INTRODUCTION

The material described comes from the Wealden clays of the Hainaut district of Belgium. It represents part of an excellent collection of fossil plants (pteridophytes and gymnosperms) which were being described by the late Professor C. Bommer in the early part of the present century, and to which Seward makes brief reference in « La flore wealdienne de Bernissart » (1900). The work was unfortunately never completed, and no account except a short note on *Weichselia* was published. However, a large number of plates were prepared and printed. The figures reproduced here on plates I and II are taken from Bommer's photographs, and figures 1, 2 and 3 on plate III are from his drawings.

The fossils are preserved in clay as a kind of lignite. They are only moderately compressed, and lend themselves to detailed anatomical study. The technique employed in obtaining sections involved softening in alcoholic potassium hydroxide, embedding in celloidin and cutting on a sledge microtome. Usually the material presented no difficulty, but in the case of *Pityostrobus bommeri*, which was of a hard coaly nature, it was found necessary to control the rate of softening with the utmost care in order to conserve the internal structure and at the same time to obtain good infiltration.

The actual degree of compression varies considerably; many specimens being scarcely at all distorted, whilst others are flattened to perhaps a quarter of their original thickness. Some of the cones of *Pityostrobus corneti* have been particularly severely compressed (e.g. Pl. V, fig. 4), and there is evidence (set forth below in the section on this species) suggesting that a certain amount of lateral spreading may have occurred in the plane of compression. As far as I know this kind of distortion in plant fossils has not hitherto been reported.

The tissues themselves, although usually showing signs of having been subjected to pressure, are for the most part remarkably well preseved. Only the softest parts such as the phloem and very thin walled parenchyma have collapsed, whilst the more resistant cells have, with few exceptions, retained their original form, even at times to show details of pitting.

Of these three species of Abietaceous cones, two are pine-like in their general external and internal organisation, and the third is superficially like a *Cedrus* or *Abies* cone, but presents a combination of anatomical characters not found in either of these genera. As all the cones are isolated and there is at present no evidence on which they can be related to the associated vegetative material of leaves, twigs and secondary wood, it appears best to place them in a form-genus for cones. NATHORST's (1897) genus *Pityostrobus* is appropriate. This has no precise definition but is used for any cone showing general Abietaceous characters. It is to be hoped that a more precise classification will be possible eventually.

All the material described here forms part of the collection of the Institut royal des Sciences naturelles de Belgique in Brussels. The microscopic preparations are also in this institute.

I should like to express my sincere appreciation of the valuable assistance and advice rendered to me by Professor T. M. HARRIS, under whose guidance this work has been carried out.

THREE ABIETACEOUS CONES

FROM

THE WEALDEN OF BELGIUM

Pityostrobus andraei (Coemans) Seward.

Pinus andraei Coemans, 1866, p. 12, pl. V, fig. 1.
? *Pinites andraei* Gardner, 1886, p. 244, pl. VII, fig. 1.
Pinus andraei Fliche, 1896, p. 115, pl. X, figs. 3 and 4.
Pityostrobus andraei Seward, 1919, vol. IV, p. 388.

This species was created by E. Coemans in 1866 for some very well preserved cones from La Louvière, Belgium. He placed it in the genus *Pinus* from which it was later transferred to Nathorst's form-genus *Pityostrobus* by A. C. Seward.

The species has only twice been recorded since its erection by Coemans. A small cone was recorded by Gardner in 1886 from the Gault of Folkestone; and Fliche in 1896 described some specimens from the Albo-Cenomanian of l'Argonne. The English record cannot be regarded as well founded, since the single specimen was not sufficiently well preserved to show the characters of the scales. The French record is more satisfactory, as one of Fliche's specimens showed the typical external features; the identity of the other specimen however seems less certain.

Most of the specimens described here come from La Louvière, but some are from Houdeng-Aimeries. The species was found in great abundance in the former locality; Bommer photographed over forty cones, many of which are shown here on plates I and II.

The specimen shown on plate I, figure 1, was figured by Coemans. It is probable therefore that some of the other examples may have been amongst this author's collection.

Diagnosis. — An abundance of well preserved material has allowed a thorough investigation to be made of both the external form and also the internal structure. As a result of this study the diagnosis given by COEMANS can now be emended to the following :

Abietaceous cone typically cylindrical (but smaller specimens ovoid), length of typical specimen 12 cm (extremes 5 and 14 cm), breadth 2-3 cm.

Scales imbricated, spirally arranged, 2-3,5 cm long, 7-11 mm broad; apophysis typically with a transverse ridge just above the centre and a concavity beneath (some specimens with the ridge very near the distal margin, and a few with smooth, almost gibbous scales), margins faintly striated radially; umbo absent.

Axis 5-6 mm in diameter.

Seeds 4-5 mm long, 2 mm broad; wing typically about 10 mm long (extremes noted, 8 and 18 mm), nearly symmetrical about middle line; sclerotesta very slightly ridged, about 0,15 mm thick, with a funnel-shaped micropyle.

Vascular supply to the bract leaving the axial cylinder at the bottom of the « leaf-gap »; supply to the ovuliferous scale horseshoe-shaped, departing at the top of the gap. Single wide vascular strand at the base of the scale dividing at and above the level of the seeds to form about 12 small strands which turn abruptly outwards and end in the transverse ridge.

Sclerenchyma at the base of the scale massive on the abaxial side, diminishing above the seeds. Groups of thick-walled cells present in the cortex of the axis.

Resin canals in the cortex of the axis and probably also in the wood; canals dilating markedly on entry into the scales, confined to the abaxial sclerenchyma in the basal region, and at higher levels probably distributed throughout the ground tissue, some of them dilating to form conspicuous cavities.

Detailed description : External form. — The remarkable range of size and form exhibited by this large collection of cones is adequately represented on plates I and II. Many of the specimens are incomplete, so that their true length cannot be determined. Considering only those that are more or less entire, we find that the length varies from about 5 cm to about 12 cm (Pl. I, fig. 1), but COEMANS recorded the maximum length as 14 cm. The diameter is usually between 2 and 3 cm, although badly abraded specimens may be slightly narrower.

In shape the cone is almost always cylindrical, but tapers distally, usually rather abruptly, to either an obtuse or pointed apex. The base may be drawn out into a narrow neck-like region bearing small scales (Pl. I, fig. 5 and Pl. II, fig. 2), or it may be more truncate (Pl. I, fig. 3). In the shorter cones the cylindrical form is often lost, and the outline may then be more or less ovate (Pl. I, fig. 3 and 9). The marked curvature, especially towards the base, of some of the specimens probably indicates a pendant habit; the elongated pendant cones of recent species of *Pinus* such as *P. lambertiana* DOUGLAS and *P. wallichiana* JACKSON are very frequently curved in a similar manner. Erect cones of comparable size are rare in recent pines, but occur in *P. koraiensis* SIEBOLD and ZUCCARINI and appear to be typically straight.

The arrangement of the scales is clearly spiral, and may be described as either (5+8) or (5+3), since there are 5 spiral ranks running in one direction and 3 or 8 in the other. These numbers, it will be noticed, are members of the familiar series 1, 2, 3, 5, etc. In about half the specimens, the five row system forms a right-handed spiral, and the three- and eight-rows systems left-handed ones (Pl. I, fig. 1). In the rest the directions are reversed (Pl. I, fig. 2). It has been found that the same variation occurs in the cones of a least some living conifers, e.g. *Pinus wallichiana* JACKSON.

The appearance of the apophysis of the scale varies considerably. Although much of this variation is probably due to bad preservation of the surface, there are genuine differences of form. The transverse ridge which in the typical *andraei*-type exists as a curved or V-shaped elevation just above the middle of the exposed portion (Pl. I, fig. 1, 2, 6, 7, 8 and 10; Pl. III, fig. 5), in some cases occurs very near the distal margin of the scale (Pl. II, fig. 8 and 11). An intermediate condition is seen in the specimen in figure 6 on plate II. The apophysis below the ridge is usually concave, but occasionally this feature is not prominent. In the better preserved cones (e.g. Pl. I, fig. 6) faint radial striations can be seen round the edge of the apophysis especially above the ridge.

A proportion of the cones figured do not show the transverse ridge typical of the species; in fact the apophyses sometimes merely follow the outline of the cone (e.g. Pl. II, fig. 3, 4 and 9). In such specimens the exposed parts usually bear distinct signs of abrasion or partial decomposition, often appearing rough and minutely pitted (Pl. III, fig. 7). Tiny particles of sand, which are frequently found embedded in the surface are probably directly responsible for this pitting, having been pressed into the eroded and softened tissues prior to fossilisation, perhaps while the cones were being rolled along the sandy bed of a stream. That some of the cones have been very considerably worn away there can be no doubt; the one shown in figure 3, plate II for example, is obviously badly abraded and at the same time conspicuously narrow. Such specimens as these have of course completely lost the external characters of the scales; but the cone in figure 9 on the same plate shows what is probably a less abraded condition, and the characteristic contour of the apophyses can vaguely be made out.

Several cones figured on plate II have scales of a kind which, although found frequently in this collection, is atypical of the species as defined by COEMANS. Examples are afforded by figures 1, 2, 5, 7, 12 and 13. Figure 13A which is of a cone photographed in light coming obliquely from the front shows the form very well. A single scale from such a cone is shown magnified on plate III, figure 6. The apophysis is convex except for a short, flat or slightly upturned extension at the apex. This sort of scale might very well have been derived from the type in which the transverse ridge is situated very near the distal margin, by the wearing away of most of the ridge. Specimens with this kind of scale often show the minute pitting and roughness which seems indicative of abrasion. The cone in figure 8 on the same plate presents a somewhat intermediate condition.

Finally the two specimens shown as figures 3 and 5 on plate I should be mentioned. In these, most of the scales have apophyses which are almost gibbous and quite smooth. The apex of one of the cones (fig. 3) bears signs of erosion, but otherwise they are more or less intact. They are probably either a rather peculiar form of *P. andraei*, or else represent another species very close to it. I do not think the differences warrant a detailed investigation, and they are certainly not sufficient in themselves to merit the placing of these cones in a distinct species.

In his original description Coemans gave the presence of an umbo as a diagnostic character (« Umbone centrali depresso, parum conspicuo »). He figured specimens, among which incidentally was the one shown here as figure 1, plate I, showing distinct marks on the apophyses which he called umbos. I have found nothing corresponding to these marks on any of the specimens I have examined, and in fact have obtained no evidence even suggestive of the existence of an umbo. Fliche (1896) describing two cones from l'Argonne, said of the umbo « non seulement il est peu visible, mais je suis fort porté qu'il n'existe pas ».

The scales are usually between 2 and 3 cm in lenght, but sometimes as long as 3,5 cm; they are between 7 and 11 mm broad at their widest point, i.e. across the middle of the apophysis. The adaxial side (Pl. III, fig. 1-4) is like that in *Pinus*, bearing two seeds each with a long, nearly bilaterally symmetrical wing. The scale is nearly always straight, and leaves the axis at a very acute angle. There is usually a median ridge running between the seeds and terminating at the tip of the scale. Above the seeds the surface is often faintly striated, and has a very well defined median ridge with sometimes one or two less prominent ones on either side (Pl. III, fig. 5-7).

The seed is aproximately 2 mm wide and 4-5 mm long. Coemans gave the lenght as 5-7 mm, but he probably included the thick basal part of the wing. My measurements were made from isolated seeds, and really represent the size of the sclerotic integument. The wing, although rather variable in size and in the shape of the distal end (Pl. III, fig. 1-4), is of the typical *Pinus* type.

Anatomy. — *a*) The Axis. — The axis is rather slender, being usually about 5 or 6 mm in diameter. In transverse section (Pl. III, fig. 8) the bases of the ovuliferous scales appear as broad protuberances. The axial vascular tissue is distributed in a broken ring which encloses a pith about 1 mm in diameter. It is represented mainly by secondary xylem, the phloem having collapsed, and appearing as a black structureless material on the outer side (Pl. III, fig. 16, bottom). Cracks are frequently found in the position of the phloem (Pl. III, fig. 8).

The origin of the vascular bundles supplying the appendages can be followed from the series of drawings in text-figures 1 and 2. The bract trace (*b*) which is quite small, arises from the axial cylinder leaving a gap above it (*g*). It passes obliquely upwards for a short distance through the cortex, and then turns and continues almost horizontally, finally bending slightly upwards again at the base of the accompanying ovuliferous scale (text-fig. 2D, *b*). No definite bracts have been seen either in section or externally on any piece of axis, but the presence of vascular traces leaves little doubt as to their existence. Text-figure 1G shows on the left-hand side a small triangular portion of tissue separated off from the scale base; this may represent the subtending bract, coming as it does above the point where the bract appears to end (text-fig. 1F). In one of the sections from which text-figure 2D was drawn, the bract trace seems to extend to the margin of the section, and the surface cells in this region appear very irregular as if the scale had broken off or decayed.

The vascular supply to the ovuliferous scale takes the form of a horseshoe-shaped strand arising from the axial cylinder at the top the « leaf-gap » (text-fig. 1 and 2, *o*). In transverse section (text-fig. 1) two masses of xylem (fig. 1B, o_1) are seen to emerge from the stele and at first look as if they were going to form separate strands, but before they break away from the stele they fuse together (fig. 2C) and then only does the combined mass separate off to form the scale trace. In text-figure 2 (A, B and C) which shows a series of tangential longitudinal sections through the axis, the origin of the vascular supply to the scales and the subtending bracts can again be followed; figure B shows the scale strand (o_1) on the point of departing from the axial system, the « leaf-gap » being closed except for three parenchymatous rays (*p*). It is difficult to determine whether the latter actually extend as far as the cortex, but they seem to do so in at least some instances. Thus although both transverse and longitudinal sections make it clear that the gap is not continued above the insertion of the scale trace, one or two broad parenchymatous rays may effect communication between pith and cortex in this region. It seems likely that the closure of the gap may have been due to the development of secondary xylem, and that in the young cones the vascular supply to the scale consisted of two distinct strands arising one from each side of the gap as in the young cones in most recent members of the *Abietaceæ* (Radais, 1894; Aase, 1915).

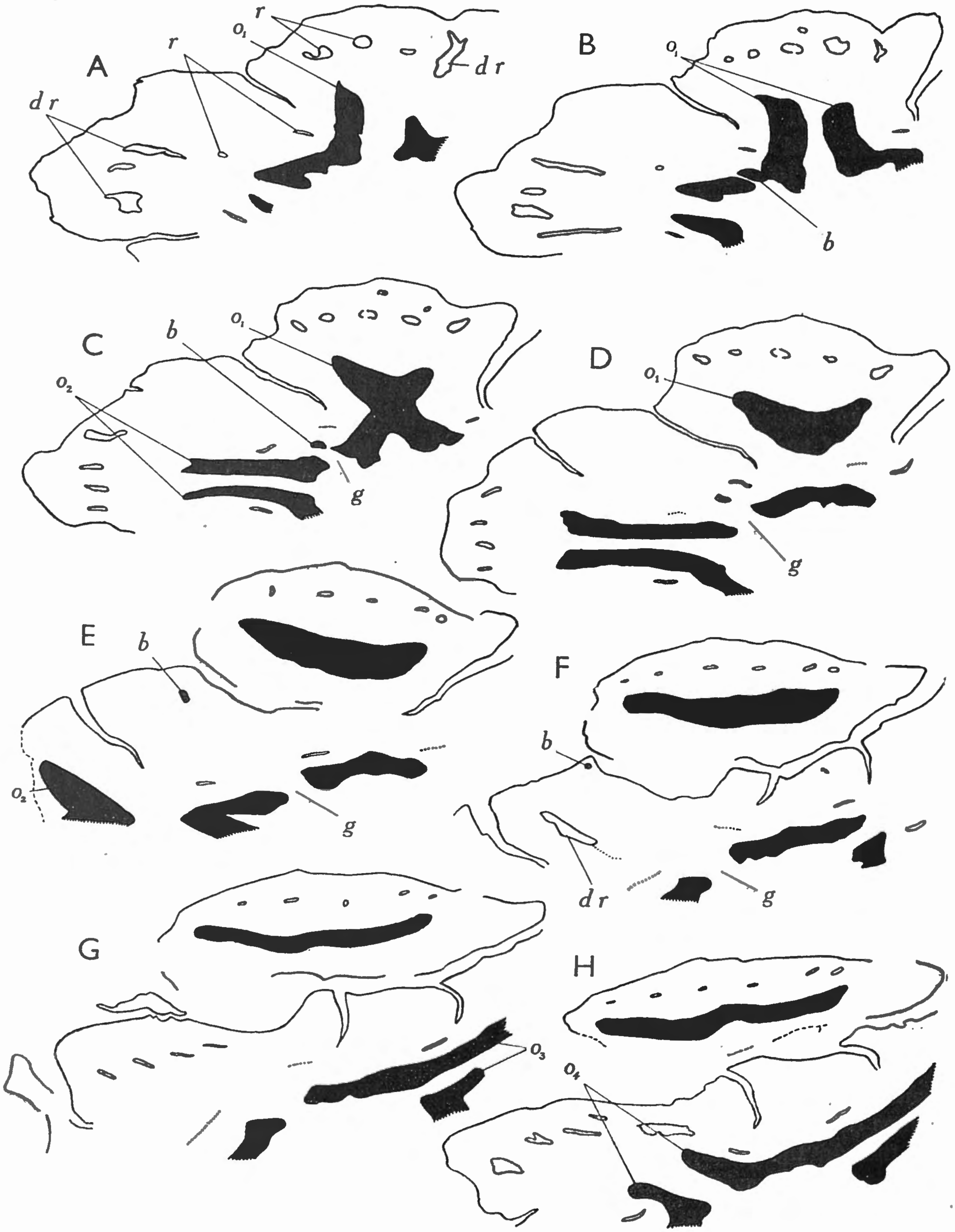


FIG. 1. — *Pityostrobus andraei* (COEMANS).

