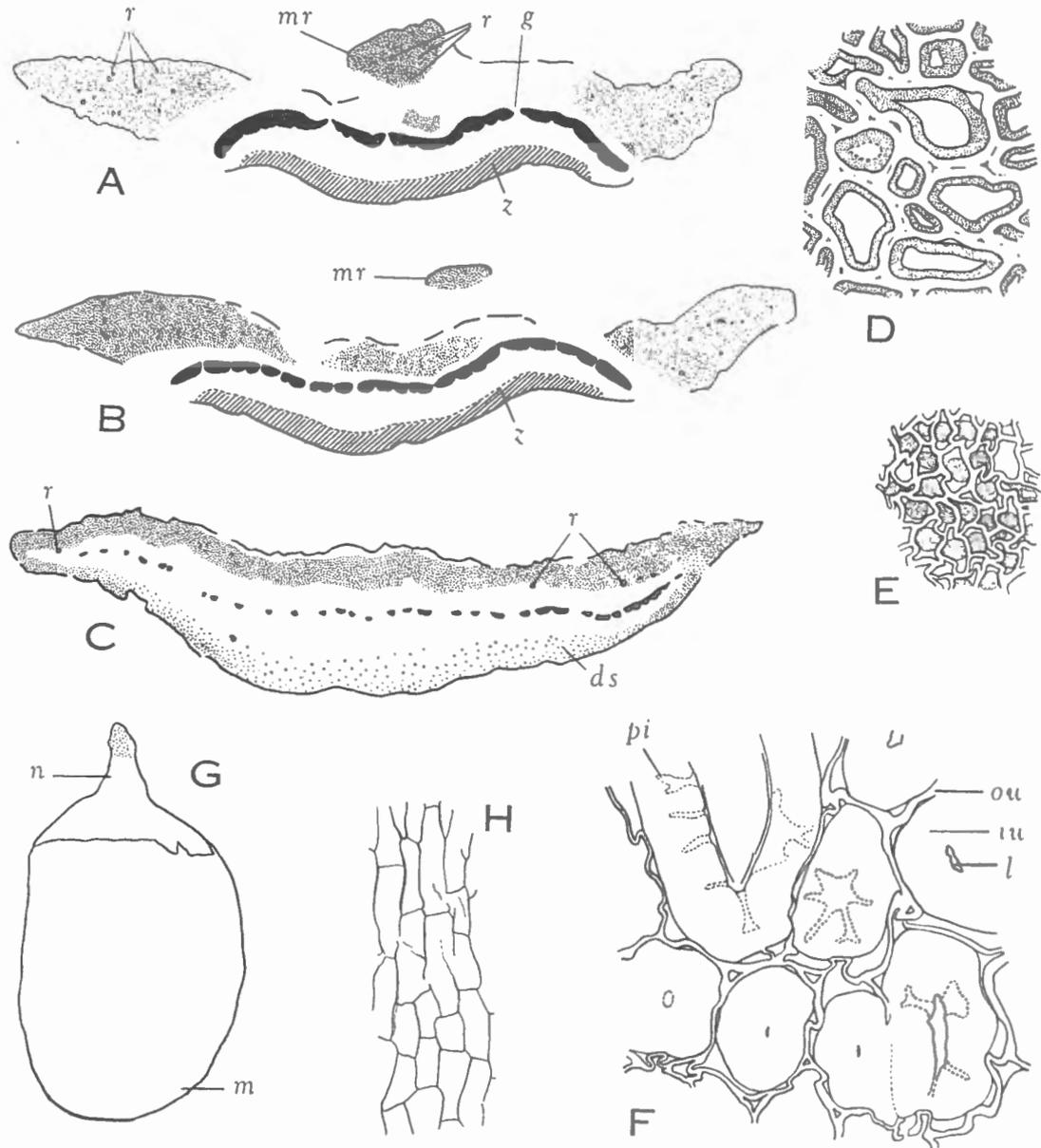


FIG. 2. — *Pseudoaraucaria heeri* (COEMANS) NOV. comb.

A-C, series of transverse sections through the upper part of the scale. *r*, resin canals; *mr*, interseminal ridge; *g*, temporary gap in the vascular system associated with a seed base; *z*, zone of thin-walled cells like those shown in figure E. Stippling indicates sclerenchyma which is more diffuse on the abaxial side above (fig. C, *ds*). From series D1; A from section 13/12; B, 15/3; C, 19/11. $\times 15$. — **D**, cells from the region immediately abaxial to the vascular strand in the lower part of the scale. Stippling here indicates dark reddish-brown contents. D4/13/10. $\times 325$. — **E**, cells from zone *z* in figures A and B. D1/9/4. $\times 325$. — **F**, cells of sclerenchyma in the scale base and in the stippled regions in figures A-C. *l*, lumen; *iw*, inner layer of wall; *ou*, combined outer layers of abutting cells; *pi*, probably distorted pits. D4/11/6. $\times 325$. — **G**, « kernel » from dissected seed. *m*, megaspore membrane; *n*, nucellus cuticle. $\times 15$. — **H**, cell outlines from the nucellus cuticle. Slide D9a. $\times 325$.

breaking away from the seeds (Pl. I, fig. 9), it was not possible to ascertain exactly where these gaps occurred relative to the seed bases. They close apparently without giving off seed traces (text-fig. 2, B), and probably correspond to similar gaps in the « sub-ovular strands » in *Pityostrobus andraei* (see ALVIN, 1953). Above the seeds the broad vascular band breaks up and eventually produces a large number of small bundles (text-fig. 2, B and C). The attenuated strands have flat or almost flat phloem faces unlike those of *Pinus* and of the pine-like species of *Pityostrobus*.

The ground tissue in the horizontal part of the scale, apart from a small region just beneath the vascular strand, is composed almost entirely of thick-walled cells which are isodiametric in the central region, but narrower and elongated elsewhere. In certain specimens the walls of these cells appear to be composed of two distinct layers; a very thick, rather spongy-looking and vaguely pitted inner layer (*iw*), and a thin outer, more compact layer (*ow*) which has in places separated from the inner (text-fig. 2, F). Middle lamellae are not visible, but small intercellular spaces occur. This kind of cell or cell preservation has been found not uncommonly in these fossil cones; it is met with in the outer part of the cortex in this species and again in *Pityostrobus villerotensis* and *P. corneti* (see ALVIN, 1953). In the case of one of the severely abraded cones (Pl. I, fig. 4), the cells in the same part of the scale have a somewhat different appearance; their apparent walls are homogeneous and rather thinner, but most of them contain a ring of more diffuse substance which may well represent the shrunken innermost layers of wall material (Pl. I, fig. 14, upper part). In figure 13, plate I, which shows part of a section of a scale from the same cone as that from which text-figure 2, F was drawn, a rather mixed and intermediate condition obtains, suggesting that there is no fundamental anatomical difference between the two types. Comparison with the appearance of the cell walls in sections through partially decayed timber has led me to believe that the fossils may have suffered some decay before preservation, and that the thick-walled cells in the lower region of the scale may originally have had compact lignified walls.

In the region immediately beneath the vascular strand the cells are rather thinner-walled (Pl. I, fig. 14, bottom), and in some material have a dark reddish-brown substance lining the walls (text-fig. 2, D); they are elongated in the longitudinal direction. This tissue extends up into the erect part of the scale (dark zone in fig. 9, Pl. I) following the abaxial face of the vascular strand. Abutting on it abaxially is another distinctive tissue composed of very narrow, elongated, thin-walled cells (text-fig. 2, E) usually containing the dark substance in a solid roundish mass. This tissue (text-fig. 1, B, and 2, A and B, z) apparently replaces the abaxial sclerenchyma found in most Abietaceous cones which plays an important role in the dehiscence mechanism.

Just above the seeds the sclerotic tissue making up most of the lower part of the scale becomes distributed in three masses, two occupying the lateral scale-wings, and the third the attenuated interseminal ridge (text-fig. 2, A and B, stippled regions). These become confluent at a higher level to form a continuous band on the adaxial side. Eventually this tissue in a more diffuse form spreads round to the abaxial side replacing the tissues described above (text-fig. 2, C). The dark ground tissue containing the vascular strands in this region of the scale is a rather irregular parenchyma (Pl. I, fig. 12).

c) The Seeds. — The shape of the seeds has already been described. The testa was probably divided into three regions, but the innermost one is difficult to distinguish. The sclerotic layer varies in thickness considerably: thus, in one cone (Pl. I, fig. 1) its

thickness is about 0.2 mm (Pl. I, fig. 10), whilst in another specimen (Pl. I, fig. 4) it is only 0.15 mm (fig. 11). The thickness of the outer layer (composed of thin-walled cells with large pits) also varies, being this time thicker in the second specimen. Although the possibility that these specimens may belong to two different but closely allied species cannot be entirely ruled out, I consider it more likely that there is merely a difference in the degree of sclerification of the testa. Another possible explanation is that in one specimen the thick cell walls have swollen during the softening treatment to a greater degree than in the other. Unfortunately, preservation is such that individual cells are difficult to distinguish, but there does appear to be a difference in the number of cells occupying the breadth of the sclerotesta (approximately 7 and 5 respectively). In both cases, the testa is thicker at the angles (as seen in cross-section, Pl. I, figs. 10 and 11), and measurements were therefore made in the middle of either the outer flat side or the curved side in contact with the scale.

