Pityostrobus macrocephalus, L. and H. A Tertiary Cone showing Ovular Structures.

BY

C. P. DUTT, B.A.,

Late Scholar of Queens' College, Cambridge.

With Plate XV and two Figures in the Text.

INTRODUCTION.

ALTHOUGH a number of cones of Abietinean affinity have been recorded from Cretaceous and Tertiary rocks, in almost all cases the internal organization of the ovules has been passed over without comment. This is, of course, partly due to unfavourable conditions of preservation, but even where slides showing a considerable amount of anatomical detail have been in existence for a long time, the older writers have generally contented themselves with a brief description of the main morphological features.

The material which forms the basis of the present description consists in the first place of a number of slides belonging to the British Museum. All but one of these are known to have been prepared from two cones which form part of the Cowderoy Collection bequeathed to the British Museum in 1852. Up to now these two cones have been regarded as representatives of two distinct species, but, as will be seen, examination of the internal structure seems to afford little justification for this view. The larger cone, *Pinites macrocephalus* of Carruthers, has furnished only thick longitudinal sections, while from the other specimen have been cut two transverse sections and two thin longitudinal sections of a small portion of the base. A third transverse section is not definitely referred to either of the above cones, but it agrees in all details with *P. ovatus*, and has probably been cut from the same cone as the others.

I should like here to record my great indebtedness to Professor Seward, who placed the slides at my disposal and who has throughout given me much valuable assistance and advice. Further, owing to the kindness of Dr. Arber I received permission to have sections cut from a specimen of *P. macrocephalus* which was presented to the Sedgwick Museum, Cambridge, some years ago by Mr. C. H. Edgell. With the help of these slides (two

longitudinal and one transverse) a closer comparison of the two forms of cone has been rendered possible. My thanks are also due to Mr. Irwin Lynch, Curator of the Cambridge Botanic Garden, who has granted me facilities in obtaining specimens of recent cones.

It will be convenient in the following description, for the purpose of reference to the different slides, to retain the specific designations, although this can be dispensed with in the general summary. Throughout the paper the generic name *Pityostrobus* will be used instead of *Pinites*, except in the case of citations from particular authors. Nathorst's name *Pityostrobus* is adopted in preference to Feistmantel's term *Pinostrobus*, recently revived by Dr. Stopes, on the ground that the former designation is more appropriate for Abietinean cones which cannot be safely referred to any one recent genus. In the present case the characters clearly point to an affinity with *Pinus*, but nothing is known of the vegetative features of the tree on which the cone was borne.

LITERATURE.

The history of these cones shows many vicissitudes with regard to terminology as well as error in the determination of their geological horizon. Of the four specimens which have been referred to by Carruthers as *Pinites macrocephalus*, the one on which is based the original description of Professor Henslow in the Fossil Flora of Lindley and Hutton (7) is a large cone which was found in clearing out a pond near Dover. Both Lindley and Hutton agreed in assigning the fossil to the genus *Zamia*, and they gave it the name *Zamia macrocephala*. From one of Henslow's figures Endlicher (4) was led to believe that the cone differed from *Zamia* in possessing only a single ovule on each scale, and he therefore established the new genus *Zamiostrobus* for its reception, retaining the specific designation *macrocephala*. Morris (10), in his revision of the fossil Cycadeae, adopts the genus *Zamites* introduced by Presl (11) and includes under it three species of *Zamia* of Lindley and Hutton, among which is *Zamia macrocephala*. Miquel (8) and Goeppert (6) accept Endlicher's genus, the last named adding to it three of Morris's species of *Zamites*. In 1850 Unger (16) added three more, and all seven were included by Miquel (9) under *Zamiostrobus* in his 'Prodromus Systematis Cycadearum' of 1861. In the meanwhile Corda (3, p. 84) in 1846 had suggested that the affinities of the fossil lay with the Coniferae rather than the Cycadeae, but it was left for Carruthers (2), in an important paper on Fossil Coniferous Fruits, published in 1866, definitely to establish this fact, and to show that it more closely resembled the recent genus *Pinus* than any other plant. He assigned the fossil to the genus *Pinites*, used in a comprehensive sense to include all cones of Abietinean affinity. With the aid of three other