Series of transverse sections through the axis showing the mode of origin of the vascular supply to the appendages. o_{1-4}, traces to the ovuliferous scales; *b*, bract trace associated with scale trace o_4; *g*, « leaf-gap »; *r*, resin canals; *dr*, dilated canals in the bases of the scales. Indistinct cortical resin canals are indicated by dotted lines. Drawn from series A2; A from section 6/1; B, 7/2; C, 8/6; D, 9/5; E, 11/7; F, 13/1; G, 15/1; H, 17/1. All × 15.

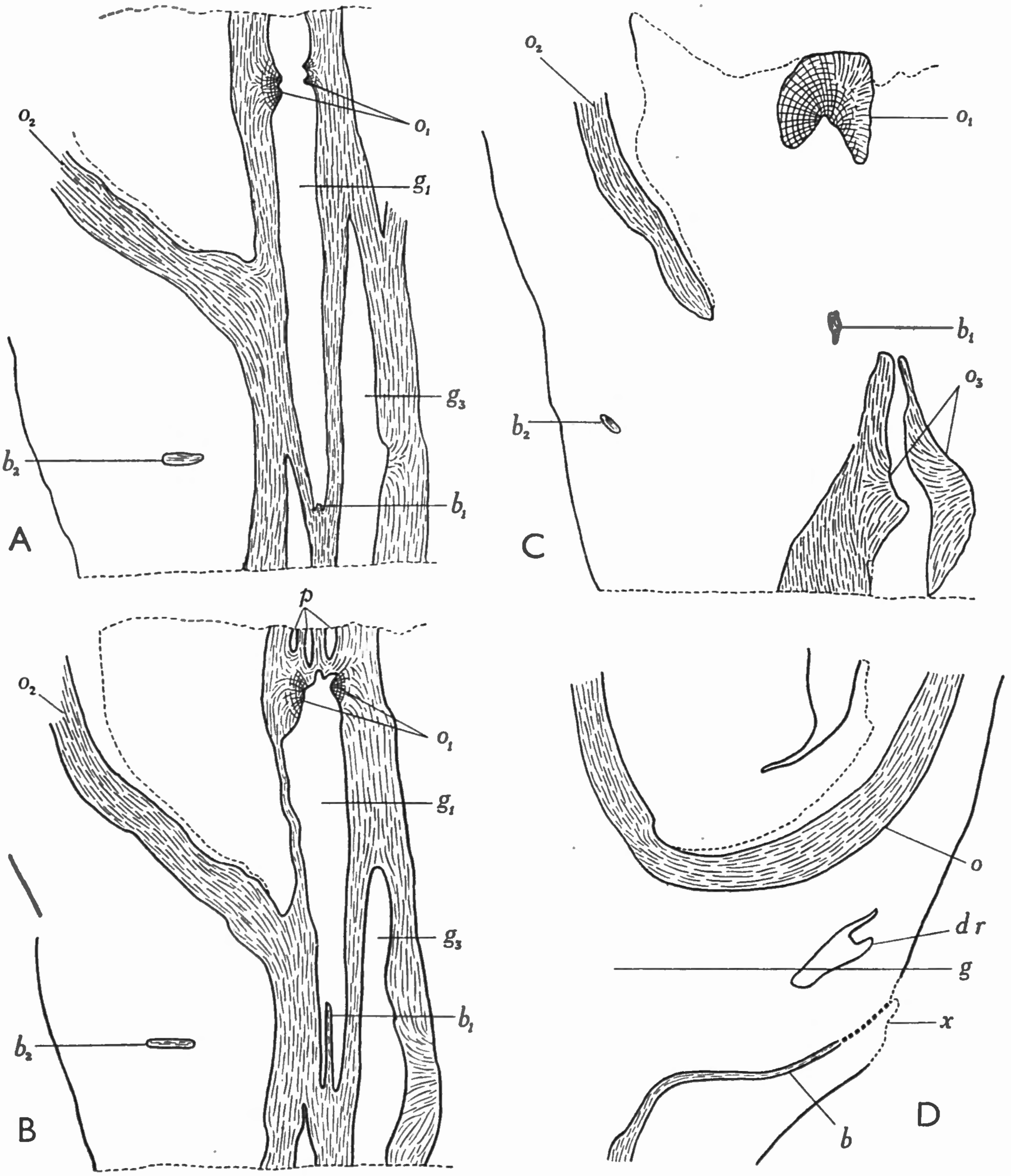


FIG. 2. — *Pityostrobus andraei* (COEMANS).

A — C, series of tangential longitudinal sections through the axis showing the mode of origin of the vascular tissue supplying the bract and ovuliferous scale. o_{1-3}, traces to ovuliferous scales; b_1, b_2, corresponding bract traces; g_{1-3}, associated « leaf-gaps »; *p*, parenchymatous rays above the scale trace. (Resin canals have been omitted.) D, radial longitudinal section through the base of a scale showing the vascular traces to the appendages; *o*, *b* and *g*, as above; *dr*, dilated resin canal; *x*, rough surface, probably the scar of the bract. All drawn from series A3. A from section 12/3; B, 13/1; C, 13/3; D is a composite drawing from sections 15/3-5. All ×15.

The ground tissue of both pith and cortex consists mainly of large-celled parenchyma, and is generally not very well preserved. The cells, which have moderately thick walls, are irregular in shape probably due, partly at any rate, to compression. They frequently contain a dark brown, semi-opaque substance. I was unable to recognise the epidermis, but the cells towards the outside are smaller and less irregular than those of the interior. This distinctive outer tissue extends inwards and downwards into the cortex at the margins of the appendages below the level at which these separate from the axis. Thus, in transverse sections groups of small dark cells are sometimes seen apparently immersed in the large-celled parenchyma of the cortex (Pl. III, fig. 11, *p*). Their appearance in longitudinal section is shown in figure 9 on plate III.

Here and there in the cortex are small groups of sclereids with very thick walls. In transverse section they appear round or oval (text-fig. 4 A; Pl. III, fig. 11, bottom left-hand corner); they are not clearly visible in longitudinal sections, but seem to be fairly short. Apart from these cells sclerenchyma is confined to the scales.

Large resin canals occur in the cortex; their distribution is shown in text-figure 1. As they are invariably more or less compressed (Pl. III, fig. 11 and 12, *r*) they are difficult to see, but their recognition is facilitated by the regularity with which they occur, and also by the fact that they usually contain a small amount of yellowish substance which is probably fossil resin. Two cortical canals are associated with each oviluferous scale; these apparently each divide into two, one part passing into the scale, and the other continuing in the axis. The appendicular branches dilate markedly in the scale base, becoming about three or four times their normal size (text-fig. 2 D; Pl. III, fig. 10). It is uncertain whether resin canals exists in the xylem of the axis, but there are rather conspicuous cavities which are strongly reminiscent of small canals (Pl. III, fig. 16).

b) The Scale. — At the base of the scale there is a single broad vascular strand lying close to the adaxial surface (text-fig. 3, A and B). The phloem is towards the upper side, being represented, as in the axis, by a black structureless material, or merely by a crack. At the level of the seeds the strand divides into three, forming a small central bundle which soon becomes V-shaped (text-fig. 3, C, D and E). The broad lateral strands then divide into two, the inner ones of which lie directly beneath the seeds. These divide again forming two small bundles which I have called the sub-ovular strands (text-fig. 3, *s*; Pl. III, fig. 17). Above the level of the seeds these strands soon reunite into V-shaped bundles similar to the central one (G and H, *su*). The parenchyma between the sub-ovular strands may therefore be homologous with a leaf-gap, although no actual seed trace departs at its proximal end. In most recent members of the *Abietaceæ*, according to Radais (1894), a small ovular strand exists, but

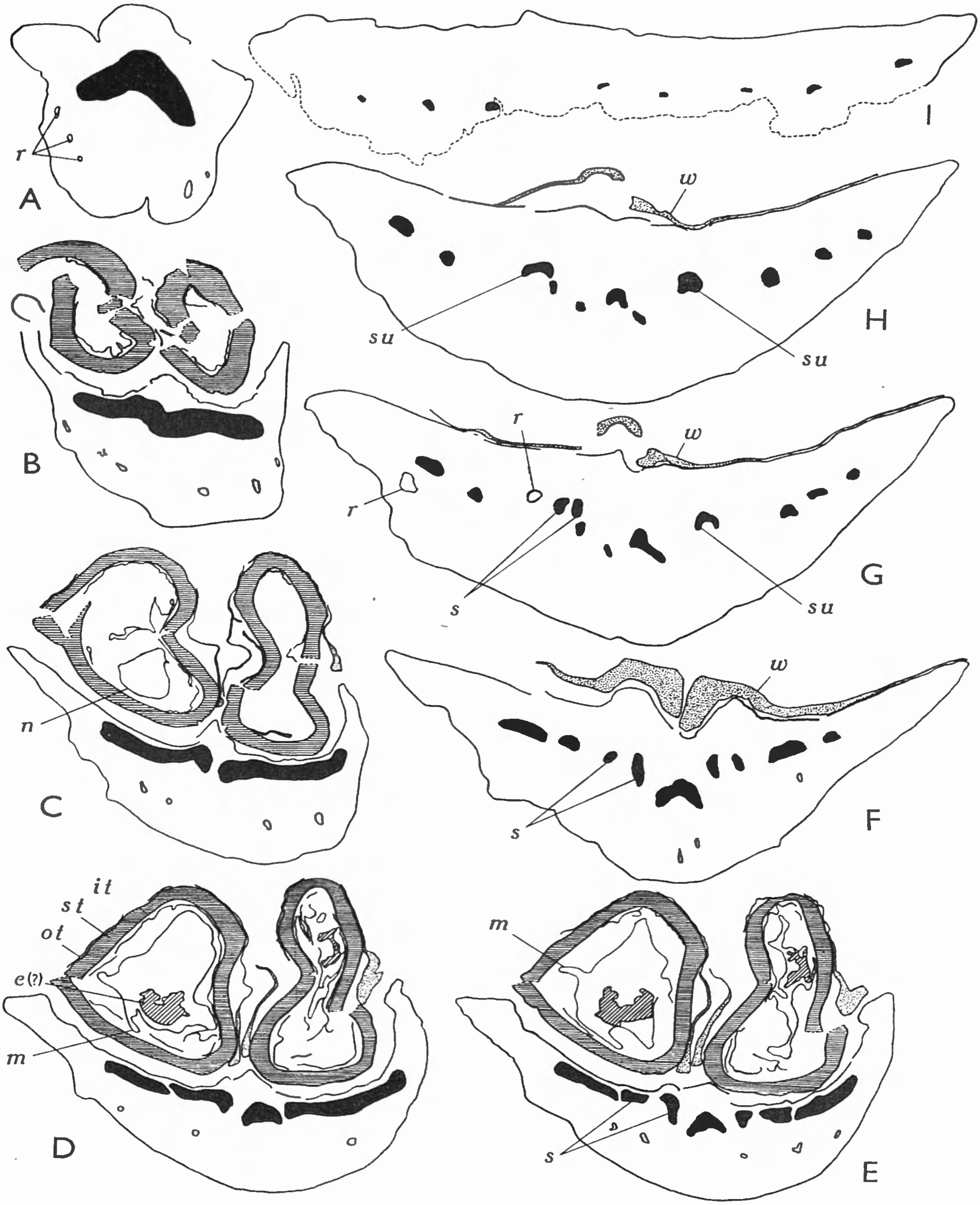


FIG. 3. — *Pityostrobus andraei* (COEMANS).

Series of transverse sections through a scale showing the ramification of the vascular bundles, the distribution of resin canals and the structure of the seeds. *s*, sub-ovular strands; *su*, united sub-ovular strands; *r*, resin canals; *ot*, outer soft layer of the integument continuous with the wing (*w*); *st*, sclerotesta; *it* thin inner soft layer of the integument; *m*, megaspore membrane; *n*, nucellus; *e*, dark body representing the remains of the embryo. The broken line in fig. I indicates the abraded outer surface of the scale. Drawn from series A6; A from section 9/3; B, 14/5; C, 18/7; D, 22/4; E, 23/6; F, 32/9; G, 38/7; H, 39/12; I, 50/13. All ×15.

except in a few instances does not actually enter the seed. In our fossil, there is at the chalazal end of the seed a definite perforation occupied by a black structureless substance (Pl. III, fig. 17), but there seems to be no vascular strand.

Further ramification of the vascular system takes place in the upper part of the scale, resulting in the formation of about ten or twelve small strands distributed in an irregular row (text-fig. 3, H and I). The strands are semi-circular in shape, the curved side being adaxial and separated from the ground tissue by a conspicuous crack which presumably indicates the position of the phloem. The ground tissue at this level contains groups of thick-walled cells some of which appear to possess bordered pits and may be transfusion tracheids; but they are thicker-walled and more scattered than is usual amongst recent pines. The mode of termination of the bundles could not be ascertained from the series of sections shown in text-figure 3, as the scale, which was from the same cone as the scale shown in figure 7, plate III, was too badly abraded; text-figure 3, I shows the vascular bundles lying very close to the worn surface (indicated by a broken line). In order to observe the destination of the bundles in the apophysis, the scale shown in figure 5, plate III was sectioned (series A7). Although incomplete at the base and devoid of seeds, it corresponded in its anatomy with the one described above. It was found that the attenuated strands continued deeply immersed in the ground tissue until the thickest part was reached (i.e. the region of the transverse ridge), where they bent abruptly outwards and ended just beneath the surface. This mode of termination supplies evidence against the existence of an umbo (the morphological apex of the scale) in the hollow below the ridge. The fact that the bundles do not converge towards the middle but end at points along the ridge suggests that the ridge itself represents the true apex of the scale, and that it did not bear a central umbo like that found in the recent « hard » pines.

The distribution of resin canals in the scale follows a similar pattern to that shown by *Pinus sylvestris*. In the basal region they are confined to the abaxial sclerenchyma, but above the seeds, where this tissue diminishes in amount, they seem to become more or less evenly distributed through the ground parenchyma; since however the latter is somewhat compressed and not very well preserved, small resin canals are difficult to detect. Sometimes broad canals appear here and there containing a small amount of substance probably fossil resin (Pl. III, fig. 13). Enlarged canals of this kind exist in the scale of *Pinus sylvestris*, often between the vascular strands.

The abaxial sclerenchyma at the base of the scale is composed of fibres a few of which are shown in text-figure 4, B and C. The walls of these cells are thick but not visibly pitted; their outlines (or middle lamellae) are usually indistinct (B), but have been thickened in drawing C for the sake of clarity. Sometimes the fibres appear to have dark contents which, in longitudinal section, is often seen localised at one end of the cell. In the part of the scale above the seeds this sclerenchyma disappears and is replaced by a small-celled tissue similar to that found in the axis in the outer part of the cortex. On the upper side, beneath the wings is a thin layer or fairly large cells with moderately thick walls.

c) The Seed. — The seeds are on the whole poorly preserved, the contents, apart from certain cutinised membranes having almost completely disappeared.