There is some suggestion that the thickened corners of the sclerotesta may have a rib-like organisation similar to that in *Pseudoaraucaria loppinetti* FLICHE (ALVIN, 1957), but the preservation is not good enough to say definitely.

Nor is it possible to say with certainty whether resin cavities were present in the testa. At the chalazal end there are hollows in the sclerotesta (Pl. I, fig. 9; Pl. II, figs. 4 and 5) which may possibly have contained resin; but they are usually empty and devoid of any of the yellowish material often found inside the resin canals. There is some suggestion of a tissue of thin-walled cells at the chalazal end beyond the sclerotesta, but the preservation in this region is very poor. In *P. loppinetti* and *P. major* FLICHE (ALVIN, 1957) the sclerotesta is pitted at the base in the same manner, but beyond it there is an extensive cushion of delicate parenchyma which appears to have broken down in places to form irregular cavities; but there is no evidence that these spaces ever contained resin. In *P. benstedii* (MANTELL) ALVIN (1957), on the other hand, it is almost certain that secretory cavities of some kind are present (Pl. II, fig. 7); they occur in the outer layer of the testa and occupy shallow depressions in the sclerotesta, just as they do in *Pityostrobus corneti* (COEMANS) ALVIN (1953) and also in those recent members of the family which have seed resin cavities.

As regards the seed contents, little has been preserved except the cutinised parts shown in text-figure 2, G. The nucellus in the dissected « kernel » is usually sharply pointed, and its cuticle (H) shows fairly short cells with thin outlines. In some seeds sectioned a very poorly preserved and unidentifiable cellular mass was visible apparently inside the megaspore membrane. No pollen has been found.

DISCUSSION.

Dehiscence of the cone. — In view of the rather peculiar structural features of *Pseudoaraucaria*, some brief consideration of its probable mode of dehiscence is perhaps worth while.

The commonest mechanism found amongst recent Abietaceae is that resulting in a separation of the scales by their bending abaxially so as to allow the winged seeds to escape between them. The bending is due to different degrees of shrinkage of two bands of elongated thick-walled cells in the base of the scale. In most cases (eg. in *Pinus* and *Picea*) the more resistant adaxial band is in fact the xylem, the cells of which have extremely thick walls, and the more contractile band is the larger-celled abaxial sclerenchyma. This latter is separated from the xylem by a variable amount of relatively thin-walled parenchyma. In many pines the actual opening is violent because the epidermises of abutting scales have

become, during growth, very intimately appressed and probably cemented by a resinous secretion (RADAIS, 1894), thus allowing a tension to be built up in the scale bases. In some species the scales are so firmly adherent that the cones do not ordinarily open at all (the « serotinous » type of cone of SHAW, 1914).

Another method (*Abies*, *Cedrus* and *Pseudolarix*) is for the cone to break up at maturity by the separation of the scales from the axis. The breakage is probably caused by a tendency for the scales to change their shape by the differential shrinkage of tissues as in the other members of the family. In *Cedrus* the break occurs at the extreme base of the scale which is laterally constricted and where there appears to be an abrupt change in the orientation and shape of the thick-walled cells from elongated fibre-like cells in the axial cortex to isodiametric or radially elongated cells in the scale base. In *Abies* the tissue of the cortex and scale base is relatively delicate, and according to RADAIS (1894) contracts on drying so that the scales just before they fall are held on only by their fairly slender vascular traces.

It is difficult to imagine *Pseudoaraucaria* conforming to the typical Abietaceous mode of dehiscence involving a simple bending of the scales, since a bending confined to the part of the scale above the seeds (the lower portion could scarcely have undergone any change of shape) would not have permitted the escape of the seeds. Indeed, for this to happen the upper part of the scale must have become torn either completely away from the lower or at least partly so. In the first case, dehisced cones would have had the same general appearance as the specimens shown on plate I, figures 4 and 5, and in the second case, the laminoid part of the scale would have remained attached only at its lowest point. It is interesting to note that there is a strong tendency for the scales to break in this manner both in the untreated fossils and also during the softening treatment employed in preparing material for sectioning. Although it is not impossible, it seems unlikely that incomplete cones like those shown do represent dehisced specimens, since firstly, seeds are usually still present, and secondly, both intermediate as well as more advanced stages of incompleteness are found. The mechanism leading to such a break in the scale is not easy to conceive; presumably the elongated thin-walled cells on the abaxial side might have tended to shrink on dessication thus tearing the soft tissues lying immediately adaxial to the xylem flange. The sclerotic upper extension of the interseminal ridge would probably have been left behind just as it has in softened scales in which such a break has occurred; this would be facilitated by the fact that the sclerenchyma (indicated by stippling in text-fig. 2, A and B) was discontinuous across the adaxial side.

Another possibility is of course that the scales were deciduous. There is some evidence suggesting this : firstly, the scales do separate fairly easily from the axis in some specimens, and secondly, at the somewhat constricted union the resin ducts lying around the vascular strand show inflation (text-fig. 1, G). Thus, there might very well have existed a plane of weakness at the extreme base of the scale. However, no abrupt change in the character of the tissues such as is found in *Cedrus* has been observed in the fossil. Some change of shape in the scale would probably have been necessary to effect the break as apparently in the living examples with deciduous scales, and this could, it seems, only have been an outward bending movement of the upper part of the scale.

It seems then that there are two possibilities that could result from a tendency for the abaxial tissues to shrink upon dessication : either the upper part of the scale could be torn partially or completely away from the lower, allowing the seeds to escape, or else the whole scale could detach itself from the axis. Both possibilities assume that the abaxial tissues which, it must be remembered, are fairly delicate, were strong enough to overcome

the resistance of the xylem flange and the adaxial tissues. There is of course no means of determining this, but it is interesting to compare the change of shape in softened scales with the similar change observed in fossil cones which have the normal thick-walled abaxial tissue.

Comparison with living conifers. — Although the general organisation of *Pseudoaraucaria* with its more or less free bract and ovuliferous scale carrying two winged seeds leaves no ground for doubting its affinity with the Abietaceae, it is so distinctly different from the cone of any living member of the family, mainly because of the peculiar form of the basal part of the scale, that no close relationship to any recent genus is suggested. Even its other characters, most of which, at least when taken separately, occur amongst living representatives, when taken collectively present a combination found in no present-day cone.

It is proposed to make some brief comparison with each of the nine genera living to-day. Unfortunately, our knowledge of the structure of the mature cone is scanty, and in order to supplement it I have carried out a number of brief anatomical investigations. The following comparison is based mainly upon these and also those of RADAIS (1894) and JEFFREY (1905).

Pinus. — In general appearance the fossil is closely similar to a short-coned pine of the section *Strobis* (e.g. *P. peuce* GRISEBACH). Points of resemblance are the cylindrical rather than conical shape, and the thin, non-reflexed scales with their terminal umbos, (although the umbo in the fossil is perhaps larger than that in most of the « soft » pines). The ribbed organisation of the integument which is so striking in *Pseudoaraucaria loppinetti* (see ALVIN, 1957) and which is probably similar in the other species as well, is present only in *Pinus*. But with these characters the resemblance to *Pinus* ends, for structurally the cone is quite different from that of a pine. The main differences are as follows: — (1) The interseminal ridge in *Pinus* is very poorly developed, being smaller than in all other genera. (2) The distribution of resin canals in the scale base is entirely abaxial, whereas in the fossil it is entirely adaxial. (3) The abaxial sclerenchyma, well developed in *Pinus*, is replaced by a tissue of thin-walled cells. (4) The cambia of the vascular strands in the upper part of the scale are markedly curved in *Pinus*, but flat in the fossil. (5) The vascular system of the axis is less dissected than in the fossil. (6) The « leaf-gaps » in the mature cone are scarcely continued above the insertion of the scale trace. (7) Resin ducts occur in the xylem. (8) The scale is straight.

Thus, apart from its generally rather massive structure, there is nothing but the two characters mentioned to indicate a close relationship between *Pinus* and *Pseudoaraucaria*.

Picea. — This is no more like *Pseudoaraucaria* than is *Pinus*, although (1) the bract is more comparable in size, being larger than in *Pinus* where it is minute; (2) the interseminal ridge is larger, though still small in comparison with *Pseudoaraucaria*; (3) the vascular strands towards the top of the scale have flat cambia. The main differences between *Picea* and the fossil genus are: — (1) the lack of an umbo; (2) the scales being only slightly curved at the base, so that the seeds are almost vertical; (3) the distribution of resin ducts in the scale base, which is largely abaxial; (4) the well developed abaxial sclerenchyma. The presence of resin ducts in the xylem is probably not a constant feature of *Picea*: e.g. *P. glauca* Voss, which I have examined, may lack them.

Pseudotsuga. — This small genus with its long tridentate bract and thin round scales is unlike the fossil. There is, however, a similar distribution of resin canals in the scale base.

Larix. — The cone of *L. decidua* MILLER is similar to that of *Pseudotsuga*, but there is a zone of dark resin-filled cells between the xylem and the abaxial sclerenchyma. Both the axis and the scale bear abundant hairs of which there is no indication in the fossil.

Tsuga. — Most living species of *Tsuga* have small delicate cones, dissimilar in form and structure to those of *Pseudoaraucaria*. Two points of agreement are: (1) a similar distribution of resin canals in the base of the scale; (2) vascular strands in the upper part of the scale with flat cambia (although the strands are considerably smaller than in the fossil).