specimens, apparently identical with *Zamia macrocephala*, L. and H., Carruthers was enabled to give a more accurate description and to correct an error regarding the geological age of the fossil. Henslow, deceived by the appearance of the sandstone in which his specimen was embedded, had referred the fossil to the 'Greensand Formation'; but Carruthers was able to fix the horizon as Eocene, for two of the three other specimens available to him were found *in situ* in a similar sandstone of this age. Of these two, one is in the Bowerbank Collection and comes from Sheppey, the other is a fossil which was found by Mr. Dowker near Canterbury, at about the junction of the Woolwich and Thanet beds. The third specimen, a water-worn fossil of unknown locality, belonging to the Cowderoy Collection, furnished the slides of *Pinites macrocephalus*, Carr., used in the following description. Since then several other specimens have come to light; Mr. Edgell's specimen of *P. macrocephalus*, in the Sedgwick Museum, was obtained from the London Clay at Reculvers, Kent.

A cone similar to *Zamia macrocephala*, L. and H., though somewhat smaller, which was found on the Kent coast near Faversham, was described by Lindley and Hutton (7, vol. iii, p. 189, Pl. 226 A) in the Fossil Flora under the name of *Zamia ovata*. Owing to its resemblance to *Zamia macrocephala* they referred it also to the Greensand. This fossil has accompanied the other in all its vicissitudes of generic terminology and was also placed by Carruthers in the genus *Pinites*. He considered it, too, to be of Tertiary age, both on account of its resemblance to *P. macrocephalus* and on account of the locality from which it was derived. The place of origin of the specimen of *P. ovata* in the Cowderoy Collection is also unknown.

Since the work of Carruthers little has been added to our knowledge of these cones. Mr. Starkie Gardner (5) in his Monograph of the British Eocene Flora in 1886 includes both cones in the recent genus *Pinus*, preferring to retain the name *Pinites* for coniferous remains from the Secondary rocks. Except that he regards *P. ovata* as only 'possibly a distinct species' he introduces practically no change into Carruthers' description.

GENERAL DESCRIPTION.

The shape of the cone can be seen from the longitudinal section of *Pityostrobus macrocephalus* (Fig. 2, Pl. XV). It is broadly ovoid-cylindrical and obtuse at both ends. This section, 9.3 cm. in length by nearly 5 cm. in breadth, has been prepared from a considerably water-worn specimen; the occurrence of part of a large seed at the very base makes it probable that the cone from which it was cut was incomplete. The cone from the Sedgwick Museum is about the same length though slightly broader, and certainly represents only the uppermost part of a much larger

specimen. Carruthers records one of the cones as being over six inches in length. *P. ovatus* is described as smaller and with a more tapering apex.

The axis of the cone is very slender, being usually less than 5 mm. in diameter, i. e. occupying hardly one-tenth of the total diameter. It is also noticeable that the axis maintains its very slender proportions almost unchanged throughout the whole length of the cone. A characteristic feature of all transverse sections is the conspicuous ring of large resin-canals surrounding the vascular cylinder.

Broad, sessile, and closely imbricated cone-scales leave the axis almost at right angles and curving sharply round the seeds continue almost vertically, though with a slight outward direction, for a distance of 4 to 5 cm. In transverse section, the cone-axis is seen to be enclosed by a whorl of four to five ovule-bearing sporophylls. Outside these is a zone, often more than 1 cm. in thickness, consisting of the erect distal portions of closely imbricated scales.