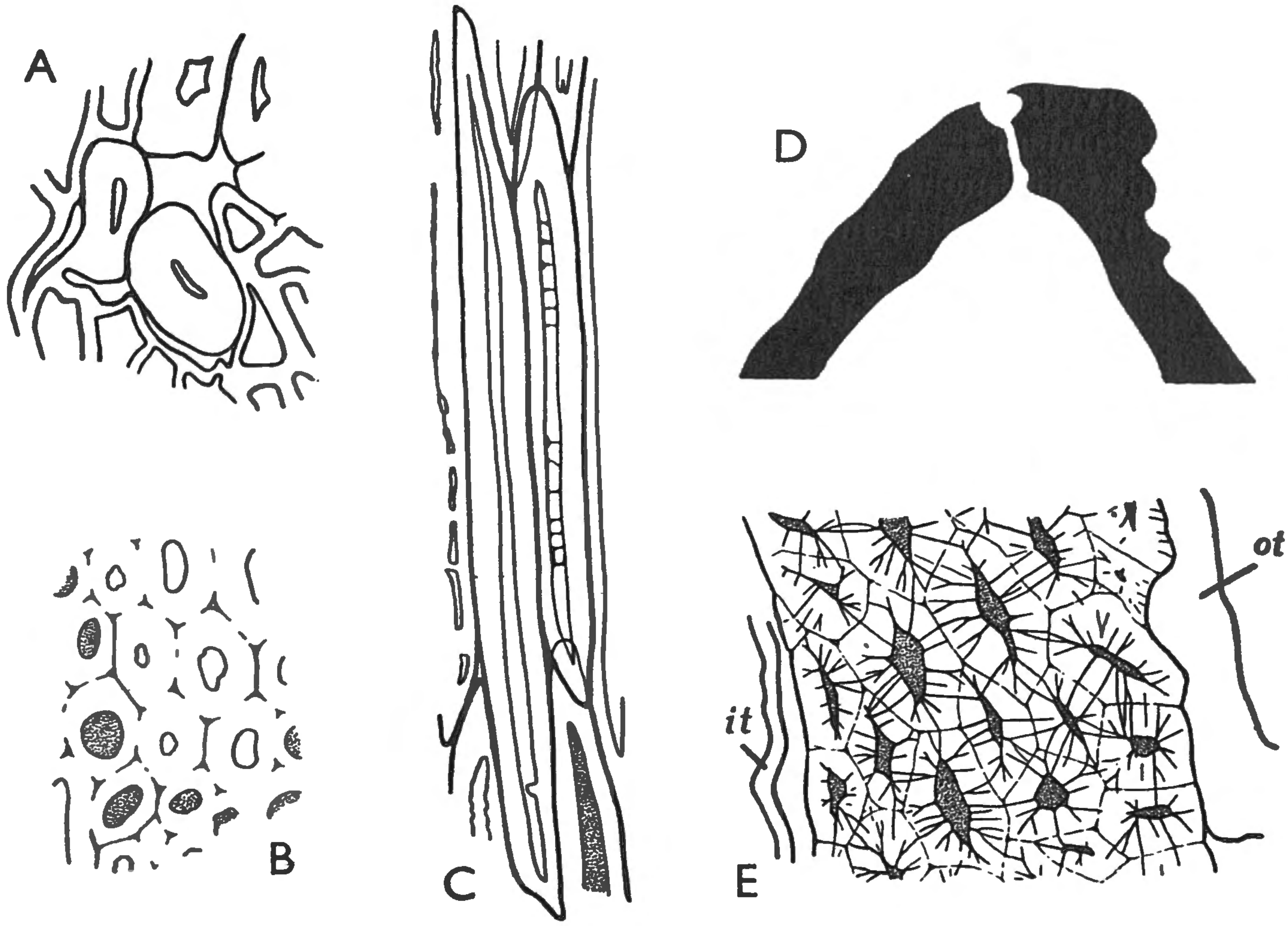


FIG. 4. — *Pityostrobus andraei* (COEMANS).

A, group of sclereids from the cortex of the axis as seen in transverse section. A2/12/3. ×325. B, fibres from the abaxial sclerenchyma of the scale as seen in transverse section, showing the thick walls without pits and the indistinct outlines. Stippling indicates dark contents. A2/11/6. ×325. C, same in longitudinal section. (Here the cell outlines have been thickened for the sake of clarity.) A3/14/2. ×325. D, longitudinal section through the micropylar end of the seed (sclerotesta only). A5/6/5. ×38. E, part of integument in transverse section. *ot*, outer soft layer; *st*, sclerotesta; *it*, inner soft layer. A6/21/8. ×325.

Although the seeds are disappointing when sectioned, a certain amount of information can be obtained by examining the contents whole. It was found that the « kernel » consisting of cuticles and a certain amount of carbonised matter, would fall out when the testa was carefully cracked open. Examination of the « kernel » under a dissecting microscope reveals two parts, a large oval yellowish membrane about a third of which is covered by a brownish cap-like one (text-fig. 10, D). The membranes are resistant to a mixture of nitric acid and potassium chlorate provided they are not left in the mixture for more than a few hours; this, followed by a weak solution of a caustic alkali removes carbonised matter and makes the membranes clearer. The oval membrane, when examined under a microscope, is seen to bear the minute papillations characteristic of megaspore membranes of gymnosperms (THOMSON, 1905). The cap-like membrane is seen to show distinct cellular outlines (text-fig. 10, C); this, by comparison with the seed of *Pinus wallichiana* JACKSON treated in a similar manner, was identified as the nucellus cuticle (text-fig. 10, B). The culticle lining the inside of the integument, which in *P. wallichiana* is easily distinguishable from the nucellus cuticle by its larger but fainter cell outlines, has not been observed.

The integument is composed of three layers as in recent conifers : a soft outermost one continuous with the wing (text-fig. 3 and 4E, *ot*), a thick middle one (the sclerotesta) consisting of stone cells with conspicuous pits, and a thin innermost layer (*it*). The cells of both soft layers have collapsed. The micropyle in the sclerotesta is distinctly funnel-shaped (text-fig. 4D). In a section of the seed the megaspore membrane can always be identified, and sometimes also can the nucellus where it is free from the integument. In the centre is sometimes found a dark amorphous object which may represent the remains of the embryo (text-fig. 3D, *e*). No pollen grains have been seen.

Discussion. — *Pityostrobus andraei*, besides being one of the most abundant of Mesozoic Abietaceous cones, perhaps presents a rather wider range of external form than most other types. Nevertheless, the degree of variation, although apparently somewhat greater than that shown by most living conifers, does not seem to be beyond the capacity of a broadly defined species; for the variable characters appear not to be correlated one with another. Further, it must be borne in mind in considering this large collection of cones, that many of the specimens have obviously been badly abraded, so that the true extent of variation may be less than one might at first suppose.

The main differences are those associated with the form of the apophysis of the scale; but these, if all specimens showing signs of abrasion are neglected, amount very largely to fluctuations in the position of the ridge. As has been pointed out, there is anatomical evidence for believing that the ridge represents the morphological apex of the scale (like the umbo in present-day pines), so that variations in its position represent different degrees of reflexion of the scale tip. In recent pines such as *Pinus armandi* FRANCHET in which there is usually a slightly reflexed apex, the actual degree of displacement varies considerably from one cone to another and also very often in one and the same specimen, being greater towards the base than at the apical end. Although there is not so much variation as in the fossil species, it is noteworthy that this kind of flexibility occurs in modern conifers.

The only specimens that are of doubtful classification are those with gibbous scales shown in figures 3 and 5 on plate I. The apophysis in these is markedly thickened but devoid of a transverse ridge except at the base of the cone where some of the small scales might be said to possess one very close to the distal margin. In other words, the tips of the scales are in the main not reflexed except at the base of the cone where they may be very slightly so. It seems to me, upon what has been said above, that such a distinction is insufficient to warrant the creation of a separate species.

From the general form of the cone *Pityostrobus andraei* falls at once into the *Abietaceæ*. Although no bract scale has been seen, it is almost certain from the small size of its vascular trace that it was poorly developed. This, together with the characters associated with the ovuliferous scale and the seeds, restricts comparison to the genera *Pinus* and *Picea*. On external characters alone the strongest resemblance is to *Pinus*, the thick type of scale with a reflexed tip occuring only in this genus. Anatomical characters, particularly those associated with the resin canals, tend also to indicate a closer affinity with *Pinus* than any other. RADAIS (1894) who made a study of the female cone in certain conifers, found that *Pinus* could be distinguished from other members of the family by the characteristic distribution of resin canals at the base of the scale. He found that canals were confined to the abaxial side, whereas in all the other genera at least some canals were to be found on the adaxial side of the vascular tissue. Another feature found to be characteristic of *Pinus* was the shape of the vascular strands in the upper part of the scale, which were markedly curved on their inner (phloem) sides. Both of these characters are typical of *Pityostrobus andraei*.

The mode of origin of the vascular bundles supplying the appendages varies little within the family, the bract trace always arising at the bottom of the gap in the axial cylinder, and the supply to the ovuliferous scale departing at the sides. Usually in the young cone there is only one strand from each side, although AASE (1915) found the number to vary in *Pinus* according to the position of the particular appendage on the axis. In the old cone the strands have combined producing a horseshoe-shaped bundle open at the bottom and closed across the top of the gap, but in some pines, e.g. *Pinus sylvestris* LINNÉ and *P. banksiana* LAMBERT, the strand becomes cylindrical due to the incorporation of the bract trace. Our fossil presents the condition typical of the *Abietaceæ* generally.

Published work on the anatomy of the mature cone in the *Abietaceæ* is very scanty, and it was considered desirable to cary out a brief investigation on a number of different types. The following ten species of *Pinus* were examined :

P. flexilis JAMES;
P. bungeana ZUCCARINI;
P. strobus LINNÉ;
P. peuce GRISEBACH;
P. monticola DOUGLAS;
P. wallichiana JACKSON;
P. radiata D. DON;
P. attenuata LEMMON;
P. pinaster AITON;
P. sylvestris LINNÉ.

Although certain minor features were found to vary from one species to another, there was on the whole remarkable constancy of anatomical construction, and there appeared to be no character of outstanding taxonomic importance. No anatomical character was found for example upon which the major sections of the genus might be separated. RADAIS (1894) gave the respective presence and absence of resin canals in the secondary wood of the axis as a character upon which the *Pinaster* section could be distinguished from the *Strobus* section, but I have found the presence of canals to be a consistent feature of all the species I have examined.

Thus, the anatomical characters of *Pityostrobus andraei*, although they confirm the gross external features in suggesting an affinity with *Pinus*, give no indication of a closer relationship to any sub-division of the genus. In its shape and form, the ovuliferous scale bears a closer resemblance to that of the « hard » pines, but on the other hand, the cylindrical shape of the cone is more characteristic of the « soft » pines.

Several other fossil cones of approximately the same geological age as *Pityostrobus andraei* have been described, but very few have been studied anatomically. As far as I know only two comparable species have been investigated in detail : *Pityostrobus sussexiensis* (MANTELL), an account of which was given by STOPES (1915), and *P. macrocephalus* (LINDLEY and HUTTON) which was studied by DUTT (1916). Both of these are externally unlike our species, being altogether larger; but the shape of the apophysis in *P. sussexiensis* was rather similar, and neither species had umbos. Their anatomy differed in several respects from that of *P. andraei*, but was still essentially pine-like. In both species for example, the resin canals at the base of the scale were not embedded in the sclerechyma, but were distributed in the parenchyma just behind; (this, incidentally, is the commoner condition amongst living pines). *P. macrocephalus* is peculiar in having only a very small amount of vascular tissue and an almost sclerotic pith.

Several fossil cones have been described which show external resemblances to *P. andraei*. SAPORTA (1877) described one from the Aptian near Havre under the name *Pinus mammilifer*, and FLICHE (1896) recorded three other examples of this species from l'Argonne. The cones are rather like our specimens with gibbous scales shown on plate I, figures 3 and 5, but are considerably stouter, being about 4,5 cm in diameter. It is interesting to note that FLICHE, after placing a certain specimen in *P. andraei*, later transferred it to *P. mammilifer;* he probably realised therefore that the dividing line was not very clearly defined. Recently BOUREAU (1948) has described in greater detail a cone belonging to this species from the Albian of Perte-du-Rhône, and has made it sufficiently clear that the species is distinct from *P. andraei*.

Pinus quenstedti HEER (1896) from the Cretaceous of Moravia is a cone of much the same size and shape as some of the specimens described here, but the transverse ridge on the apophysis apparently bore a definite umbo. The seed was larger too.

The resemblance of our cones to those of *Pinus longissima* Velenovsky (1885) as regards their diameter and the form of the scale is very close, but the length of one of the type specimens of this species is enormously greater than that of any cone of *P. andraei*, being as much as 31 cm.

Pityostrobus purvesi Stockmans (1946) is a cone whose size and external characters make it strongly reminiscent of our species; but unfortunately the specimen, which was a cast, would not allow of any detailed study. It seems not to be distinguishable from *P. andraei* on any known character.

Several other Mesozoic and Tertiary pine-like cones might also be compared with *P. andraei* (e.g. *Pinus rhombifera* Cornuel, *P. elongata* d'Orbigny, *P. parseyi* Saporta), but since they are for the most part very imperfectly known, it seems that nothing would be gained from such a comparison.

Further discussion is reserved till after the descriptions of the other species.

Pityostrobus bommeri nov. sp.

This species which seems sufficiently distinct from all other fossil cones described up to the present time, has been named after the late Professor Bommer who collected the specimens.

Diagnosis. — Abietaceous Cone, cylindrical in shape, 2-3 cm in diameter; apex almost truncate.

Scales uniformly thin, imbricated, arranged in (5+8) spiral ranks, 2-2,7 cm long, 1,2-1,4 cm broad; apex rounded with median point; both surfaces finely striated.

Bracts pointed, 1-2 mm long.

Axis 4-8 mm in diameter.

Seeds pear-shaped, 5 mm long, 3 mm broad; sclerotesta smooth, about 0,65 mm thick; wing of elongated narrow *Pinus*-type, usually about 13 mm long.

Pollen grains winged; wings about 50 μ broad at the base and about 30 μ high, with reticulate markings.

Vascular Supply to the bract leaving the axial cylinder at the bottom of the « leaf-gap »; supply to the ovuliferous scale horseshoe-shaped, departing at the top of the gap. Single wide vascular strand at the base of the scale, dividing at and above the level of the seeds to form a row of small strands which fade out near the apex.

Resin Canals in the cortex of the axis and round the edge of the pith associated with the primary xylem; canals in the base of the scale confined to the abaxial side of the vascular tissue.

Sclerenchyma, small-celled, in the lower part of the scale on the abaxial side. Sclereids, isodiametric, occurring usually in short columns in the pith.

Horizon. — Wealden.

Locality. — Bernissart (Puits Négresse), Hainaut, Belgium .

Type Material. — Institut royal des Sciences naturelle de Belgique, Brussels.

Detailed description. — The material upon which this new species is based was unfortunately rather badly broken when it came into my hands, and in fact did not include an intact cone. The three best specimens are shown on plate IV, fig. 1, 2 and 3; but in addition to these there were many fragments consisting of pieces of axis, some with scales attached, and an abundance of loose scales and seeds. Preservation is of a kind which has given the material a hard coaly texture, and rendered it extremely brittle. Although cracks invariably developed as a result of the softening treatment, cellular details were found to be clearly visible in thin sections.

In shape the cones are almost perfectly cylindrical, scarcely tapering towards the extremities. The apex is so obtuse as to be almost truncate (Pl. IV, fig. 2 and 3). They were probably of a pendant habit as is suggested by the asymmetry of the basal part; this is to be suspected from the narrowly elongated shape. The diameter of the cones is between 2 and 3 cm. The actual length cannot be determined from the material at present available, but it must, in some cases at least, have exceeded 14 cm, the length of the specimen in figure 1, plate IV.

The scales are spirally arranged in eight steep ranks in one direction and five in the other. Again it has been found, as in *P. andaei* and in at least some recent conifers, that the direction of the spirals varies from one specimen to another. In size and shape the scales are remarkably constant, but at the extreme base of the cone there occur small, poorly developed scales which are considerably shorter than the others. The scale has no thick apophysis, and the apex, which in outline is typically like that shown in figure 5, plate IV, is not reflexed; it is in fact closely similar to that of the « soft » pines (e.g. *Pinus strobus* Linné), except that it has no distinct umbo but only an apical tooth like that in certain species of *Picea*. Both surfaces are finely striated (Pl. IV, fig. 4). In general appearance the adaxial surface is remarkably like that of a pine such as *P. strobus;* the two seeds which when removed leave shallow depressions at the base of the scale, bear long wings which taper asymmetrically at their distal ends (Pl. IV, fig. 6). The seeds are larger than in *P. andraei*, and are well protected by the scales (text-fig. 6 F).

The small pointed bract scales are clearly visible on the piece of axis bearing the bases of the ovuliferous scales shown in figure 7, plate IV.

Anatomy. — *a*) The axis. — The axis, which varies in diameter from about 4 to 8 mm has a xylem cylinder about 7 mm thick, enclosing a large pith of 2-4 mm. There are two rings of resin canals, one in the cortex, and one at the edge of the pith apparently associated with the primary xylem (Pl. IV, fig. 8 and 9). No resin canals are visible in the secondary xylem.

The vascular trace to the bract departs from the axial cylinder at the bottom of the gap in the usual way. It passes through the cortex in a downward direction and turns up into the base of the combined appendage, where it appears to terminate (text-fig. 6 G, *b*). A resin canal is associated with the trace, but disappears as it passes through the cortex (text-fig. 5 A, 6 A).