Pseudolarix. — This genus, which is represented by only a single rare species, is highly distinctive, presenting a peculiar combination of characters. Unfortunately, I was able to obtain only loose, seedless scales which did not lend themselves well to anatomical study. Although structurally the scale appeared to be quite different from that of the fossil, an interesting point of resemblance was discovered in the form of the scale base. The scale is sharply bent near its base so that it joins the axis at right-angles, and the interseminal ridge, which is considerably larger than in any other living member of the family, forms, with the wing-like lateral portions, two deep hollows in which the seeds rest. The horizontal part of the scale is, however, short, and the seeds are apparently not orientated along it, but lie almost parallel to the axis.

Structurally the scale of *Pseudolarix* is peculiarly spongy and quite unlike the fossil. Firstly, the tissues themselves are soft except for a poorly developed abaxial sclerenchyma and some isolated thick-walled elements in the interseminal ridge; and secondly, the vascular tissue which is very scanty is apparently associated with large intercellular cavities. The distribution of resin ducts could not be ascertained definitely from the material available, but according to JEFFREY (1905) canals are scattered around the small vascular strands in the lower part of the scale. Further, in the gross features of the cone *Pseudolarix* is not especially reminiscent of the fossil. The cone is small and the scales, which are few in number, are sharply pointed and without umbos. The bract is of a rather different shape and has a serrate margin.

Abies. — This is unlike the fossil in most respects except that the seeds lie horizontally (although the scale is not very sharply bent) and that the resin ducts are confined to the adaxial side at the base of the scale. In one species at least (*A. forrestii*, CRAIB) the axial vascular cylinder is greatly dissected by the extension upwards of the gaps as in the fossil. In *A. magnifica*, A. MURRAY and *A. apollinis*, LINK, according to JEFFREY (1905), the cylinder is again greatly dissected, but the xylem contains conspicuous resin ducts.

Cedrus. — Here the seeds are again orientated at right-angles to the cone axis; the scale is more sharply bent than in *Abies* although still not as abruptly so as in the fossil. Two points of structural resemblance should be mentioned: — (1) The cambial sides of the vascular strands in the scale are flat. (2) The abaxial side of the scale just above the seeds is sharply divided into two zones, although the tissues themselves differ in character from those in the fossil (ALVIN, 1953).

The vascular tissue is somewhat reduced in *Cedrus* and the axial cylinder is highly dissected. Moreover, the distribution of resin canals in the scale base is entirely abaxial except for a single canal running in the small interseminal ridge.

Keteleeria. — The cones of the two species of this genus differ structurally from each other (ALVIN, 1953), but neither bears any strong resemblance to the fossil.

It will be clear that *Pseudoaraucaria* whilst having more features in common with some genera than with others, cannot be said to be especially closely related to any one of them; in fact it appears to be as distinctive in its cone organisation as any of the living genera. Unfortunately, the genera of the Abietaceae do not fall readily into obviously natural groups or sub-families, so that it is not easy to discuss the wider affinities of the fossil. However JEFFREY (1905) recognised two sections in the family which he distinguished as follows :—

Pineae	Abietae
<p>(<i>Pinus</i>, <i>Picea</i>, <i>Larix</i> and <i>Pseudotsuga</i>)</p>	<p>(<i>Tsuga</i>, <i>Abies</i>, <i>Cedrus</i>, <i>Keteleeria</i> and <i>Pseudolarix</i>)</p>
<ol style="list-style-type: none"> 1. Resin canals present in the cortex and the secondary wood of the stem, root and cone-axis 2. Cone scales persistent 	<ol style="list-style-type: none"> 1. Resin canals usually absent from the secondary wood except in the cone-axis of species of <i>Abies</i> 2. Cone scales deciduous (except in <i>Tsuga</i> and <i>Keteleeria</i>)

Exceptions to the first distinguishing character were recognised by JEFFREY in the genus *Abies*. I have found others : e.g. in *Picea glauca* and *Larix decidua* there were no resin canals in the secondary wood of the cones I examined. It has also been found that the timber of *Keteleeria* does contain resin canals. JEFFREY suggested that another difference lay in the greater thickness of the integument in the Abietae, but I do not believe this is true; in fact the converse may hold : certainly the sclerotesta is thickest in *Pinus* and *Picea*. There are, however, distinctions not mentioned by JEFFREY which may be more reliable. These are :— (1) the presence of resin cavities in the seed-coat in members of the Abietae and their absence in the Pineae, and (2) the presence of a vascular supply to the seed in the Abietae, and its absence in the Pineae. These may hold good universally, but I have no information about *Pseudolarix*.

The apparent absence of resin ducts from the xylem would suggest that *Pseudoaraucaria* might have affinity with the Abietae rather than the Pineae. Similarly, if the scales were in fact deciduous, as seems not unlikely, this too would point in the same direction. Moreover, I have reported the presence of a seed-trace in *P. loppinetti* (see ALVIN, 1957), although in other species, perhaps due to poorer preservation, no seed traces have been observed. It is unfortunate that we cannot say with certainty whether or not there were secretory cavities in the seed-coat in three species of the genus, but it is fairly clear that they existed in the fourth (*P. benstedii*).

It is by no means certain of course that the Abietae and Pineae represent truly natural groups in each of which all genera are more closely related to one another than to members of the other group. It is not even clear that they are « natural » in the sense that

they agree in a considerable number of morphological characters, for there are many similarities between genera falling into different groups in both vegetative as well as cone characters.

The following table summarises the comparison with the recent members of the Abietaceae :—

Characters of <i>Pseudoaraucaria</i>	Occurrence in living genera
Umbo present (<i>P. heeri</i>)	Only in <i>Pinus</i>
Small, simple bract	<i>Pinus, Picea, Tsuga, Cedrus</i> and <i>Pseudolarix</i>
? No resin canals in the xylem	Abietae group (with some exceptions)
Resin canals entirely adaxial in the scale base	<i>Larix, Pseudotsuga, Tsuga</i> and <i>Abies</i>
Seeds at right-angles to axis	<i>Cedrus, Abies</i> and <i>Keteleeria</i>
Vascular strands in the scale with flat cambia	<i>Picea, Tsuga, Abies, Cedrus</i> and ? <i>Pseudolarix</i>
Massive interseminal ridge	Greatest in <i>Pseudolarix</i>
Scales { if persistent	Pineae group, <i>Tsuga</i> and <i>Keteleeria</i>
{ if deciduous	<i>Abies, Cedrus</i> and <i>Pseudolarix</i>
Resin { if present (<i>P. benstedii</i>)	Abietae group
in the seed { if absent	Pineae group
Ribbed testa	<i>Pinus</i> only
Thick sclerotesta	Pineae group, especially <i>Pinus</i> spp.
Seed trace present (<i>P. loppinetti</i>)	Abietae group

Comparison with other fossil cones. — A number of other Abietaceous cones have been described from the Cretaceous which bear some resemblance to *Pseudoaraucaria* as regards external features, but as even the gross internal structure of most of these is unknown, little is to be gained from a comparison with these.

Two cones described under the name *Takliostrobus alatus* by SAHNI (1931) appear to bear some resemblance to *Pseudoaraucaria* in the form of the cone scale, the basal part of which carries two seeds which are probably embedded in it. But owing to the fragmentary and eroded nature of the specimens and the rather poor preservation, it has not been possible to determine, upon examination of the type-material in the British Museum (Natural History), whether there is a true likeness. It seems probable that the part of the organ labelled « ovuliferous scale » in SAHNI'S text-figure 13 may be merely the thick outer part of the integument (which in *Pseudoaraucaria benstedii* is very thick), and that the part labelled « bract scale » may in fact be the ovuliferous scale. The tissues are too badly preserved to enable vascular bundles to be identified with any certainty.

Some other fossil cones from the Wealden of Belgium described by COEMANS (1866) bear a close resemblance to *Pseudoaraucaria heeri*, chiefly in the form of their scales, e.g. « *Pinus* » *gibbosa*, « *P.* » *depressa* and « *P.* » *toillezi*, but until these have been studied further, no useful comparison can be made.

Genus PITYOSTROBUS NATHORST.

This form-genus was considered most appropriate for the following species, in view of the fact that the cone cannot be said to belong definitely to any recent genus of the Abietaceae, although, like several other Mesozoic species, it appears to be closer to *Pinus* than to any other.

Pityostrobus villerotensis nov. sp.

The cones described under this new specific name are not unlike some described by COEMANS (1866) as *Pinus omalii* and *P. briarti*. At first it was thought they might be identical to one or other of these species. However, examination of the type material has made it clear that this is not so.

The species is named after the chief locality (Villerot) where a great many specimens were collected.

Diagnosis. — Abietaceous cone typically 4 cm long (extremes : 2.2-4.8 cm), 1.3 cm broad (extremes : 0.7-1.7 cm); cylindrical, narrowing terminally; apex obtuse, often minutely apiculate.

Bract minute.

Scales arranged in (2 + 3) spirals; 9-15 mm long; straight; exposed part typically 9 × 3.5 mm, scarcely striated except in abraded or poorly preserved specimens where striations are prominent.

Seeds. — 2-3 mm long, 1 mm broad; wing nearly bilaterally symmetrical, 4-6 mm long, reaching only about half way up the scale; sclerotesta 0.08 mm thick.

Vascular system of the axis little dissected; supply to the ovuliferous scale and its bract united at first into a cylinder but dividing in the cortex into a simple bract trace and a horseshoe-shaped scale strand. Single row of small bundles with curved phloem sides in the upper part of the scale.

Resin canals in the axial cortex large; distribution in the scale base abaxial to the vascular tissue except for a few in the lateral parts of the scale. Canals distributed in two rows in the upper region, one lying just beneath the abaxial surface, the other in line with the vascular strands with which the canals regularly alternate.

Sclerenchyma well developed on the abaxial side at the level of the seeds. Isodiametric sclereids abundant in the upper region on both sides of the line of vascular strands.

Pollen of *Pinus* type.

Horizon. — Wealden.

Localities.

1. Villerot (clay workings at a place called Culot).
2. Hautrages.

Detailed description. — In all about fifty cones belonging to this species have been examined; of these a selection is shown on plate III, figures 2-8 to give a general picture of the variation of size and shape and the degree of preservation. Three of these cones (figs. 2, 4 and 6) are entire or almost so; others lack their basal parts.

The typical cone is more or less cylindrical in shape but tapers at both ends, usually fairly abruptly (fig. 2), but sometimes at the apical end more gradually (fig. 3). The apex

itself is sometimes bluntly pointed (figs. 3 and 8), but is usually rounded and obtuse (figs. 2 and 4-7) and often has a small terminal apiculus (figs. 4 and 6). The very short and relatively broad cone in figure 4 has been obliquely compressed but is otherwise typical.

The exposed parts of the scales are always broader than they are high. In well preserved specimens they may show faint striations but are sometimes more or less smooth. The scales in some cones however bear pronounced vertical striations (fig. 8). This seems to be due to poor preservation of the surface as a result of some abrasion or of decomposition of the superficial layers of cells to expose the ridged harder tissues beneath. The cone in figure 7 presents an intermediate condition where the surface layers are represented here and there as black patches.

The scales vary in length up to about 1.5 cm according to the size of the cone and their position on the axis; (towards the apex and base they become smaller). The scale is straight except below the seeds where the base bends inwards to the axis (Pl. III, fig. 10). The apex is usually rounded and there is no sign of an umbo. The adaxial surface resembles that in most species of *Pinus*. It bears two seeds the wings of which cover only about half the area of the scale (fig. 9). The inner surface is smooth, and the interseminal ridge extremely small and inconspicuous (fig. 11).

The cones in figures 5 and 6 were selected for anatomical study.

A n a t o m y .

a) The Axis. — The axis, although slender, is not disproportionately so in comparison with the size of the cone (Pl. III, fig. 12). The vascular cylinder (about 1 mm in diameter) is little dissected (fig. 13), for the « leaf-gaps » are very small. The cortex contains a ring of about seven large and conspicuous resin canals. I have seen no undoubted resin canals in the xylem, but the preservation is not sufficiently good to enable me to rule out the possibility of the occurrence of small ones.

The cells comprising the pith are large towards the centre, but towards the periphery they become smaller and probably thicker-walled. The cortex is composed of cells similar in appearance to those shown in text-figure 4, C which come from the abaxial tissue at the base of the scale. These are probably thick-walled cells which have partially disintegrated in such a way that the layers of wall material have separated leaving conspicuous gaps. The cells in both the pith and the cortex frequently contain the dark reddish-brown substance found so often in this material.

An interesting anatomical feature of the cone is the presence of small dark cells apparently loose around the scales, axis and seeds. These can be seen clearly in figure 13, plate III. Some of these are probably epidermal, for where two scales are in contact, two clear lines of such cells closely appressed are often visible. A strikingly similar condition obtains in the cones of some living conifers (e.g. *Pinus pinaster* ARON and *Picea abies* KARST) where the epidermal cells are completely filled with a dark, probably resinous, substance.

The vascular supply to the bract is at first united with that of the ovuliferous scale, the whole taking the form of a short cylinder in which the hollow represents the continuation of the « leaf-gap » (text-fig. 3, I and J); but further out in the cortex the parts separate into a simple bracteal portion and the usual horseshoe-shaped scale trace. In text-figure 3, A-G an acropetal series of transverse sections through the axis at the base of a scale shows the origin of the vascular traces. The bract trace is seen isolated in figure A; this is because it takes a slightly downward course through the cortex after separation from the united

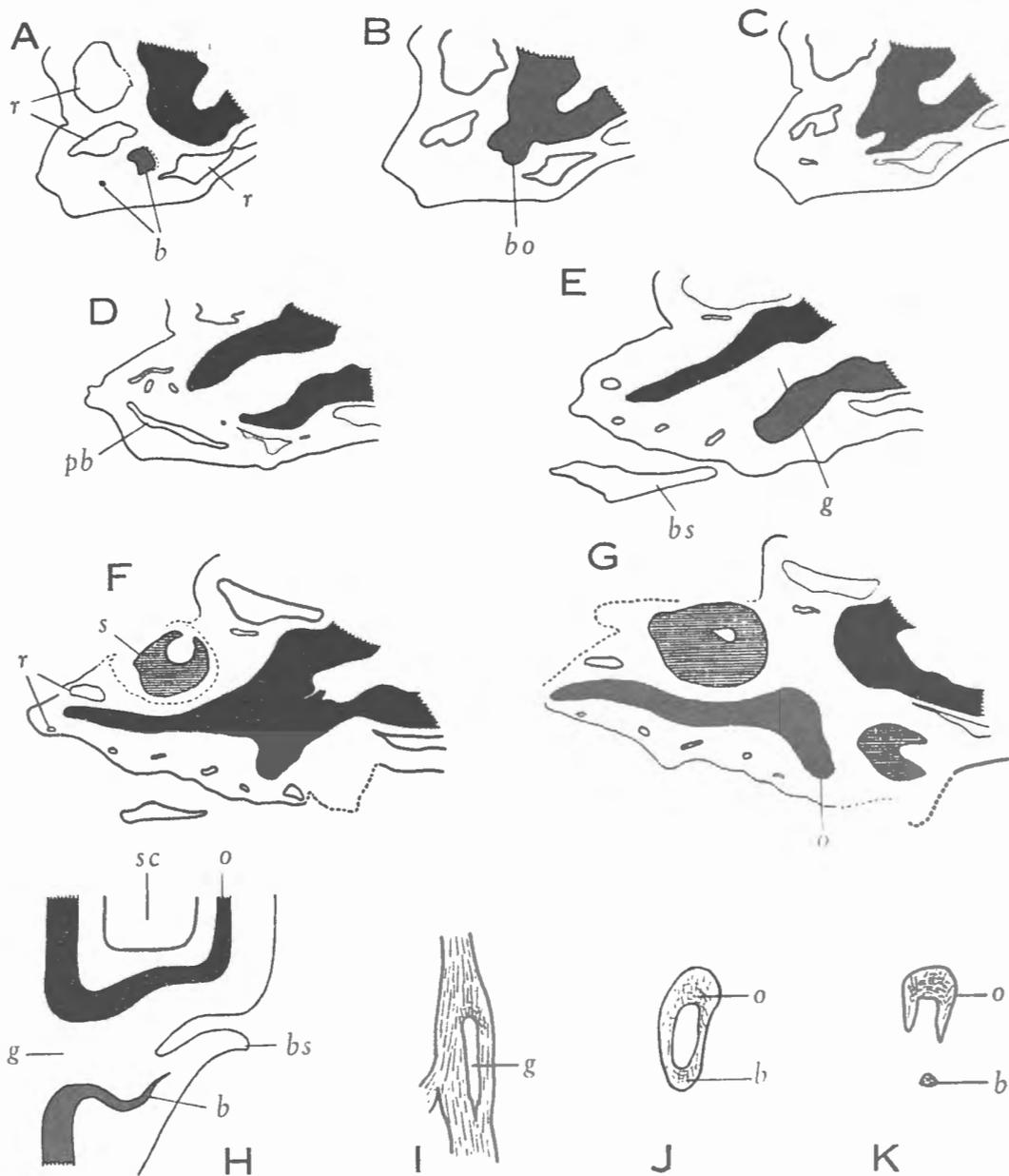


FIG. 3. — *Pityostrobus villerotensis* nov. sp.

A-G, series of transverse sections through the axis at the base of a scale showing the mode of origin of the vascular traces and of the system of resin canals in the scale. *b*, bract trace; *o*, ovuliferous scale trace; *bo*, base of combined cylinder; *g*, « leaf-gap »; *bs*, bract scale; *pb*, pocket between bract and scale; *r*, resin canals; *s*, seed. From series E3; A from section 4/6; B, 5/2; C, 5/4; D, 6/1; E, 7/1; F, 7/6; G, 8/3. $\times 20$. — **H**, median longitudinal section through the base of a scale; *sc*, seed cavity; other labelling as before. Reconstructed from series E4. $\times 20$. — **I-K**, series of vertical sections through a trace to a scale and its bract; labelling as before. From series E4; I from section 8/1; J, 9/1; K, 9/5. $\times 20$. (In I-K xylem is indicated by line shading, in others it is solid black.)

cylinder (text-fig. 3, H). In figures B and C the planes of section pass through the bottom part of the horizontal cylinder; in D and E they pass through the middle (i.e. through the « leaf-gap »); in F the top of the cylinder is reached, and in G the separated arc is seen in the scale base.