Two primary strands indicated by resin canals (text-fig. 5 D and 6 A) are associated with the vascular supply to the ovuliferous scale; but the strand is actually horseshoe-shaped due presumably to the development of secondary xylem (text-fig. 6 B, *o*). This, as has already been stated above, is apparently the normal condition in the *Abietaceæ*. The « leaf-gap » is not continued above the point of departure of the scale trace (text-fig. 5 E and F). The lower part of the gap is very narrow, especially just below the level at which the primary strands to the scale (text-fig. 6 A, *po*) are inserted; this is due to the presence of two flanges of xylem (*f*) directed towards the centre of the pith, which are continued in the scale trace as two hooks at the ends of the horseshoe (text-fig 6B). Sometimes these flanges appear almost to meet so as to make the strand cylindrical (cf. *Pityostrobus corneti*). The resin canals associated with the primary strands may divide once or twice, but eventually disappear (text-fig. 6C).

The system of resin ducts in the scale is supplied by two from the cortex which divide some distance below the insertion of the appendage. The dilation of the canals on entry into the scale base is not striking in this species (text-fig. 5 B). There are no resin canals in the bract.

As regards the finer anatomical details of the axis, the most prominent feature is the presence in the pith of isodiametric sclereids which usually occur in short columns, but sometimes in irregular groups or isolated. Figure 14, plate IV shows a small part of the pith in longitudinal section, and several of these striking cells can be seen. The lumina are small and irregular, and there is a suggestion of pitting (text-fig. 6 E). The rest of the pith is made up of fairly thick-walled rectangular parenchyma. The cortex is composed mainly of rather similar parenchyma, but towards the outside the cells become narrower and more elongated. Many of the cells in both the pith and the cortex contain

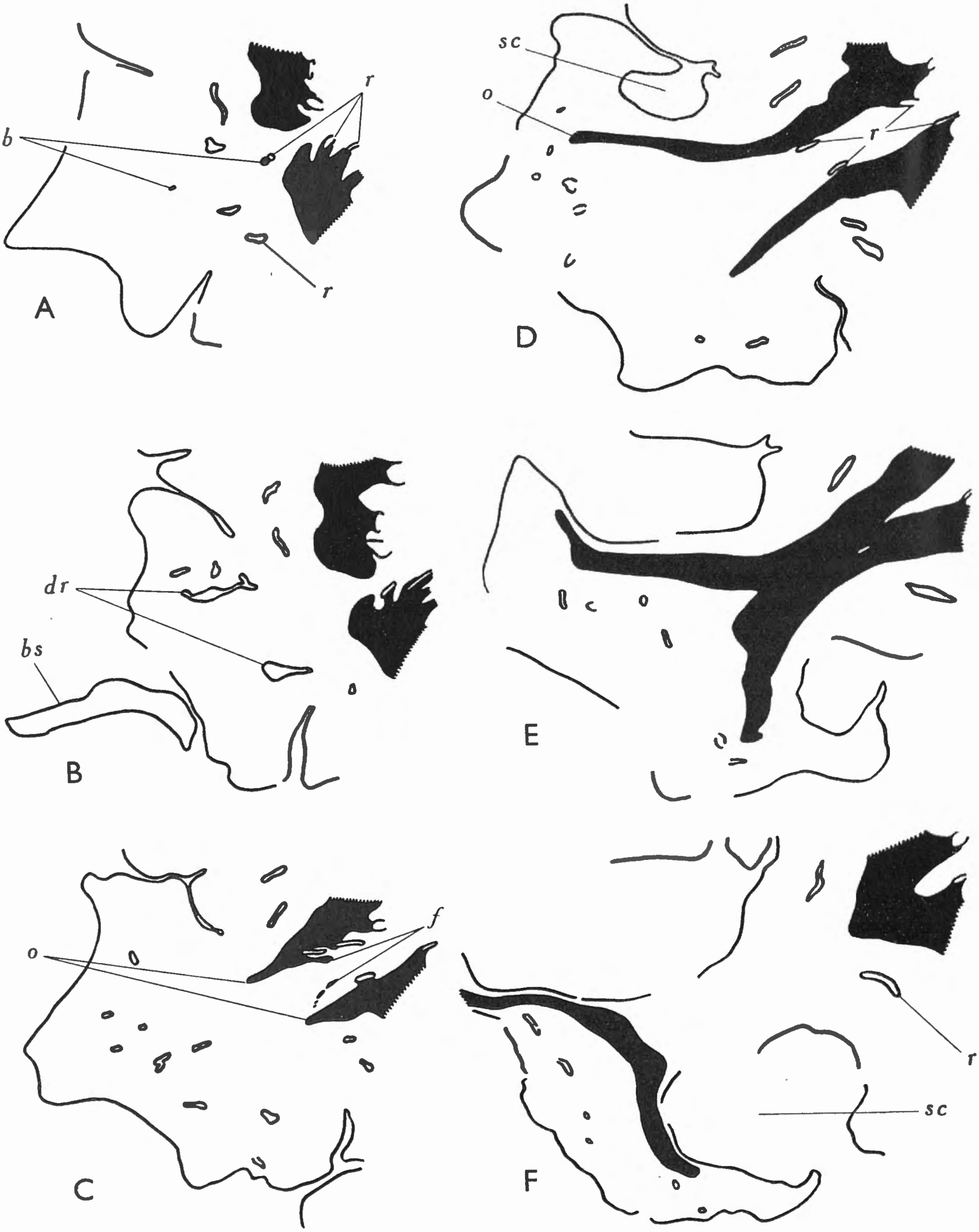


FIG. 5. — *Pityostrobus bommeri* nov. sp.

Series of transverse sections through the axis showing the mode of origin of the vascular supply to the bract and ovuliferous scale. *b*, bract trace; *o*, scale trace; *bs*, bract scale; *r*, resin canals; *f*, inwardly directed xylem flanges associated with the scale trace; *sc*, cavity left by seed Drawn from series B7; A from section 10/8; B, 11/6; C, 12/8; D, 13/7; E, 14/7; F, 15/6. All ×15.

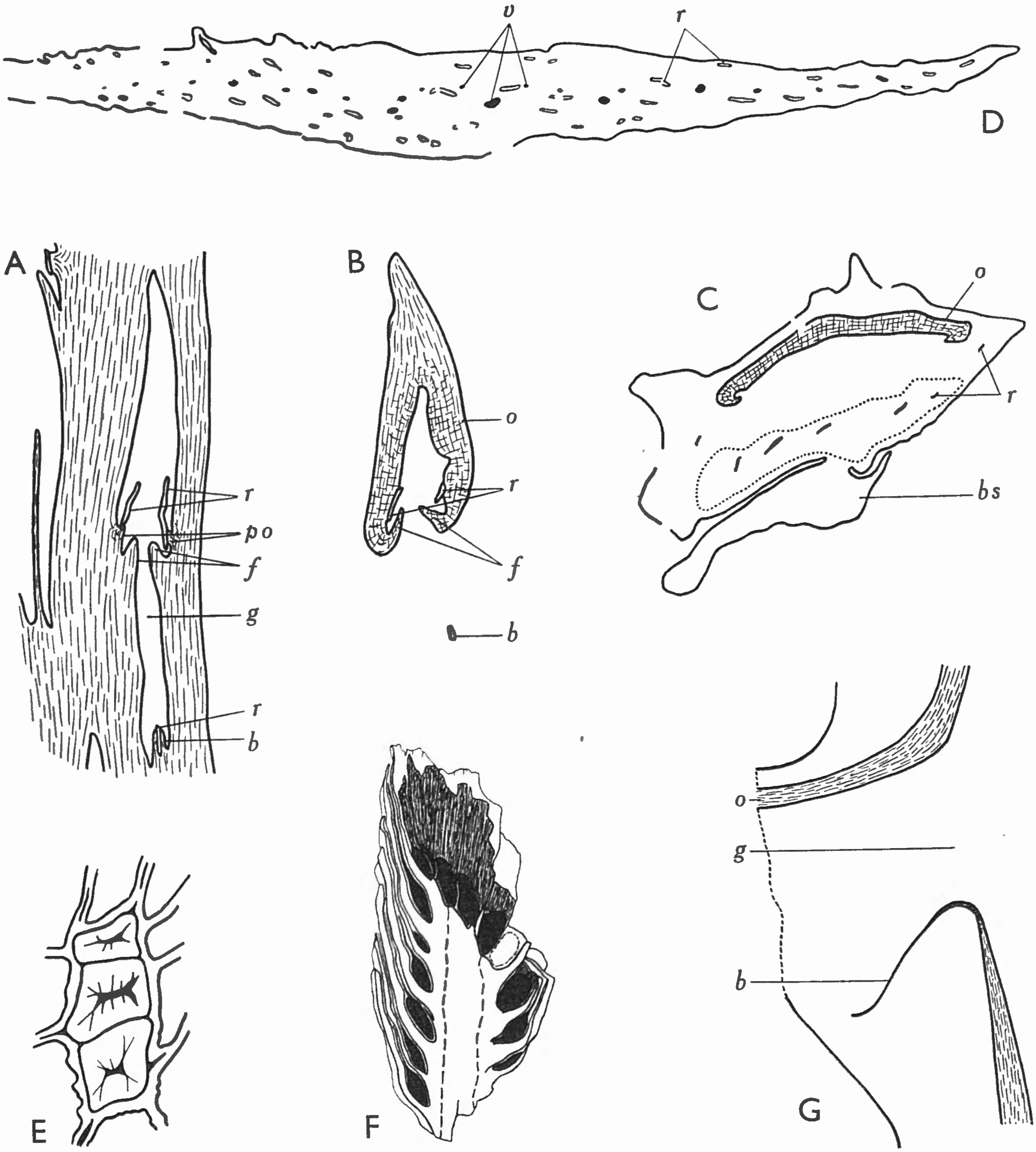


FIG. 6. — *Pityostrobus bommeri* nov. sp.

A and B, tangential longitudinal sections through the axis showing the mode of origin of the vascular traces to the appendages; (cortical resin canals have been omitted). C, vertical section through the base of a scale and accompanying bract. D, transverse section through the upper part of a scale E, group of sclereids from the pith of the axis. F, part of a cone cut longitudinally. G, radial longitudinal section through the base of a scale; *po*, primary strands to the scale; *f*, inwardly directed flanges of xylem associated with the scale trace; *g*, « leaf-gap »; *r*, resin canals; *v*, attenuated vascular strands in the upper part of the scale. The dotted line in fig. C indicates the extent of the sclerenchyma. A—C drawn from series B6; A from section 8/3; B, 7/2; C, 1/5; all ×15. D from B1/33/5; ×15. E from B6/13/5; ×325. F, ×1½. G is a composite drawing from slides B6/12 and B6/13; ×15.

a dark, almost opaque substance which may or may not be of natural origin (Pl. IV, fig. 14). It is this substance which seems to be responsible for making the tissues so hard and compact; it is especially abundant in the lower part of the scale and in the outer part of the cortex.

b) The Scale. — In structure no less than in external form the scale conforms to the *Pinus*-type. At the base, in the region of the lower part of the seeds, there is an unbroken band of vascular tissue (phloem side upwards), an abaxial block of sclerenchyma and a row of large resin canals which are at first immersed in the sclerenchyma (text-fig. 6 C) but which later emerge and run in the broad zone of parenchyma (Pl. IV, fig. 12). Above the seeds the tissues become more evenly distributed (Pl. IV, fig. 13; text-fig. 6 D); the band of vascular tissue, which begins to break up just below the upper limit of the seeds, gives rise to a large number of small bundles distributed in an irregular row, and the sclerenchyma gradually diminishes. The resin canals ramify greatly above the seeds and become dispersed in the ground tissue; some of them come to lie very close to the surface and run in what are presumably the externally visible ridges.

The sclerenchyma is composed of thick-walled, elongated cells of small diameter. Here and there are dark patches which may be islands of parenchyma (Pl. IV, fig. 12). The xylem is very compact, and made up of very thick-walled tracheids arranged in parallel rows between which lie occasional narrow rays. The phloem has become disorganised. The ground tissue in the upper part of the scale consists of fairly thick-walled cells with reddish brown contents; these become smaller towards the outer (abaxial) surface. There appears to be no distinct epidermis, the surface cells on both sides being very irregular.

c) The Seed. — The seeds when sectioned are disappointing; even the massive sclerotesta is not well preserved, and its structure, although apparently similar to that in *P. andraei*, is far from clear. Inside, the cutinised megaspore membrane is usually visible, and so also are parts of the nucellus and the inner soft layer of the integument. As in the case of *P. andraei*, it was found possible to remove the cutinised membranes from the seeds by simply cracking open the sclerotesta. These « kernels » are of a similar type to those of the last species, and some of the cell outlines from the nucellus cuticle are shown for comparison in text-figure 10 F. The cuticle lining the inside of the integument, which in *Pinus* is much more delicate than that of the nucellus, has not been definitely observed. Occasionally fragments of a very thin membrane have been seen round about the pollen mass, but these have never shown clear cell outlines.

Many of the « kernels » of *P. bommeri* were found to bear at the tip of the cap-like nucellus membrane a dark mass of pollen grains which readily separated after treatment in nitric acid + potassium chlorate followed by alkali. (The pollen mass can be seen clearly in fig. 11 on Pl. IV.) A drawing of a single pollen grain is shown in text-figure 10 E. Grains from several different seeds have been examined and found to be of the same form and size; it is therefore probably fairly safe to assume that they belong to the same species as the cones. It will be seen from the drawing that the grain is of essentially the same type as in *Pinus*, with two sublateral wings bearing distinct reticulate markings.

Discussion. — *Pityostrobus bommeri*, in its general apearance, recalls strikingly the cones of several recent members of the *Abietaceæ*, particularly those of certain species of *Pinus* and *Picea*. There is perhaps also a superficial resemblance to *Keteleeria*, but the broader scales, the relatively strong development of the bract and the different anatomy in this genus excludes the possibility of a close relationship. Anatomically, the fossil presents those characters indicated by RADAIS (1894) as being typical of the genus *Pinus* : namely, the confinement of resin canals in the basal region of the scale to the abaxial side of the vascular tissue, and the markedly curved inner (phloem) sides of the vascular strands in the upper part of the scale. (These characters have been found constant in those species listed on page 17.)

As was pointed out above, anatomical characters of the cone seem to be of little value in indicating sub-generic relationships in *Pinus*. The external features of *Pityostrobus bommeri*, however, particularly the cylindrical shaped cone and the thin non-reflexed scales, suggest a close affinity with the *Strobus* pines. It is interesting to note that one rather striking anatomical feature of the fossil, namely, the presence of a ring of large resin canals round the edge of the pith, occurs in *Pinus strobus* LINNÉ. Although a more or less clearly defined ring of canals is found in the older xylem in a number of species (e.g. *P. peuce* GRISEBACH, *P. monticola* DOUGLAS, *P. flexilis* JAMES and *P. radiata* D. DON), only in *P. strobus*, amongst those species investigated, have I found the canals protruding into the pith as they do in the fossil. *P. strobus*, however, possesses a few resin canals in the secondary xylem, and seems in this respect to differ from the fossil; but these canals are very small, and it is doubtful if similar ones would be visible in the fossil.

Perhaps the most distinctive anatomical character of *Pityostrobus bommeri* is the presence of sclereids in the pith. I have found nothing comparable in any of the species of *Pinus* I have examined, but STEINBOCK (1926) described strikingly similar cells in the pith of vegetative shoots of *P. banksiana* LAMBERT.

Another feature of some interest in the fossil is the great thickness of the sclerotesta in proportion to the size of the seeds. Amongst living pines the thickness is usually between 0,15 mm (*Pinus strobus, P. radiata*) and 0,45 mm (*P. pinaster* AITON). In *P. pinea* LINNÉ it is about 1 mm, but the seed is very much larger than in the fossil.

Although several fossil cones of the same general form as *Pityostrobus bommeri* have been described, none has been studied anatomically. Perhaps the best known species to which there is a very strong resemblance is *Pityostrobus dunkeri* (MANTELL) SEWARD which was created in 1843 for two cones from Brook in the Isle of Wight. These specimens together with some others from Tilgate Forest were later re-described by CARRUTHERS (1866). I have examined the collection of cones belonging to this species in the Natural History Museum in London, and find that they differ from the Belgian cones in being somewhat larger. Their average diameter is about 3 cm and the length of the scales is often over 3 cm. The form of the scale, very few of which remain intact, is essentially the same as in *P. bommeri*. Although there is this strong resemblance between the two forms, I would not combine them under one specific name in view of the slight differences and of the fact that nothing is known of the anatomy of the English cones.

A group of species instituted by GARDNER in 1886 were thought by SEWARD (1919) to be identical with *P. dunkeri*; they comprised : *Pinites carruthersi, P. valdensis, P. cylindroides* and *P. pottoniensis*. STOPES (1915) re-examined the specimens upon which the latter two species were based and apparently regarded them as distinct.

Several species erected by FONTAINE for some cones from the Cretaceous of America were grouped together by BERRY (1911) under the name *Abietites macrocarpus*. Although in the main they were poorly preserved, their general appearance was not unlike that of our cones.