The main system of resin ducts in the scale have their origin in branches from two cortical canals. In text-figure 3, A (bottom) one such cortical canal is seen just dividing.

b) *The Scale.* — The vascular arc flattens on entry into the scale, and at the level of the seeds begins to break up into a number of small strands which become curved on their phloem sides. There are no seed traces, but two of the strands running beneath the base of the seed sometimes reunite a little further on, thus recalling a « leaf-gap ». [Cf. *Pseudoaraucaria heeri* and *Pityostrobus andraei* (see ALVIN, 1953)]. The resin canals in the basal part of the scale lie mainly abaxial to the vascular system, but there are also a few in the lateral wing-like portions (text-fig. 4, A). These have origin in the two outermost members of the row of canals in the scale base (text-fig. 3, E-G). There are no canals between or beneath the seeds (text-fig. 4, A and B). As the vascular band becomes dissected, so resin canals begin to take up positions between the derivative strands (text-fig. 4, B) where they remain throughout the upper part of the scale. Above the seeds a second series of canals arises just beneath the abaxial surface (Pl. III, figs. 17 and 18). These do not appear to be in connection with the primary series, but to begin and end blindly.

The resin ducts in the upper part of the scale are often exceptionally well preserved. Figure 19 on plate III shows a single canal greatly magnified. There is a fibrous sheath of one or sometimes two layers of thick-walled cells, and an inner layer of dark but thin-walled cells probably representing the epithelial layer.

The abaxial sclerencyma at and just above the level of the seeds is well developed and composed of thick-walled fibres (text-fig. 4, D). In some material the cell walls have disintegrated as shown in text-figure 4, C, and as a result, the appearance of the tissue is somewhat reminiscent of a greatly distorted parenchyma. The lumina, however, which usually contain the reddish-brown substance (shown stippled), assist in the interpretation.

In the upper part of the scale, stone cells are present distributed in two zones, one on each side of the line of vascular bundles (Pl. III, fig. 17). These cells which first appear just above the seeds (Pl. III, fig. 18) and become more abundant in the upper part, are angular and isodiametric (text-fig. 4, E). They sometimes show pitting. In addition to these there are some fibres distributed mainly on the adaxial side and immediately abaxial to the vascular strands (Pl. III, fig. 18). There is also a certain amount of thin-walled parenchyma.

c) *The Seeds.* — Sectioned seeds are not rewarding, but as in the case of other cones described, « kernels » consisting of the cutinised parts of the interior together with a certain amount of carbonised matter, have been removed from the whole seeds. As before, only two membranes have been found, the megaspore membrane, characteristically minutely papillate, and the cap-like nucellus cuticle showing clear but fairly delicate cell outlines (text-fig. 4, F). At the top of the nucellus in some cases a dense mass of pollen was found. The pollen is of the winged Abietaceous type (Pl. III, figs. 15 and 16; text-fig. 4, G and H). The following table shows the measurements (in microns) of twelve of the best grains found :

Diameter of body						Breadth of bladder						Height of bladder					
48	53	30
50	48	—
43	41	39

Diameter of body		Breadth of bladder		Height of bladder	
—	...	49	...	40	
50	...	68	...	44	
56	...	65	...	35	
58	...	53	...	—	
41	...	58	...	38	
56	...	65	...	—	
54	...	63	...	36	
59	...	70	...	33	
63	...	64	...	38	
Average : 53		58	...	37	

There is considerable variation from one grain to another, but this may to some extent be due to distortion. Where no measurement is given, the grain was too distorted to allow one to be made. The average size and the size of the majority of the individual grains fall within the limits given by WODEHOUSE (1935) for *Pinus*; the grains of *Picea*, *Cedrus* and *Abies* are considerably larger.

Discussion. — *Pityostrobus villerotensis* represents another example of a cone pine-like in its broad structure but distinctly different in several respects from the cone of any living species of *Pinus*.

The distribution of resin canals in the base of the scale, which has been regarded (RADAIS, 1894) as an important systematic criterion in the Abietaceae, resembles that in *Pinus monticola* DOUGLAS ex LAMBERT and *P. bungeana* ZUCCARINI possibly among several others. These species, like the fossil, have a few resin canals in the lateral parts of the scale beyond the vascular tissue, whereas most species (e.g. *P. sylvestris* LINNÉ and *P. strobus* LINNÉ) have canals confined to the tissues abaxial to the xylem band. The genus as a whole is distinguished from all others in the family in having no canals on the adaxial side in the lower part of the scale.

Regular alternation of the vascular strands with resin canals in the upper part of the scale occurs in *P. sylvestris* LINNÉ and *P. greggii* ENGLEMANN : but in most of the species I have examined, the canals are more or less irregularly scattered.

The combination of the bract and scale traces to form a cylinder in the cortex of the axis has been reported from *P. banksiana* LAMBERT (see AASE, 1915) and I have found the same condition in *P. sylvestris* LINNÉ. The union between the two traces in the fossil occurs only for a short distance, whereas in *P. sylvestris* it persists into the base of the combined appendage before the bracteal trace separates off and enters the free part of the bract. It seems unlikely that this feature is of fundamental importance, since in the young cone of *Pinus* there are always separate scale and bract strands, except sometimes near the base of the cone (AASE, 1915), and the union between the strands such as occurs in *P. sylvestris*, apparently takes place during later development, and may depend upon the size of the « leaf-gap » or the relative proximity of the primary traces in relation to the degree of development of secondary xylem.

The main points of difference between the fossil and *Pinus* are : a) the apparent lack of an umbo; b) the small size of the cone; c) the sclereids in the scale.

As regards the first of these, it must be pointed out that the umbo is notably inconspicuous in a few living pines. In *P. parviflora* SIEBOLD and ZUCCARINI, for example,

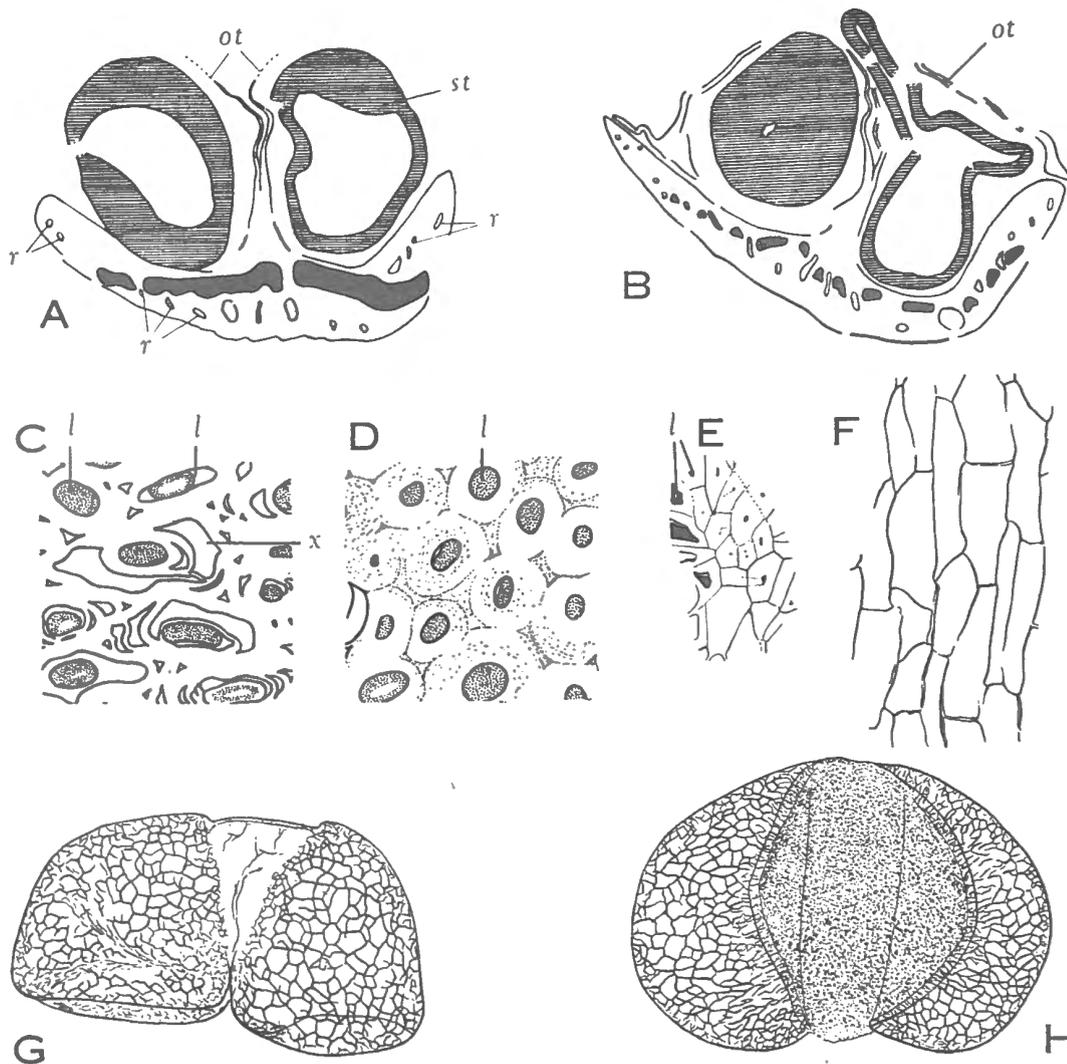


FIG. 4. — *Ptyostrobus villerotensis* nov. sp.

A and **B**, transverse sections through the base of the scale showing the ramification of the vascular system and the distribution of resin canals; *r*, resin canals; *ot*, outer layer of the integument; *st*, sclerotesta. From series E3; **A** from section 4/1; **B**, 8/1. $\times 20$. — **C**, cells from the abaxial sclerenchyma showing spaces (*x*) within the wall material; *l*, lumina. Stippling indicates dark contents. E3/10/1. $\times 325$. — **D**, cells from the same tissue in a better preserved specimen. E1/4/15. $\times 325$. — **E**, stone cells from the upper part of a scale as seen in longitudinal section. Dark contents are here shown solid black. E4/3/4. $\times 224$. — **F**, cell outlines from the nucellus cuticle. Slide E5e. $\times 325$. — **G** and **H**, pollen grains from the nucellus; that in **G** is seen in side view and is probably distorted to some extent; that in **H** is seen from the dorsal side. Both from slide E5i. $\times 715$.

the umbo does not stand out beyond the smoothly rounded or obtusely pointed scale tip, and is in fact only distinguishable by its darker colour and smoother surface. Although, therefore, I have seen no clear indication of an umbo in *Pityostrobus villerotensis*, it is just possible that there could have been one of the kind found in *Pinus parviflora*. However, other fossil species have been described as lacking umbos; among the best known of these are *Pityostrobus andraei* (see ALVIN, 1953), *P. bernissartensis* (= *P. bommeri*) ALVIN, 1953, *P. sussexiensis* (see STOPES, 1915) and *P. macrocephalus* (see DUTT, 1916). (The first and the last two of these have the thick reflexed type of scale.) It may be, therefore, that many of the early pine-like cones (including *Pityostrobus villerotensis*) were genuinely without umbos, indicating perhaps that they grew to their full size in a single season instead of the two years taken in all living species.

Although in its external form the fossil presents a general resemblance to the « soft » pines or *Haploxyton* of KOEHNE (1893) and SHAW (1914), there is no living species in this section with such small cones. *Pinus parviflora* has perhaps the smallest cones, but even there they are considerably broader, and the scales themselves are much larger than in the fossil. Amongst the « hard » pines or *Diploxyton*, however, *P. banksiana* LAMBERT has cones and scales of comparable dimensions to those of the fossil, but as with other species in the section, the cones are more conical and the scales have fairly thick apophyses with dorsal umbos. At first it was thought the fossils probably represented immature (first year) cones of a « soft » pine such as *Pinus peuce* GRISEBACH to which there is a strong resemblance, but this possibility is ruled out by the presence of mature seeds.

The outstanding structural peculiarity of the fossil is the presence of abundant isodiametric sclereids in the upper part of the scale. As far as I know, nothing comparable has been reported from any living or any other fossil pine. Although there are several species with abundant sclerenchyma in the scale, especially in the *Diploxyton*, this tissue is composed of elongated fibres like those of the abaxial sclerenchyma at the base of the scale. In the fossil the sclereidal tissue is clearly differentiated from the fibres.

Some mention should be made of the resemblance between *Pityostrobus villerotensis* and the cones of certain other living members of the Abietaceae. So striking is the resemblance to *Picea glauca* Voss, for example, that a specimen of this species was obtained and sectioned. It was found however that structurally this cone resembled that of *Picea abies* in most respects, except that the xylem lacked resin ducts. The distribution of resin canals in the base of the scale was of the pattern characteristic of *Picea* (RADAIS, 1894) and differed from that of the fossil. There is also some resemblance between the fossil and the cone of *Tsuga mertensiana* CARRIÈRE which has elongated cones. The scales and seed-wings however of *Tsuga* are differently shaped.

There are very few comparable fossil species. The resemblance to *Pinus omalii* COEMANS and *P. briarti* COEMANS is considerable, as has already been indicated. Both of these species are of the same order of size, and have a similar gross organisation. The main differences are the distinctly pointed apex, the greater height in proportion to breadth of the exposed part of the scale, and the thinner scales. *P. briarti*, of which only a single specimen is known, differs from *P. omalii* mainly in being somewhat narrower. It would not be surprising if, upon detailed investigation, these two were found to be identical to each other.

The only other fossil cone, at least amongst those that are reasonably well known, that shows any marked resemblance to *Pityostrobus villerotensis*, is that of *Pinites solmsi* SEWARD (1895). Although the structure of the cone is unknown, it is of interest because it was found attached to leafy twigs. Its external features are similar to those of *Pityostrobus*

villerotensis except that it is slightly broader, and the exposed parts of the scales are somewhat larger. It is not unlikely, especially as the cones were found attached to twigs, that they were immature and perhaps not fully grown. The twigs themselves were not strikingly like those of the living species of *Pinus*, although there were apparently needle-bearing dwarf-shoots. The unfavourable nature of the material, which was very severely compressed, made it impossible to determine the number of leaves on each dwarf-shoot, or to say whether in fact needles were not borne directly upon the long shoots.

***Pityostrobus bernissartensis* nov. sp.**

Pityostrobus bommeri ALVIN, 1953, p. 19, Pl. IV.

The author is grateful to Dr. F. STOCKMANS for drawing his attention to the fact that the specific name « *bommeri* » was used by Dr. STOCKMANS (1936) for a cone of *Pinus* from the Eocene of the Brussels district of Belgium. It is therefore proposed to change the name of the Wealden pine-like species of *Pityostrobus* to *P. bernissartensis*, a name derived from the locality.

CONCLUSION

The two cones described here add to the evidence that the Abietaceae was a well-established family in Lower Cretaceous times, and that it presented a wide range of cone-form. Like certain previously described species, they indicate that the family was represented, at least to a very great extent if not entirely, by species and genera which to-day no longer exist. Thus, *Pityostrobus villerotensis*, like *P. andraei*, *P. bernissartensis* and *P. sussexiensis*, although they show clear affinity with the recent genus *Pinus* and may indeed belong to it, do not conform in all respects to the genus as represented by the living species; for example, all four of these fossils appear to lack the umbo which is characteristic of all recent species. Certainly no recent species of *Pinus* has been shown to extend back as far as the Lower Cretaceous. As regards the other genera, we have yet no clear indication that any of them were established in pre-Tertiary times: the few well known non-pine-like fossil cones (*Pseudouraucaria* and *Pityostrobus corneti* are perhaps the best known) have no specially close affinity with any one of the recent genera, and are almost certainly representatives of extinct genera.

It is noteworthy that of the many Abietaceous cones that have been described from the Cretaceous, most of them are pine-like, at least as far as their superficial characters indicate. Whether of course all of these are structurally more like *Pinus* than any other genus, we do not at the present time know. It may however be that *Pinus* is the most ancient of the recent genera and that it was well represented in Lower Cretaceous times whilst the other living genera were not yet established. Some of the non-pine-like cones may represent species from which the other living genera later evolved.

But at the present time our knowledge of the Cretaceous fossils is not sufficient to allow us to obtain any broad view of the family as it existed at that time, for only a few isolated cones, some leaves and a number of woods are known in any detail. The rest of the material that has been referred to the family is known only very imperfectly. But there exists a great abundance of good material, and there is every reason to hope that our knowledge of the family will increase greatly in the future.

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PLATE I

EXPLANATION OF PLATE I.

Pseudoaraucaria heeri (COEMANS) nov. comb.

- FIG. 1. — Slightly abraded cone with some scales removed. $\times 1$.
- FIG. 2. — Entire cone, but probably charred. $\times 1$.
- FIG. 3. — Cone with the upper parts of the lower scales broken off. $\times 1$.
- FIG. 4. — Abraded cone with only the basal parts of the scales remaining. $\times 1$.
- FIG. 5. — A cone similar to that in fig. 4 showing the form of the scale-bases, two of which have lost their seeds. $\times 2$. (After BOMMER.)
- FIG. 6. — Scale from the cone in figure 1 showing the seeds in situ. (Umbo missing) $\times 2\frac{1}{2}$.
- FIG. 7. — Undamaged upper part of a scale showing the umbo. $\times 3$. (After BOMMER.)
- FIG. 8. — Basal part of a scale showing the bract. $\times 10$ (approx.). (After BOMMER.)
- FIG. 9. — Longitudinal section through the basal part of a scale from the cone in figure 1. Section D6/7/5. $\times 10$.
- FIG. 10. — Transverse section through the basal part of the scale. Section D4/12/5. $\times 14$.
- FIG. 11. — Part of a tangential longitudinal section through the cone in figure 4. Section D7 6/2. $\times 8$.
- FIG. 12. — Part of a transverse section through the upper part of the scale. Section D5,2/10. $\times 37$.
- FIG. 13. — Part of a section close to the one in fig. 10, showing three resin canals and the thick-walled cells of the basal part of the scale. Section D1/9/8. $\times 90$.
- FIG. 14. — Part of a similar section from the cone in figure 4, showing at the top, the thick-walled cells, and at the bottom the thinner-walled cells which lie beneath the vascular strand. Section D7/6/2. $\times 90$.
-

EXPLANATION OF PLATE II.

***Pseudoaraucaria heeri* (COEMANS) nov. comb.**

(All after BOMMER.)