Those species of *Pityostrobus* which have been studied anatomically are unlike *P. bommeri* in external appearance; nor do they show any special anatomical resemblance. I think therefore that little is to be gained from a detailed comparison with these species.

Pityostrobus corneti (COEMANS) comb. nov.

Pinus (*Cedrus*) *corneti* COEMANS, 1866, p. 11, pl. IV, fig. 3.

There is no doubt that the cones described here are specifically identical with COEMANS' specimens from the same geological formation in Belgium. NATHORST's genus *Pityostrobus* is considered appropriate since it is by no means certain that these cones are related to the recent *Cedrus*.

The diagnosis given by COEMANS appears to be adequate for most of the external features except the diameter of the cones; this (given as 2-3 cm, and 3-4 cm in severly compressed specimens) was probably exaggerated somewhat. The minimum diameter is not more than 1,5 cm (fig. 3, Pl. V) and only in greatly compressed (and probably distorted cones) is it as much as 3 cm. I would therefore substitute :

Diameter typically 1,5-2,5 cm, but in severaly compressed specimens up to 4 cm.

Apart from this, the following additions based mainly on an anatomical study of the cone shown in figure 3, plate V should be made :

Axis 5-6 mm in diameter; vascular cylinder 3-4 mm in diameter; pith small (1 mm); cortex with large resin canals. Vascular supply to the scale cylindrical, departing closely above the simple bract trace; « leaf-gap » between very small.

Bract extremely small, partly adherent to the base of the scale; two resin canals in the bract.

Scale with a stalk-like base making an angle of 110°-120° with the upper laminoid portion; vascular system cylindrical at first but soon giving rise to a broad strand lying towards the upper side, and dividing at and above the level of the seeds to form many small bundles; resin canals at the base probably three in number, ramifying profusely above the seeds and becoming evenly distributed through the ground tissue; mechanical cells absent from the basal region, but abundant on the abaxial side just above the seeds and becoming dispersed in the parenchyma in the higher part. Seeds lying horizontally in the cone along the stalk-like base of the scale; sclerotesta 0,4 mm thick, longitudinally furrowed; outer soft layer of the seed coat supplied with resin ducts.

Detailed description : External form. — The specimens shown on plate V, figures 1-4 give an indication of the range of cone form and size presented by the species. One of these (fig. 4) has been particularly severly compressed and has a maximum thickness of only 8 mm; it is also considerably broader than the others and has an oval rather than oblong outline. This type of cone occurs very commonly in the collection, for Bommer photographed eight others in a similar condition. It is to be strongly suspected that these cones have collapsed under severe pressure in such a way as to spread out laterally. Further evidence suggesting this is found in the scales lying at the sides (i.e. with their long axes in the plane of compression) : these are less sharply bent than scales from intact cones, the stalk-like part making an angle of about 140° with the upper laminoid part, as though this had been forced outwards, so producing the increase in cone diameter. It should be pointed out that there is no reasonable doubt that all these cones belong to one species, for the general organisation is similar in all kinds, and the very peculiar scale trace has been seen in one of the distorted specimens as well as in the small cone shown in figure 3, plate V which was used for the detailed anatomical study.

The scales, which are arranged in a close spiral, and which are imbricated so that only their broad tips are exposed, resemble closely those of *Cedrus* or *Abies*. In surface view (Pl. V, fig. 5-8) the isolated scale appears fan-shaped, the stalk-like base being set at an angle of about 110°-120° to the fan; the seeds lie along this basal part with their long axes almost horizontal. The seed wings are very thin, and in the case of the small cone in figure 3, intimately in contact with the surface of the scale. The broken line in figure 5, plate V indicates what is believed to be the outline of the wings, but they are not easily seen.

The part of the scale exposed in the cone is variable in size, being anything between 1,2 and 2,4 cm in width and 2-5 cm in height. Some of this variation might perhaps be due to spreading in the more compressed specimens since this would presumably have involved some increase in the surface area of the cone.

The bract is small and inconspicuous; its pointed tip reaches only as far as the point of inflection of the scale.

Anatomy. — *a*) The Axis. — The axis (Pl. V, fig. 10) possesses a thick, scarcely interrupted cylinder of xylem (mainly secondary) enclosing a pith just over 1 mm wide. The cortex is relatively thin, and contains a ring of conspicuous resin canals; it is usually separated from the xylem cylinder by a crack which has presumably resulted from the decomposition of the phloem.

As can be seen from text-figure 7H, the vascular strands supplying the appendages pass through the cortex in an obliquely downward direction, thus making a series of transverse sections somewhat difficult to interpret : text-figure 7 (A-E) shows such a series. In A the bract trace (*b*) can be seen on the inside of the accompanying ovuliferous scale trace (*o*) as it passes into the appendage. Figure B is drawn at a slightly higher level where the bract trace unites with the axial cylinder. It will be noticed that the « leaf-gap » left by the departure of the bract trace is very small in both width and height (text-fig. 7, C, D and F, *g*). The supply to the ovuliferous scale is of an unusual type being completely cylindrical (text-fig. 7, A, B and C, *o*); in figure D, which is at a level a little above the point of separation, it can be seen as a loop-like extension of the axial cylinder; just below this the sides of the loop break and close over to form a ring. Presumably the phloem, which is not preserved, existed as a continuous layer round the outside of this trace, but it may have been thicker on the upper (adaxial) side as is indicated by the crack (*c*) shown in text-figure 7, G.

The precise mode of origin of the resin ducts supplying the scale is not clear because of the poor conservation of the softer tissues. Nevertheless, it appears that two cortical canals play a prominent part; these, shown in text-figure 7G, r, seem to give off single branches which subsequently run laterally to the vascular cylinder in the base of the scale (text-fig. 8A, *r*). There is a suggestion that a third canal may enter the scale from above and run in a median position on the adaxial side. The origin of the two canals in the bract has not been ascertained.

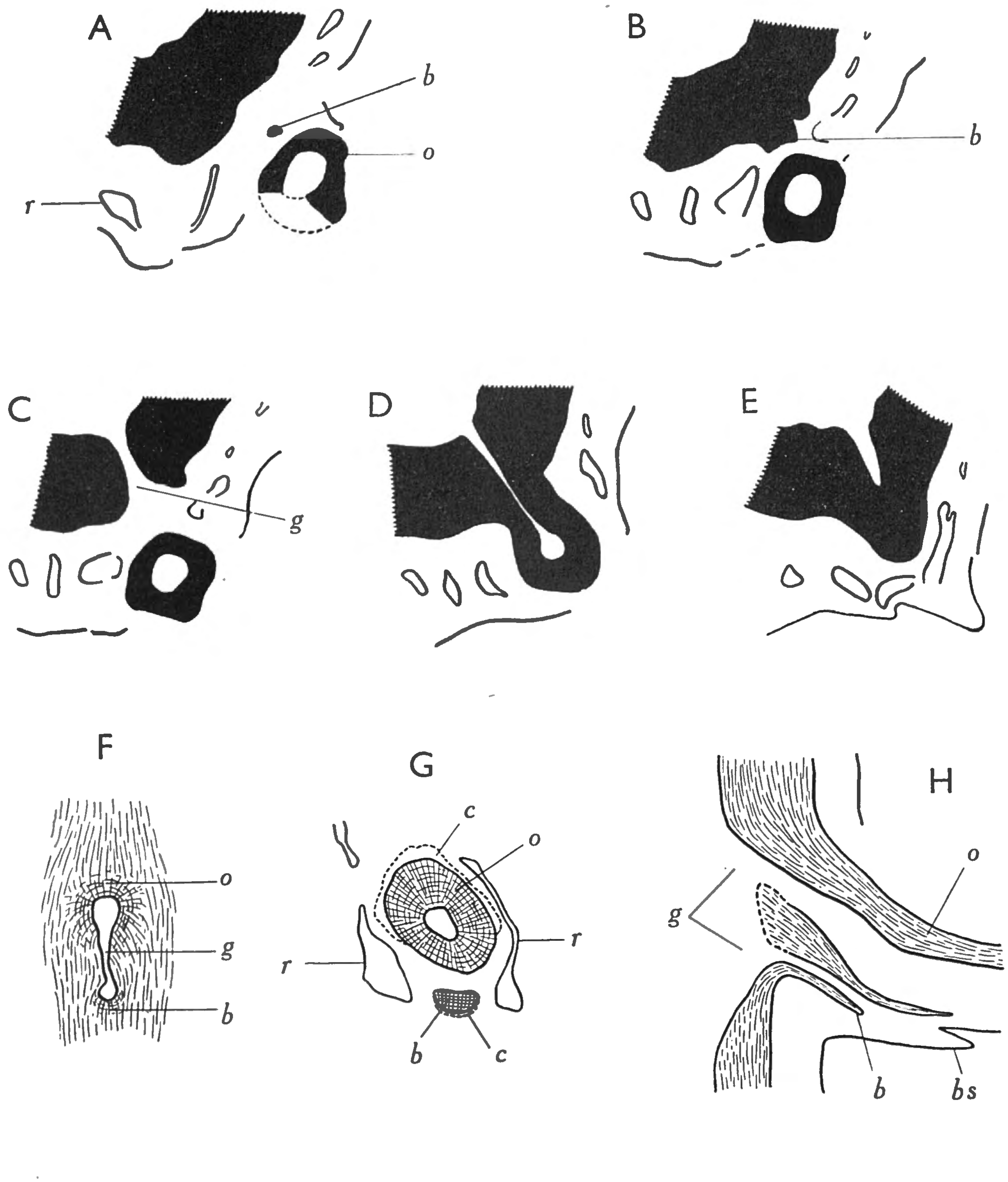


FIG. 7. — *Pityostrobus corneti* (COEMANS).

A — E, series of transverse sections through the axis showing the mode of origin of the vascular supply to the appendages. F and G, tangential longitudinal sections through the axis. H, radial longitudinal section through the base of the scale. *b*, bract trace; *bs* bract scale; *o*, ovuliferous scale trace; *g*, « leaf-gap »; *r*, resin canals; *c*, crack probably indicating the position of the phloem. A — E drawn from series C2; A from section 4/5; B, 6/3; C, 6/7; D, 7/7; E, 10/2. F — H drawn from series C4; F from section 5/1; G, 8/2; H is composite from slide 14. All ×15.

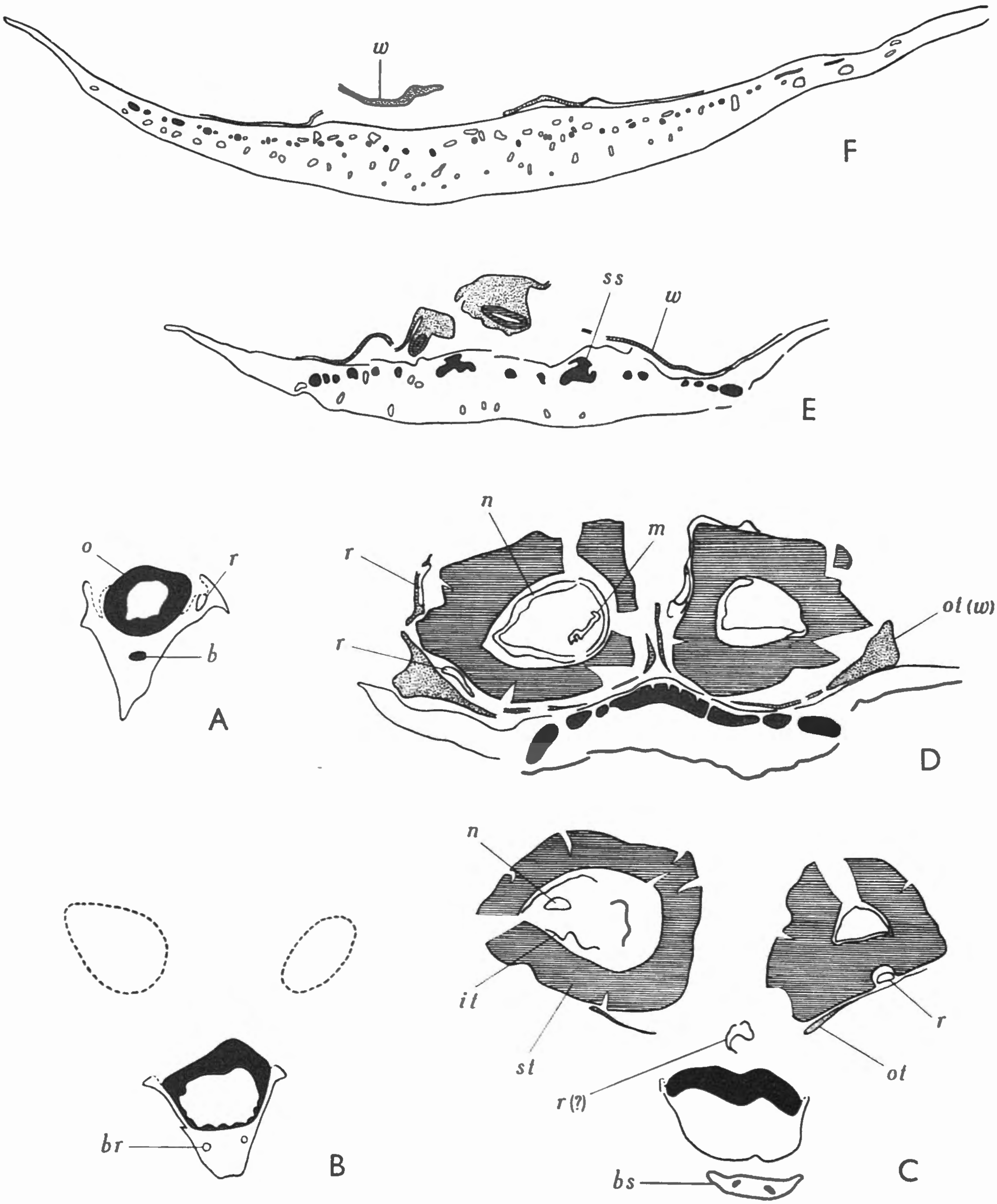


FIG. 8. — *Pityostrobus corneti* (COEMANS).
Series of transverse sections through a scale showing the ramification of the vascular tissue, the distribution of the resin canals and the structure of the seeds. *b*, bract trace; *bs*, bract scale; *o*, vascular supply to the ovuliferous scale; *ss*, vascular supply to the seed; *r*, resin canals; *br*, resin canals of bract; *ot*, outer soft layer of the integument continuous with the wing (*w*); st, sclerotesta; *it*, inner soft layer of integument; *n*, nucellus; *m*, megaspore membrane. (The seeds have been displaced slightly in softening.) Drawn from series C1; A from section 1/7; B, 4/4; C, 7/2; D, 14/1; E, 19/10; F, 26/9. All ×15.

The cells making up the ground tissue of the cortex are of two kinds, thick-walled fibres similar in appearance to those described from the scale (*q.v.*) and irregular parenchyma which is interspersed with the fibres in the inner part. The pith, both of the axial cylinder and of the scale traces, is composed of a farly thick-walled parenchyma, the cells of which are usually filled with a dark brown substance. There are also, especially round the edge, a few fibres like those in the cortex.

b) The Scale. — The cylindrical vascular supply in the basal region of the scale (text-fig. 8, A and B) soon becomes asymmetrical by the attenuation of the abaxial side; the cylinder does not open out from below as one might expect, but the xylem here gradually diminishes and eventually fades out. The small bract trace ends before reaching the free portion of the bract.

The major part of the parenchyma in this part of the scale is continuous with the pith of the axis through the cylindrical trace, and is composed of cells with dark contents like those in the pith. The tissue continuous with the cortex, which probably lay mainly lateral and adaxial to the vascular trace, is not well preserved, and consequently the exact distribution of resin canals is not easy to ascertain. However, it has been noticed that the linings of resin ducts in this species have a rather distinctive appearance (Pl. V, fig. 12), and seem to be more resistant to decay than some of the softer tissues (e.g. the outermost layer of the integument). A dark membrane like the lining layer of a resin canal has been found on the upper side of the scale between the seeds (text-fig. 8, C; 9, A, *r*). Thus, there were probably three resin canals in the basal region of the scale, two lateral to the vascular strand and one adaxial probably occupying the ridge between the seeds.

At a level about midway along the seeds where the scale broadens, the vascular arc begins to break up to give rise to a number of strands which, in the distal part of the scale, come to lie evenly spaced in a single median row (text-fig. 8, D-F). Towards the upper end of each seed, a small vascular strand is given off which becomes splayed out just beneath the chalaza without actually entering it (text-fig. 8 and 9, *ss*). The resin canals, of which there appear to be two systems, one from each side of the scale (Pl. V, fig. 11), become evenly distribued through the ground tissue in the upper part. There is a definite tendency in the distal region for two resin canals to become associated with each attenuated vascular bundle (text-fig. 8, F, left-hand side). According to one of the drawings given by Radais (1894) of a section through the scale of *Keteleeria fortunei* Carrière, the same tendency is found in this recent conifer.

Just above the seeds on the abaxial side of the scale there occurs a well developed mechanical tissue composed of thick-walled fibres similar to those found in the axis. Figure 11, plate 6 shows the general appearance of this tissue, and a few of the cells are shown in greater detail in text-figure 9B. It will be noticed that the cell walls appear to consist of two layers, a thin outer one similar to the walls of the ordinary parenchyma, and a much thicker inner layer which is of a lighter colour and more spongy appearance. Sometimes the inner layer is more or less separated from the outer (Pl. V, fig. **12**), especially in the upper part of the scale where the fibres occur in scattered groups in the parenchyma. It is interesting to note that cells with definitely double walls occur in a similar position in the scale of *Cedrus libani* LOUDON; here

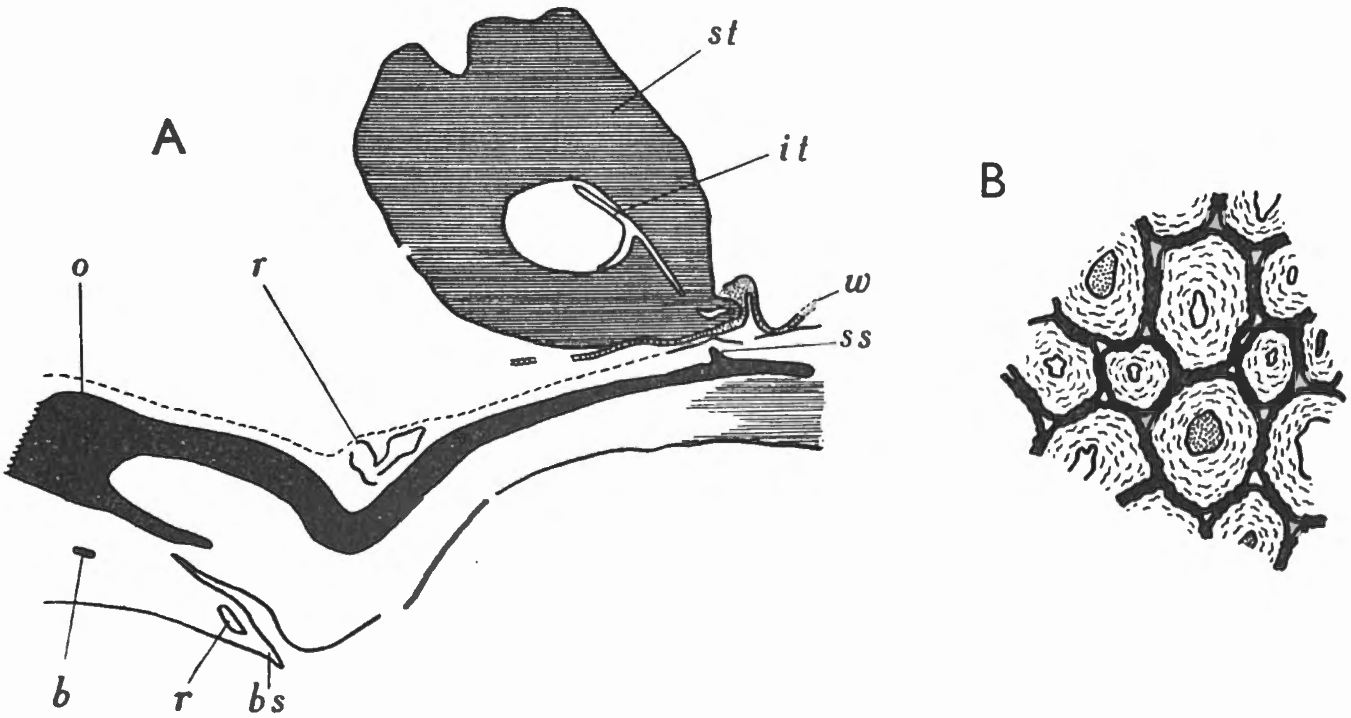


FIG. 9. — *Pityostrobus corneti* (COEMANS).

A, longitudinal section through the base of a scale showing the course of its vascular system and the distribution of mechanical tissue (indicated by thin horizental shading). *o*, vascular system of scale; *b*, bract trace; *bs*, bract scale; *ss*, vascular trace of the seed; *r*, resin canals; *w*, wing; *st*, sclerotesta; *it*, inner soft layer of the integument. (The shape of the scale has been distorted by the softening treatment, the seed normally being in contact with the base of the scale.) C3/5/6; ×15. B, group of fibres from the scale as seen in transverse section showing the apparent double nature of the walls. C1/24/3; ×325.

the outer layer is apparently an ordinary cellulosic wall, whilst the inner one is composed of a fatty material which swells up in a fat solvent such as xylol. But these cells are considerably smaller in diameter than those of the fossil, and are confined to the outer part of the scale. Again, in the fossil other cells (e.g. some of the tracheids) often show double walls, and it seems unlikely that these too would be of the same highly specialised kind as the fatty cells in *Cedrus*. It has been noticed that the thick-walled, lignified cells (fibres and tracheids) in several living conifers often appear to have two layers to their walls, the outer one of which is too thick to represent merely the true primary wall, and after prolonged pickling these layers sometimes tend to separate. It seems unlikely therefore that the cells in the fossil are anything but ordinary (lignified?) fibres showing a differentiation in their walls frequently found amongst living plants.

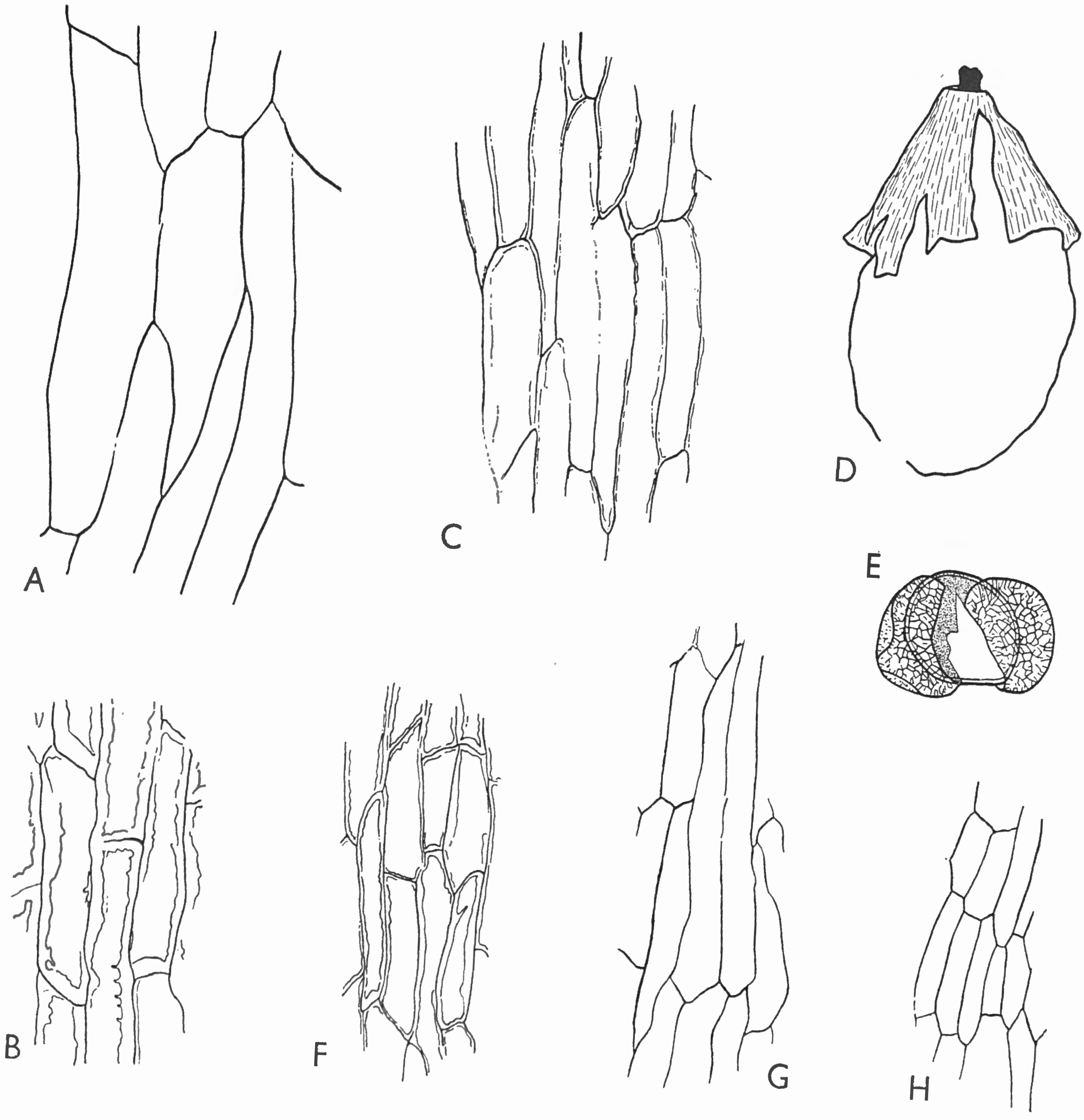


FIG. 10.

A and B, *Pinus wallichiana* JACKSON : A, cuticle from inside the integument of the seed; B, nucellus cuticle. — C, *Pityostrobus andraei*, nucellus cuticle. — D — F, *Pit. bommeri* : D, « kernel » showing the megaspore membrane, the cap-like nucellus cuticle and an apical pollen mass (black); E, pollen grain; F, nucellus cuticle. — G and H, *Pit. corneti* : G, probably the cuticle lining the inside of the integument; H, nucellus cuticle. — All except D ×325; D, ×15.

c) The Seed. — The seeds, although fully grown, were probably immature at the time the cone separated from the tree; this is indicated by the fact that the wings are still very intimately in contact with the scale, and by the ocurrence of unthickened cells in the sclerotesta of one of the seeds sectioned (Pl. V, fig. 9). The chief point of difference between this seed and those of the pine-like species described above, is that the integument is supplied with resin canals as in the recent conifers of the genera *Abies*, *Cedrus*, *Tsuga* and *Keteleeria*; the canals appear to run in longitudinal furrows in the sclerotesta (text-fig. 8, C and D).

As in the other species, « kernels » have been obtained from the seeds, but here the cutinised membranes were rather more delicate, and never was an entire nucellus cuticle observed. However, in its general form the « kernel » corresponded to the one figured from *P. bommeri* (text-fig. 10 D). Cell outlines from the nucellus cuticle are shown in text-figure 10 H; those in figure G, which are considerably larger, were drawn from a very delicate piece of membrane the identity of which was uncertain; it may have been from the cuticle lining the inside of the integument, or else from the lower part of the nucellus where the cells tend to be larger.

No pollen has been found in this species.

Discussion. — Coemans drew attention to the resemblance between these cones and those of *Cedrus* and *Abies;* and in their general appearance as well as in the form of the ovuliferous scale there is indeed a striking similarity. The cylindrical shape of the cones is more characteristic of *Abies* than of *Cedrus*, but on the other hand the bract scale, being weakly developed, is more like that of *Cedrus*.

In its anatomy the fossil presents a combination of characters found, as far as I know, in no living member of the *Abietaceæ*. Although there are a few *Cedrus*-like features, it has more in common with *Keteleeria*. *Abies*, as will be seen from the table on pages 38 and 39, is very much less like it in structure than either of these. The most notable *Keteleeria*-like characters are follows :

a) Persistant scales. Available evidence suggests that the scales of the fossil were not deciduous; this evidence includes the fact that the vascular tissue is strongly developed at the base of the scale, and that there is no tendency for the scales to separate from the axis, even in severely compressed cones.

b) Vascular cylinder of the axis. This is thick and almost uninterrupted in *K. davidiana* as in the fossil, whilst in both *Cedrus* and *Abies* it is much dissected, and in *Cedrus* the amount of xylem is small in comparison with the size of the cone.

c) Distribution of resin canals. Distribution is similar in the scale at least in the region above the seeds. At the distal end there is, in *K. fortunei* as in the fossil, the same tendency for a pair of canals to become associated with a vascular strand. In both, the bracts are supplied with canals.

d) Vascular supply to the scale. In *K. fortunei* this is radially organised as apparently in no other living member of the family, but differs from that in the fossil in being at first solid. In *K. davidiana* the strand is horseshoe-shaped as in most members of the family. In *Cedrus* it is weak and scarcely curved.

e) Sclerenchyma. The distribution of sclerenchyma in the scale of *K. davidiana* is similar to that in the fossil, and the cells of which it is composed, although rather larger, show very distinctly the two wall layers. *K. fortunei* however, according to Radais, has no well defined abaxial sclerenchyma but only scattered fibres.

f) Nucellus cuticle. In thickness and in the form of the cell outlines this corresponds more closely to that of *K. davidiana* than to that of *Cedrus libani*.

The following characters are more distinctly *Cedrus*-like :

a) General form of the cone and ovuliferous scale.

b) Bract. This is of similar size and form. Its vascular trace is single and weakly developed as in *Cedrus*. In *K. fortunei* the trace is double, but is single in *K. davidiana*; in both species it is more strongly developed than in the fossil, as also is the bract itself.

c) The seed. This is of the kind found in *Cedrus*. In *K. davidiana* the sclerotesta is poorly developed.

d) Resin canals at the base of the scale. Distribution is probably like that in *Cedrus*.

Thus, the fossil presents an extraordinary mixture of characters : whilst it is clearly like a *Cedrus* or *Abies* cone in its external form, its structure, which is unlike that of either of these (especially *Abies*), appears to conform in many respects to that of one or other of the species of *Keteleeria*. It must be borne in mind however that the two species of *Keteleeria* are anatomically dissimilar (e.g. *d*) and *e*) above), and also that the genus is very strikingly distinct from *Cedrus* not only in cone-form, but also and especially in its vegetative organisation. It would therefore be rash to assume that this fossil was closely related to *Keteleeria* on the strength of the characters listed above. On the other hand, in view of the wide structural differences, it would be equally unjustifiable to assume a *Cedrus* affinity.

Some of the features of the fossil seem to suggest primitiveness : for example, the radially organised scale trace (like that of a lateral vegetative shoot), and the grouping of the resin canals and vascular strands in the distal part of the scale, recalling the arrangement in a series of leafy appendages fused laterally. Incidentally, *Keteleeria fortunei*, which also shows these characters, has been shown by AASE (1915) to possess signs of a third ovule in the middle of the scale, a fact of some considerable significance in making comparison with the Palaeozoic conifers.

In conclusion it can only be said that *Pityostrobus corneti*, although showing an affinity with the *Abietæ* section of the family (i.e. those characterised by the absence of resin ducts from the secondary wood and their presence in the seeds), does not appear to be very closely related to any living genus.

Unfortunately, although several fossil cones having a similar appearance to ours have been described from various parts of the world, none has been studied anatomically. Most of them are considerably stouter, e.g. *Pityostrobus leckenbyi* (CARRUTHERS) SEWARD, *Cedrus lotharingica* CORNUEL and *C. lennieri* SAPORTA, all of which are 3 cm or more in diameter.

Cedrostrobus mantellii (CARRUTHERS) STOPES, from the lower Greensand of Kent, is of much the same size as the cones described here, but the shape is more ovoid and the apex is distinctly pointed.

Cedrus leei (FONTAINE) BERRY from America, is a small cone 4 cm long and between 1,5 and 2 cm in diameter which might very well be specifically identical with *Pityostrobus corneti*, but being in ignorance of its internal structure, I would not combine them under one specific name.

CONCLUSION.

It is remarkable that the Abietaceous cones of late Mesozoic age should present such a wide variety of form, and resemble in their general organisation so closely the cones of living members of the family, since in pre-Cretaceous strata Abietaceous remains are very rare. Many of the pine-like cones are especially modern in the appearance, so much so that some authors in the past have unhestitatingly placed species in the genus *Pinus*. Even the two main cone-forms found amongst living pines seem to be foreshadowed in the Cretaceous if not even in the Upper Jurassic (FLICHE and ZEILLER, 1904); thus *Pityostrobus andraei* and *P. quenstedti* HEER resemble, especially in the form of their scales, the cones of the *Pinaster* type, whilst *P. bommeri* and *P. dunkeri* are much more like the *Strobus* cones.

But the modern genus *Pinus* is a large cone, and presents great variety of cone-form, some species having cones different from, and sometimes more or less intermediate between the *Strobus* and *Pinaster* types. Amongst the fossils too there is considerable diversity, and some species which seem to be more distinct from the living pines than most, may later be shown to merit generic status : such is *Pityostrobus macrocephalus* (Lindley and Hutton) which is peculiar in its anatomical structure, possessing very scanty xylem.