- FIG. 1. — Cone showing the external features in an almost perfect state of preservation. (Specimen missing.) ×2 (approx.).
- FIG. 2. — The same cut longitudinally.
- FIG. 3. — Drawing of a dissected scale showing an intact seed-wing. ×10.
- FIG. 4. — Detailed drawing of part of the surface of a cone like that shown in figure 5, Plate I, showing the hollows in the sclerotesta. ×10.
- FIG. 5. — Drawings of seeds. ×10.
- FIG. 6. — Drawing of a scale base showing the bract. ×10.

***Pseudoaraucaria benstedii* (MANTELL) ALVIN.**

- FIG. 7. — An oblique longitudinal section through the cone showing the secretory cavities (*r*) in the testa, and the small bract (*b*). ×3.

[Photograph provided by the British Museum (Natural History), London.]

Erratum. — Fig. 7. Read : *Pseudoaraucaria benstedii* (MANTELL) ALVIN, for : *Pityostrobus benstedii* (MANTELL).

EXPLANATION OF PLATE III.

Pseudoaraucaria heeri (COEMANS) nov. comb.

FIG. 1. — Part of a transverse section through the cone-axis showing a cortical resin canal and part of the vascular cylinder and pith. Section D2/9/10. $\times 33$.

Pityostrobus villerotensis nov. sp.

FIG. 2-8. — A selection of cones. That in figure 3 is from Hautrages, the others are from Villerot. All $\times 1$.

FIG. 9-11. — Three scales showing the adaxial surface. That in figure 9 has both seeds in situ, that in figure 10 has one and that in figure 11 lacks both. All $\times 2\frac{1}{2}$.

FIG. 12. — Transverse section through the cone in figure 5, (outermost scales missing). Section E3/10/2. $\times 8$.

FIG. 13. — Central part of the same section enlarged. $\times 22$.

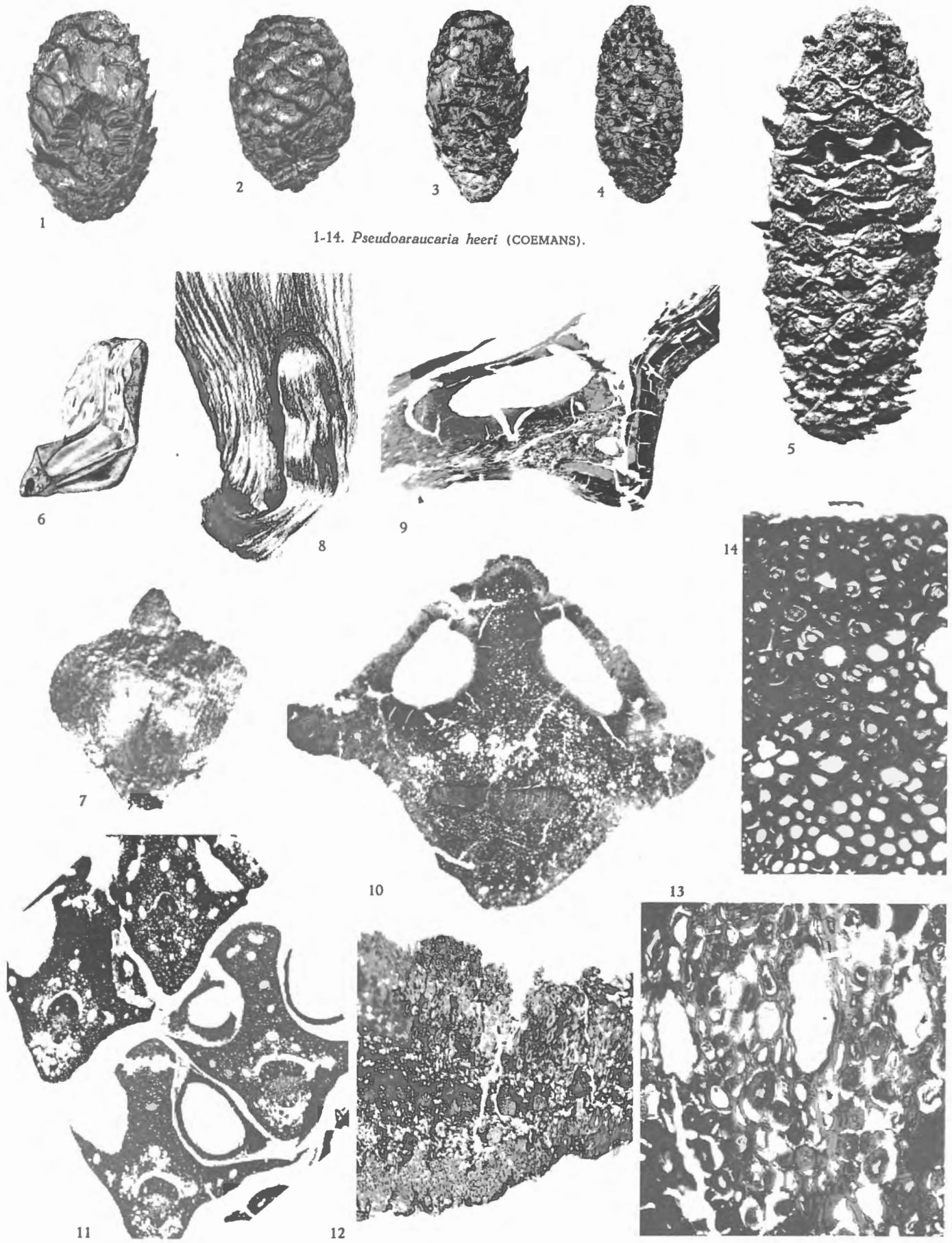
FIG. 14. — The nucellus cuticle seen from above, showing the dark central region with a cluster of pollen grains. Slide E5g. $\times 64$.

FIG. 15, 16. — Pollen grains. Slides E5j, E5h. $\times 240$.

FIG. 17. — Part of the upper region of the scale cut transversely. Section E1/8/4. $\times 43$.

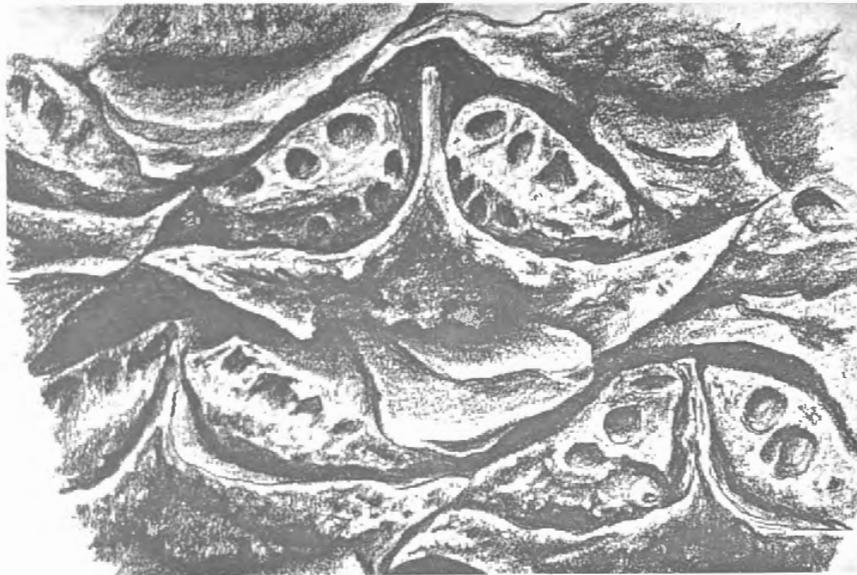
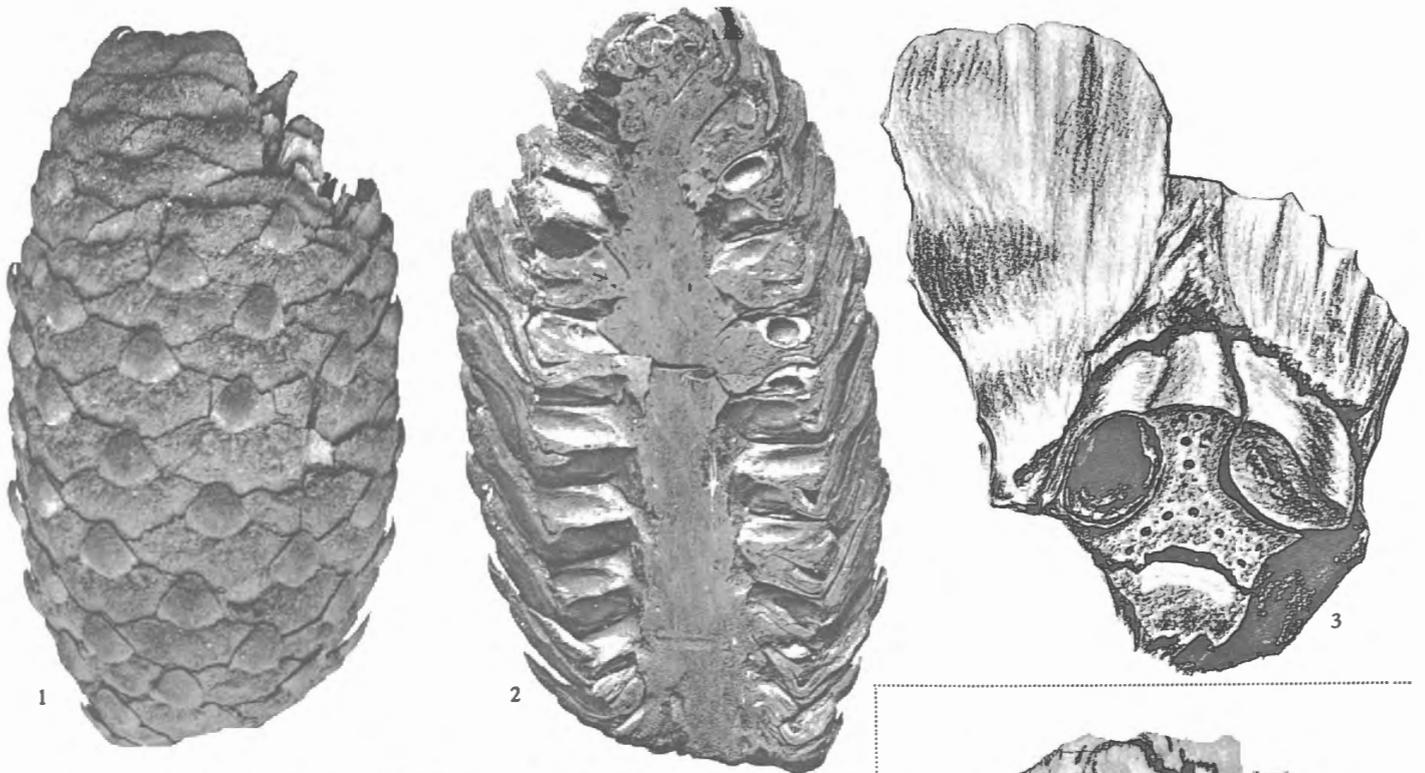
FIG. 18. — Section in the middle region of the scale. (Enlargement of part of the scale on the extreme left in fig. 12.). $\times 95$.