The absence of an umbo from the scale in a number of these early pine-like cones (including the two described here) has been regarded as an important distinction between them and the recent pines (Fliche, 1896). The umbo is that part of the scale which is exposed during the first season of growth, and represents the morphological apex whose power of growth is arrested at an early stage. It is strange that in all recent pines this should be a constant character of the mature cones, and that it should not occur in any other genus of the family. Its absence from these fossils may mean that the cones matured in a single season, as do the cones of *Picea* for example.

Most of the non-pine-like species of *Pityostrobus*, at least as far as their external features are concerned, can be compared with one or other of the recent members of the family. However, two species having a Cedrus-like appearance have now been shown to be unlike cedar cones in important respects : these are *P. corneti* which has an anatomical structure quite unlike that of *Cedrus* and more like that of *Keteleeria*, and a species named *Apterostrobus cedroides* Gothan and Nagel (from the Lower Eocene) in which the seeds lacked wings. It is not unlikely that if other species were investigated more carefully similar differences might come to light.

Concluding, we may say that the *Abietaceæ* was undoubtedly a large and important family in Cretaceous and early Tertiary times, and presented a wide variety of cones, many of which were strikingly like those of recent representatives, but some of which were clearly different, in structure if not in general external form. There is no doubt that several distinct genera were represented, but it seems undesirable at this stage to attempt to devise a more natural system of classification for these isolated cones, since so many are very imperfectly known. It is hoped that at a later date a thorough review will be made of them.

TABLE COMPARING THE MAIN CONE-CHARACTERS OF *PITYOSTROBUS*

Based on the work of RADAIS (1894)

	BRACT	SCALES	AXIAL VASC. CYLINDER	RESIN CANALS : BASE OF SCALE
Abies nordmanniana SPACH.	well developed	deciduous	much dissected	adaxial only
Cedrus libani LOUD.	very small	deciduous	much dissected	one adaxial, two abaxial or lateral
Keteleeria fortunei CARR.	fairly well developed	persistant	?	several both sides
Keteleeria davidiana BEISS...	fairly well developed	persistant	thick, ± continuous ring	?
Pityostrobus corneti	very small	persistant (?)	thick, ± continuous	one adaxial, two lateral

CORNETI WITH THOSE OF FOUR RECENT MEMBERS OF THE *ABIETACEÆ*.
and on original investigation.

RESIN CANALS : JUST ABOVE SEEDS	RESIN CANALS : BRACT	SCALE TRACE	BRACT TRACE	SCLERENCHYMA IN SCALE
adaxial only	present	arc-shaped	double	well developed at level of seeds
one adaxial, rest abaxial	absent	simple, weak	single, very weak	well developed specialised cells above seeds
both sides	present	solid, then cyl.	double	only scattered cells
both sides	present (?)	arc-shaped	single, fairly strong	fairly well developed above seeds
both sides	present	cyl.	single, weak	fairly well developed bove seeds

LITERATURE CITED

AASE, H., 1915, *Vascular Anatomy of the Megasporophylls of Conifers.* (Bot. Gaz., LX, p. 277.)

BERRY, E. W., 1911, *Revision of several Gymnospermous Plants from the Potomoc Group in Maryland and Virginia.* (Proc. U. S. Nat. Mus., XL, p. 313.)

BOUREAU, E., 1948, *Morphologie et affinités de deux cônes fossiles de la flore Albienne de la Perte-du-Rhône.* (Bull. Mus. Hist. Nat. Paris, 2e sér., XX, p. 481.)

CARRUTHERS, W., 1866, *On some Fossil Coniferous Fruits.* (Geol. Mag., III, p. 534.)

— 1869, *On some undescribed Coniferous Fruits from the Secondary Rocks of Britain.* (Geol. Mag., VI, p. 1.)

COEMANS, E., 1866, *La flore fossile du premier étage du terrain crétacé du Hainaut.* (Mém. Acad. Roy. Belg., XXXVI, p. 1.)

CORNUEL, M. J., 1866, *Des cônes de pins trouvés dans les couches fluviolacustres de l'étage néocomien du bassin parisien.* (Bull. Soc. Géol. France, 2e sér., XXIII, p. 658.)

— 1882, *Note sur les cônes de Pinus elongata découverts à Saint-Dizier (Haute-Marne) et sur des cônes de cèdre du sable vert de la Houpette (Meuse).* (Bull. Soc. Géol. France, 3e sér., X, p. 259.)

DUTT, C. P., 1916, *Pityostrobus macrocephalus* LINDLEY *and* HUTTON, *a Tertiary Cone showing Ovular Structures.* (Ann. Bot., XXX, p. 529.)

FLICHE, P., 1891, *Études sur la flore fossile de l'Argonne (Albien-Cénomanien).* (Bull. Soc. Sci. Nancy, XIV, p. 118.)

FLICHE, P. and ZEILLER, R., 1904, *Note sur une florule portlandienne des environs de Boulogne-sur-Mer.* (Bull. Soc. Géol. France, 4e sér., IV, p. 787.)

GARDNER, J. S., 1886, *Second Report of the Committee appointed for the purpose of reporting on the fossil plants of the Tertiary and Secondary beds of the United Kingdom.* (Rep. of the 56th Meeting Brit. Assoc.)

GOTHAN, W. and NAGEL, K., 1921, *Über einen cedroiden coniferen Zapfen aus dem Unter Eocen der greisswalder Oie.* (Jahr. Preuss. geolog. Landesanst., XLI, 1, p. 121.)

HEER, O., 1869, *Beiträge zur Kreide-Flora. I. Flora von Moleten in Mahren.* (Neue Denksch. Allgem. Swcheiz. Ges. gesammt. Naturwiss., XXIII.)

NATHORST, A. G., 1897, *Zur Mesozoischen Flora Spitzbergens.* (K. Svensk. Vetenskaps-Akad. Handl., XXX, No. 1.)

RADAIS, M., 1894, *Contribution à l'étude de l'anatomie comparée du fruit des conifères.* (Ann. Sci. Nat. Bot., 7e sér., XIX, p. 165.)

SAPORTA, G. DE, 1877, *Note sur les végétaux fossiles de la craie inférieure des environs du Havre.* (Bull. Soc. Géol. de Normandie, VI, p. 640.)

SEWARD, A. C., 1900, *La flore wealdienne de Bernissart.* (Mém. Mus. Roy. Hist. Nat. Belg., 1.)

— 1919, *Fossil Plants.* IV. (Cambridge.)

STEINBÖCK, H., 1926, *Über den anatomischen Bau des Markkorpers einiger Koniferen-Hölzer.* (Osterr. bot. Zeitschr., LXXV, p. 65.)

STOCKMANS, F., 1946, *Végétaux de l'assise des sables d'Aix-la-Chapelle récoltés en Belgique (Sénonien inférieur).* (Mém. Mus. Roy. Hist. Nat. Belg., No. 105.)

STOPES, M. C., 1910, *The Anatomy of Cretaceous Pine Leaves.* (Ann. Bot., XXIV, p. 400.)

— 1915, *Catalogue of Mesozoic Plants in the British Museum (Nat. Hist.); The Cretaceous Flora.* Part 2. *Lower Greensand (Aptian).* (London.)

THOMSON, R. B., 1905, *The Megaspore Membrane of Gymnosperms.* (Univ. of Toronto Studies, Biol., Ser. 4.)

VELONOVSKY, J., 1885, *Die Gymnospermum der Böhmischen Kreideformation.* (Prague.)

DEPARTMENT OF BOTANY, BIRKBECK COLLEGE, LONDON.

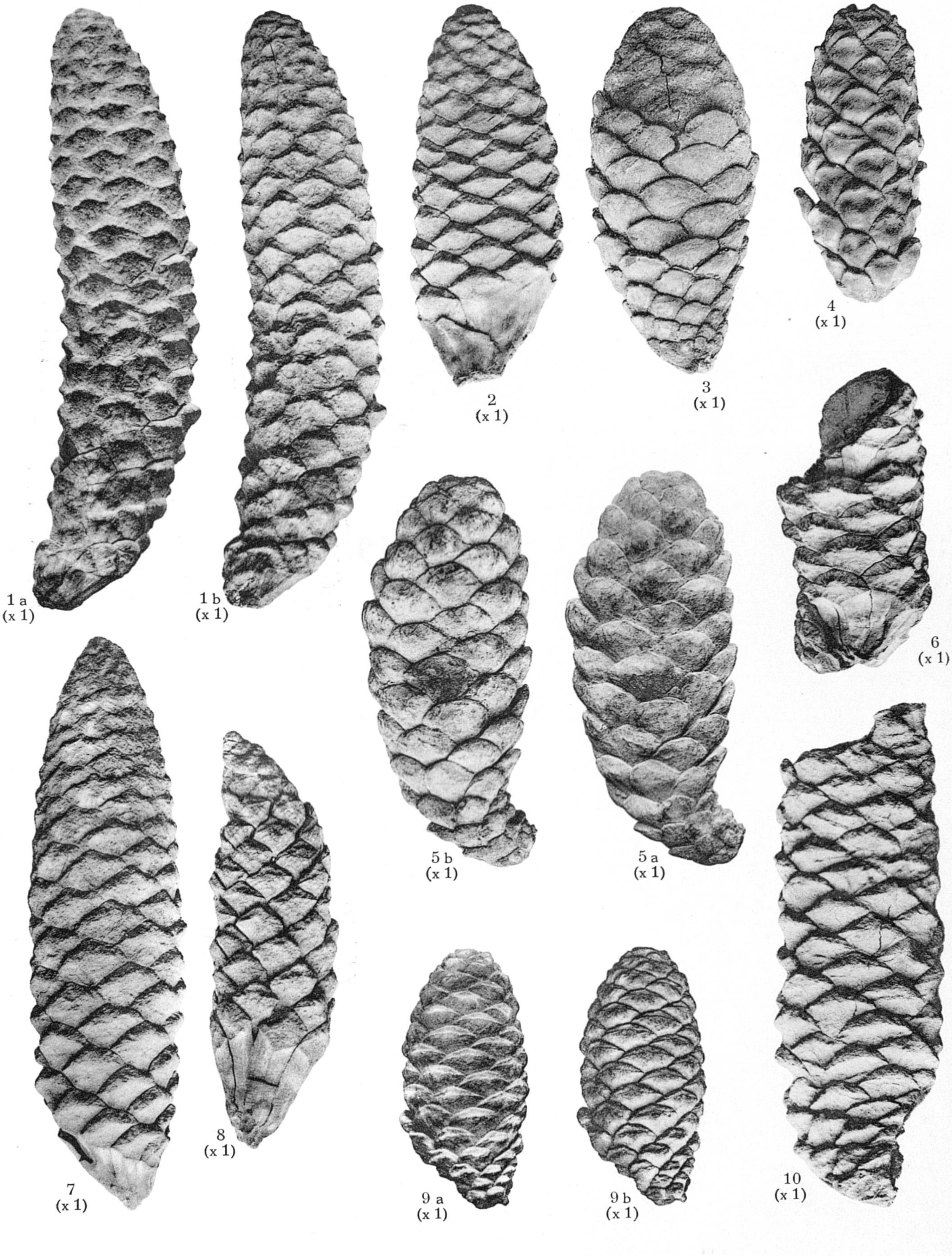
CONTENTS

EXPLANATION OF PLATE I.

Pityostrobus andraei (COEMANS).

A selection of cones from La Louvière taken from BOMMER's photographs. All ×1.

(In order to indicate accurately the form of the apophysis, three specimens (figs. 1, 5 and 9) are shown twice. In each case, fig. A shows the cone in light coming obliquely from the apex, and fig. B shows it in light coming obliquely from the base.)



K. L. ALVIN. — Three Abietaceous cones from the Wealden of Belgium.

Phototypie A. Dohmen, Bruxelles

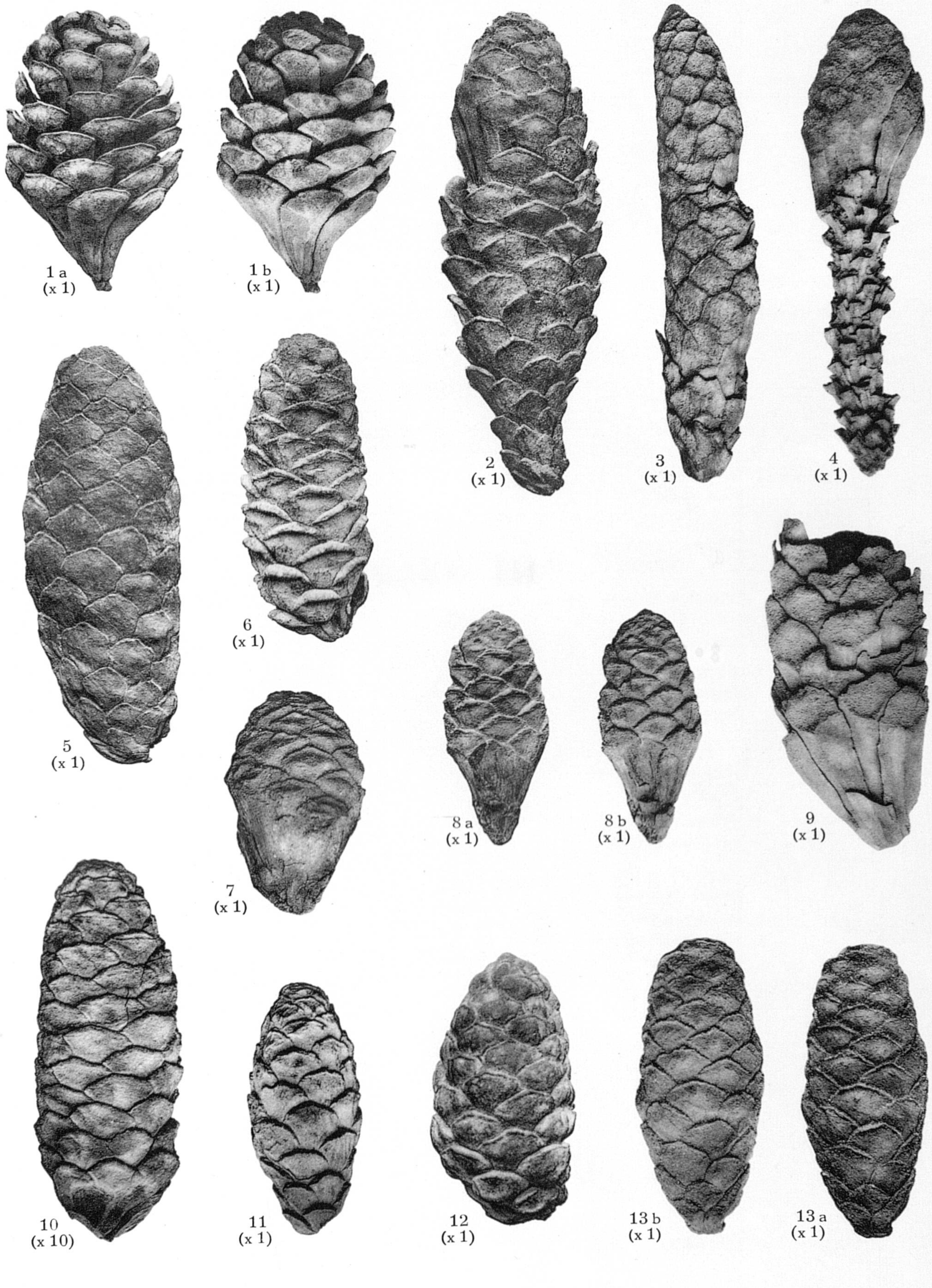
EXPLANATION OF PLATE II.

Pityostrobus andraei (COEMANS).

A selection of cones from La Louvière taken from BOMMER's photographs. All ×1.

(In order to indicate accurately the form of the apophysis, three specimens (figs. 1, 8 and 13) are shown twice. In each case, fig. A shows the cone in light coming obliquely from the apex, and fig. B shows it in light coming obliquely from the base.)

Inst. Roy. Sc. Nat. Belg. — Mém. N° 125, 1953.
Kon. Belg. Inst. Natuurw. — Verh. Nr 125, 1953.



K. L. ALVIN. — Three Abietaceous cones from the Wealden of Belgium.

Phototypie A. Dohmen, Bruxelles

EXPLANATION OF PLATE III.

Pityostrobus andraei (Coemans).

Fig. 1-4. — Scales seen from adaxial side showing the seeds in situ. (1-3 after Bommer.) $\times 2\frac{1}{2}$.

Fig. 5. — Scale with almost intact apophysis. $\times 2\frac{1}{2}$.

Fig. 6. — Scale with abraded apophysis. $\times 2\frac{1}{2}$.

Fig. 7. — A badly abraded scale whose apophysis has been completely worn away. $\times 2\frac{1}{2}$.

Fig. 8. — Transverse section through the axis. Section A2/10/3. $\times 10$.

Fig. 9. — Tangential longitudinal section through the axis showing the horseshoe-shaped vascular supply to the scale and the bract trace some distance below. p, small-celled parenchyma which extends inwards from the margin of the scale. Section A3/12/1. $\times 18$.