FIG. 19. — A resin canal from the same. $\times 350$.

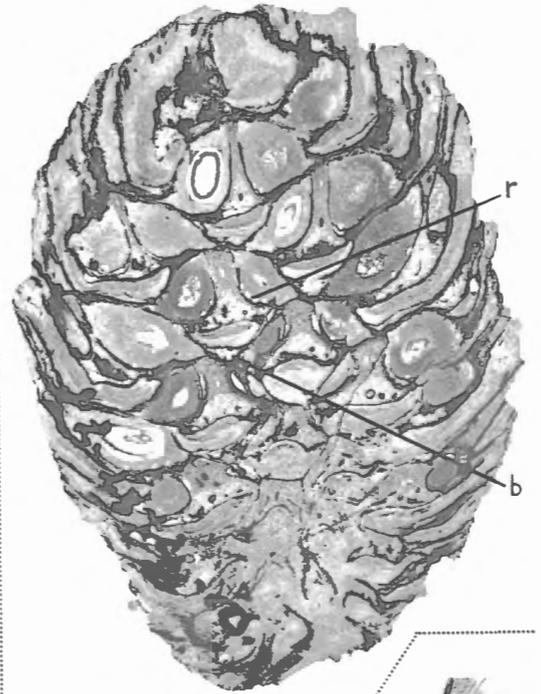


1-14. *Pseudoaraucaria heeri* (COEMANS).

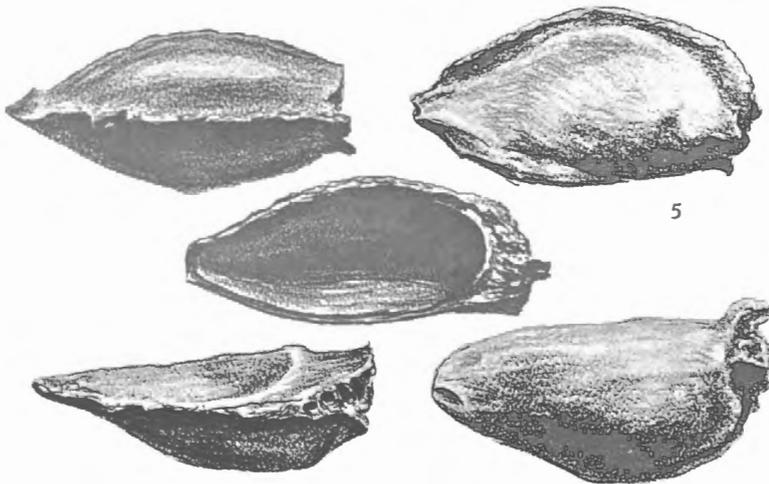
K. L. ALVIN. — On the two cones *Pseudoaraucaria heeri* (COEMANS) and *Pityostrobus villerotensis* nov. sp. from the Wealden of Belgium.



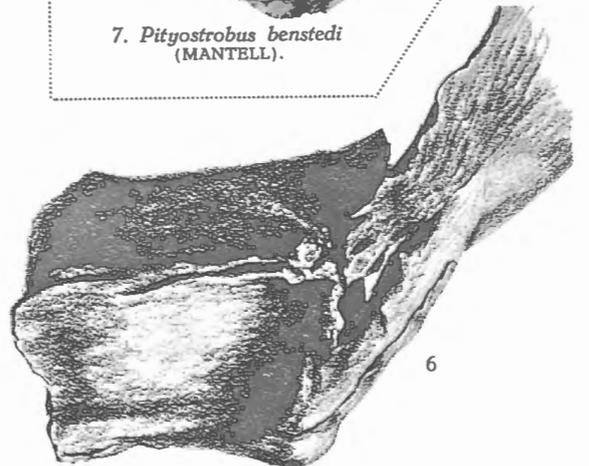
1-6. *Pseudoaraucaria heeri* (COEMANS).



7. *Pityostrobus benstedii* (MANTELL).

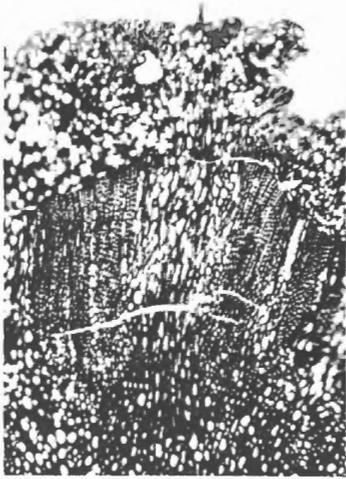


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6

K. L. ALVIN. — On the two cones *Pseudoaraucaria heeri* (COEMANS) and *Pityostrobus villerotensis* nov. sp. from the Wealden of Belgium.



1. *Pseudoaraucaria heeri*
(COEMANS).



2



3



4



5



6



7



8



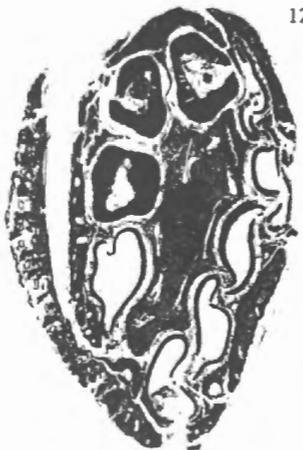
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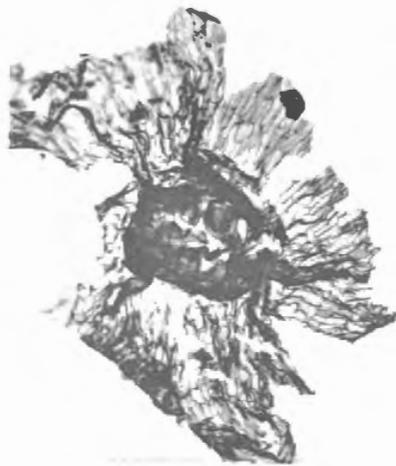
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14

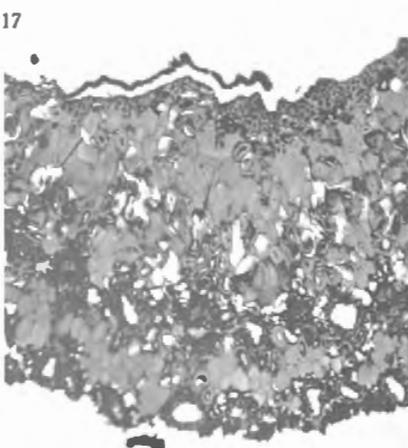


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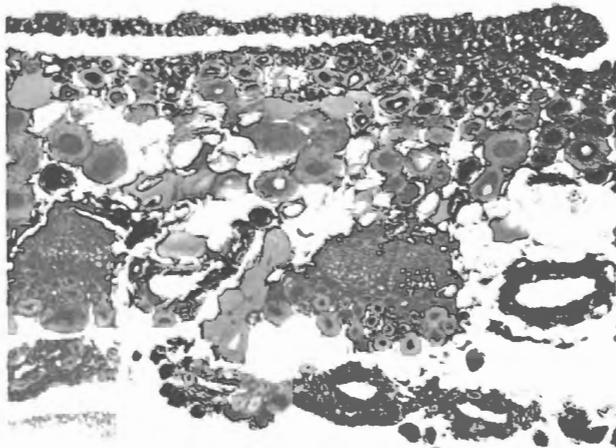


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2-19. *Pityostrobus villerotensis*
nov. sp.



17



18



19

K. L. ALVIN. — On the two cones *Pseudoaraucaria heeri* (COEMANS)
and *Pityostrobus villerotensis* nov. sp. from the Wealden of Belgium.