Fig. 10. — Radial longitudinal section through the axis showing the base of an ovuliferous scale, its vascular supply, the trace of the subtending bract and a dilated resin canal in the abaxial scelernchyma. Section A3/15/4. $\times 15$.

Fig. 11. — Part of the cortex of the axis in transverse section showing a collapsed resin canal (r) and a small group of sclereids in the bottom left-hand corner. p, as in figure 9. Section A2/12/3. $\times 100$.

Fig. 12. — Part of a transverse section through the axis showing a bract trace (top), the associated gap in the axial cylinder (centre) and a cortical resin canal (r). Section A2/10/5. $\times 65$.

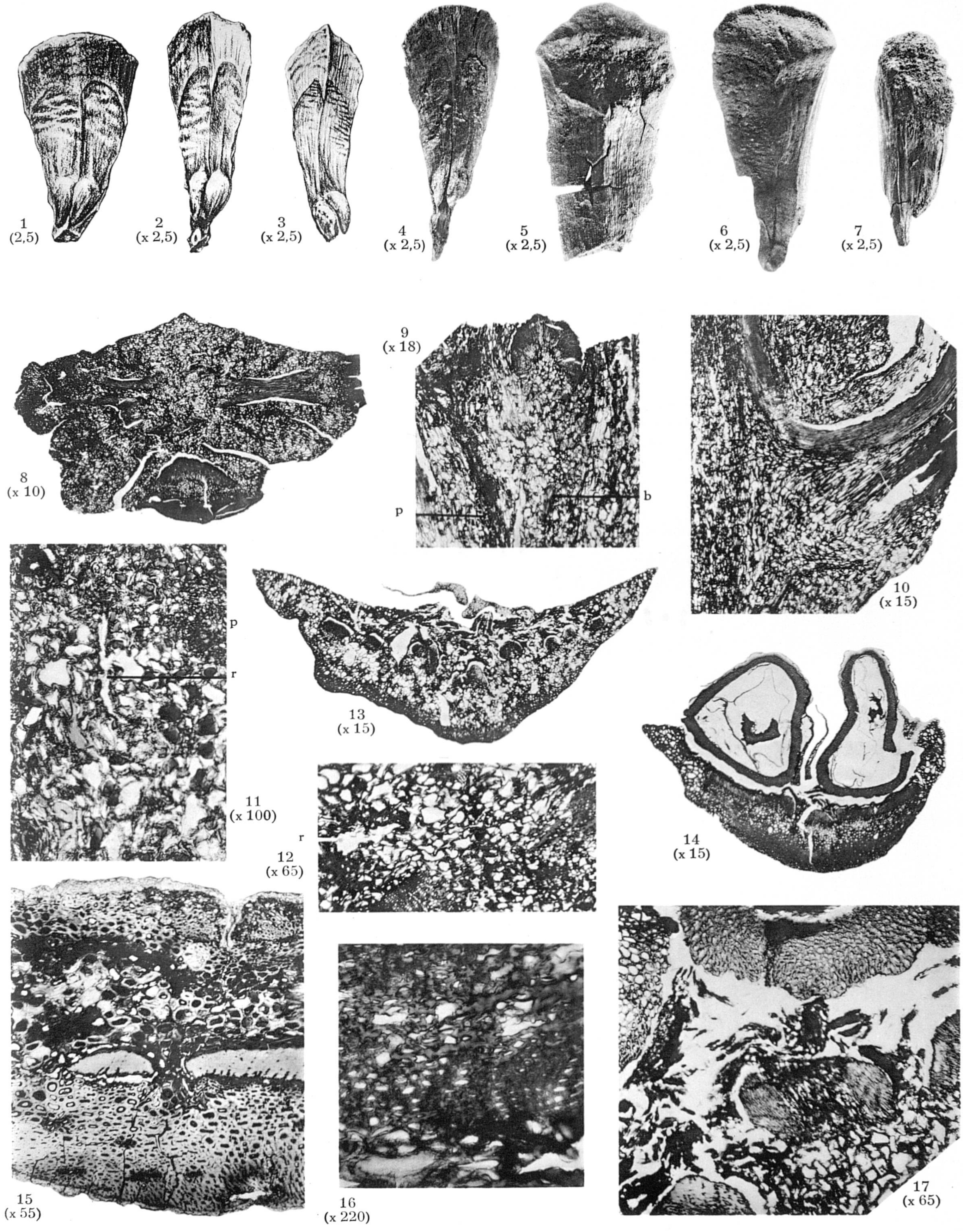
Fig. 13. — Transverse section through a scale in the region of the wings (just above the seeds). Three dilated resin canals can be seen on the left. Section A6/34/4. $\times 15$.

Fig. 14. — Transverse section through the same scale in the region of the seeds. For explanation see text-figure 3. Section A6/24/1. $\times 15$.

Fig. 15. — Part of a traverse section through the scale shown in figure 5 ,cut just above the seeds. The abaxial sclerenchyma with dark compressed resin canals and a narrow band of adaxial sclerenchyma beneath the closely adpressed seed wings can be seen. Section A7/3/9. $\times 55$.

Fig. 16. — Secondary xylem of the axis showing, just above the centre, three cavities probably representing resin canals, and at the bottom the black remains of the phloem. Section A2/10/6. $\times 220$.

Fig. 17. — Part of a transverse section through the same scale as in figures 13 and 14 showing the chalazal end of a seed with the perforation in the sclerotesta and the two sub-ovular strands beneath. Section A6/29/6. $\times 65$.



K. L. ALVIN. — Three Abietaceous cones from the Wealden of Belgium.

Phototypie A. Dohmen, Bruxelles

EXPLANATION OF PLATE IV.

Pityostrobus bommeri nov. sp.

FIG. 1-3. — Three cones (all incomplete) showing the main external features. No. 2 (and probably also 1 and 3) from Bernissart. All ×1.

FIG. 4-6. — Three scales showing the form of the adaxial surface. Figure 4 shows the fine striations characteristic of the species. The wing of the seed on the left in figure 6 is almost intact. All ×2½.

FIG. 7. — A piece of axis showing the pointed bracts and the bases of the ovuliferous scales. ×2.

FIG. 8. — Transverse section through the axis showing the vascular system and the two rings of resin canals, one in the cortex and the other at the edge of the pith. Section B7/13/5. ×7.

FIG. 9. — Part of the next section to that in figure 8 at a higher magnification. Section B7/13/6. ×23.

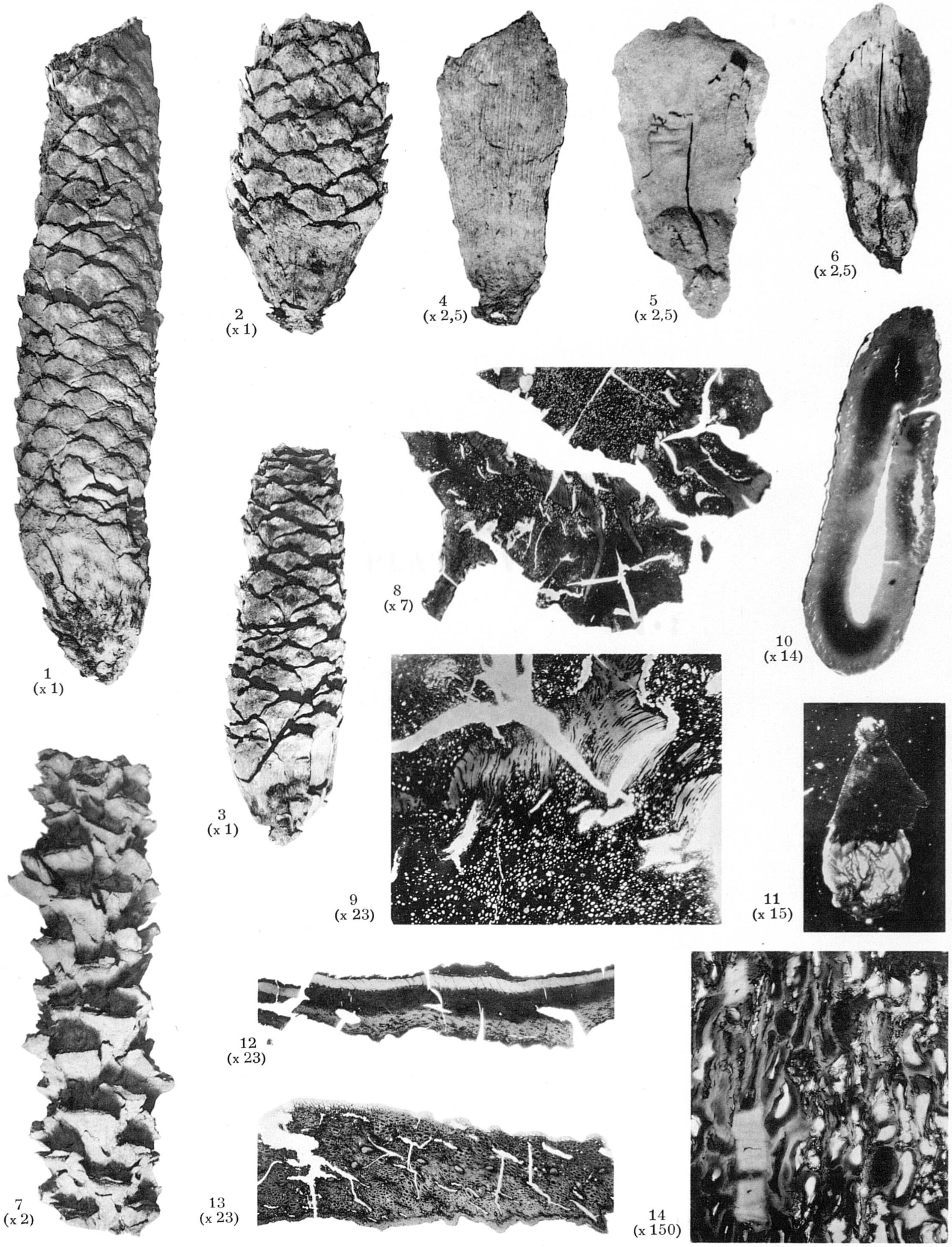
FIG. 10. — Longitudinal section through a seed showing the very thick and poorly preserved sclerotesta. Section B4/7/7. ×14.

FIG. 11. — Photograph of a « kernel » dissected from a seed showing the oval megaspore membrane and the cap-like nucellus membrane. ×15.

FIG. 12. — Transverse section through a scale in the region of the seeds showing the continuous band of vascular tissue (xylem light), and the large resin canals at the margin of the abaxial sclerenchyma. (Parenchyma is black.) Section B3/4/2. ×23.

FIG. 13. — Transverse section through the scale in the distal region showing the line of small bundles, the evenly distributed resin canals and the thin layer of small-celled tissue on the abaxial side. (The upper face was damaged by the softening treatment.) Section B1/32/4. ×23.

FIG. 14. — Small part of the pith in longitudinal section showing a few of the characteristic sclereids. Section B6/16/4. ×150.



K. L. ALVIN. — Three Abietaceous cones from the Wealden of Belgium.

Phototypie A. Dohmen, Bruxelles

EXPLANATION OF PLATE V.

Pityostrobus corneti (COEMANS).

FIG. 1-4. — A selection of cones of different sizes and showing various degrees of compression. 1, 2 and 4 from La Louvière; 3 from Hautrage. All × 1.

FIG. 5-8. — Scales from the cone shown in figure 3 to show the form of the adaxial surface. The broken line in figure 5 indicates the extent of the wings. All × 2½.

FIG. 9. — Transverse section of the scale shown in figure 6. Note the unthickened cells in the sclerotesta of the seed on the right. Cf. text-figure 12, D. Section C1/14/1. × 10.

FIG. 10. — Transverse section through the axis of the same cone. Section C2/11/2. × 10.

FIG. 11. — Transverse section through the scale just above the seeds showing the two systems of resin canals, the large ones on the adaxial side, and the smaller ones on the abaxial side in the fibrous tissue. Part of the seed wing can be seen on the upper side. Section C1/22/3. × 100.

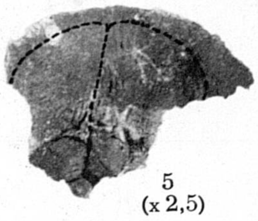
FIG. 12. — Transverse section through the scale in the distal region showing the even distribution of resin canals and fibres. Note the dark lining membranes of the canals. Section C1/30/2. × 100.

1
(x 1)

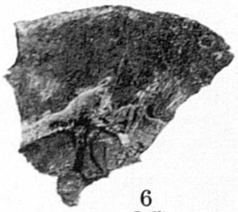
2
(x 2)

3
(x 1)

4
(x 1)

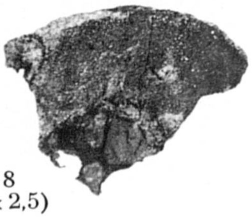


5
(x 2,5)

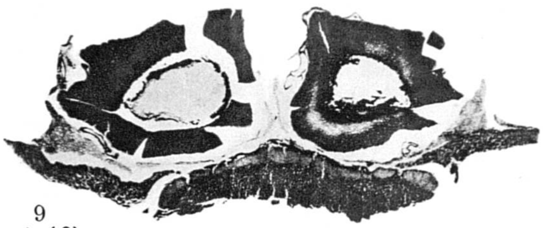


6
(2,5)

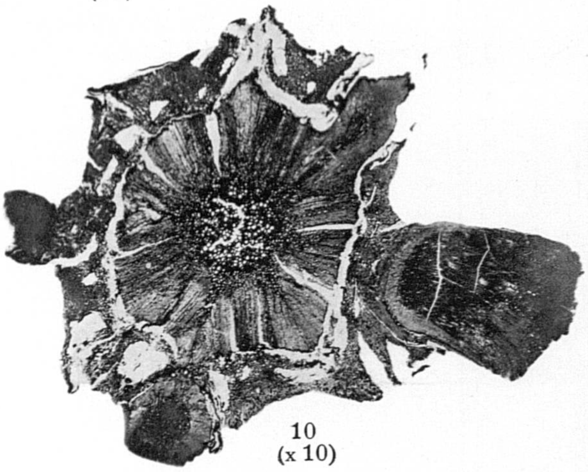
7
(x 2,5)



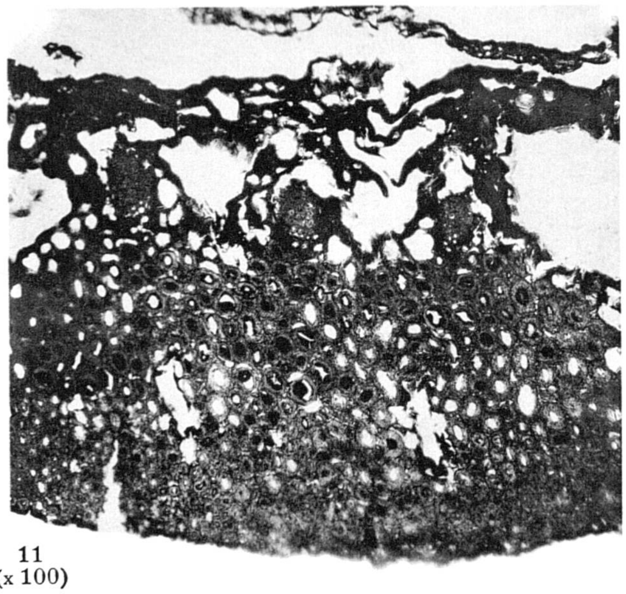
8
(x 2,5)



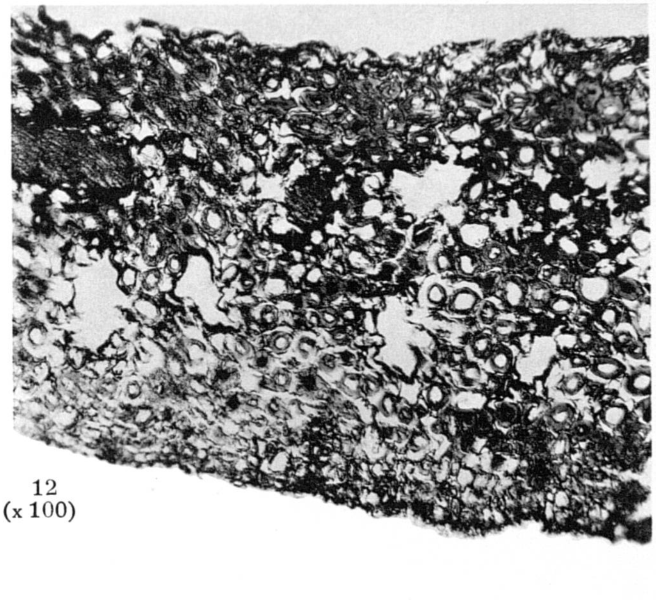
9
(x 10)



10
(x 10)



11
(x 100)



12
(x 100)

K. L. ALVIN. — Three Abietaceous cones from the Wealden of Belgium.

Phototypie A. Dohmen, Bruxelles