The presence of a short subtending bract-scale has been detected in both cones. In both cones also each of the large ovuliferous scales bears two ovules at its base occupying hollows in the upper surface. The distal end of the ovule is attached to the scale by a massive stalk-like tissue, while the blunt-ended micropyle is directed towards the centre of the cone. The lower part of the scale is also somewhat hollowed out underneath to make room for the ovules of the scale below; the basal region, however, near the point of attachment, is much thicker than the rest of the nearly horizontal portion. The long vertical portion remains thin until it reaches the surface, where it swells out somewhat to form the slightly projecting apophysis. The smooth and rounded surface of the latter does not appear to have been marked by any sharply outstanding umbo, but it is too worn definitely to settle this point.

The shape of the apophysis is supposed to constitute an important difference between the two so-called species. According to Carruthers, *P. macrocephalus* is distinguished by thick, flat, and irregularly six-sided apophyses, while those of *P. ovatus* are described as sub-quadrangular and higher than broad. Compared with figures of type specimens of the above species, the Sedgwick Museum cone appears somewhat intermediate in character (Fig. 1, Pl. XV). It has been referred to *P. macrocephalus*, but the apophyses are generally more quadrangular than hexagonal and are not infrequently higher than broad. Hence, even if allowance be made for the incomplete nature of the specimen, and it is noticeable that in Henslow's original drawing of *P. macrocephalus* the apophyses are markedly hexagonal even in the uppermost region of the cone, it is doubtful whether any great emphasis can be laid on the above distinction.

The breadth of the scale increases gradually from the base upwards, being about 2 cm. near the apophysis. Carruthers gives a fairly good restoration of the scale of *P. macrocephalus* (2, Pl. XXI, Fig. 6), but his figure seems to show too great a contrast between the breadth of the apophysis and the rest of the vertical portion. Carruthers also describes a striking feature which he says is peculiar to *P. macrocephalus* and *P. ovatus*, viz. that the basal scales are larger than those of the body. This is not found in any recent Abietinean cone. He says further, 'The basal scales are barren and the apophyses arise from their whole surface; in the series immediately above them there is a short flat body to the scale, but the greater portion of the scale is covered with the apophysis; the third series are fertile and have a larger and more ascending body'. Mr. Gardner in his monograph quotes and confirms this, but in the longitudinal sections which he figures, one of which is from the Cowderoy Collection, the base of the cone is too worn to show more than that the basal scales are at least very nearly as long as those higher up. The lowest scales in this section are not barren, but the upturned portion has the appearance of a long thin apophysis, so that it may be true to say that the basal apophyses are largest.

ANATOMICAL DETAILS.

1. *The Cone-axis.*

The greater part of the slender axis is occupied by a pith composed of rather thick-walled cells, more or less circular in cross-section, and often separated by conspicuous intercellular spaces. From the longitudinal section it is seen that the cells are elongated in the vertical direction, with horizontal or slightly oblique cross-walls, and, in fact, are closely similar to those in the axes of recent species. The weakly developed vascular cylinder has an external diameter of about 3 to 5 mm., but the width of the xylem ring is very small. The limits of the original bundles are usually well marked, even where there is a more or less complete ring of wood. The xylem consists of regularly arranged radial strands of tracheides separated by uniseriate medullary rays. There are no indications of centripetal xylem. At certain points in the ring narrow gaps mark the exit of the sporophyll-traces. The tracheides of the secondary xylem show abundant pitting on their radial walls. The large circular pits, which may extend over the whole length of the tracheide, are rather irregularly disposed. They are generally uniseriate and not in contact, but biseriate pitting is not rare, and in a few cases the pits are alternate and, exceptionally, with flattened margins. According to Thomson (14) this type of pitting occurs also in the cone-axes of recent species. He remarks: 'In the primitive regions of the latter (Abietineae) there is

a considerable amount of resemblance to the Araucarineae. Instead of opposite pitting, pitting in the cone-axis and early wood of the Abietineae has characteristically either scattered uniseriate pits or biseriate ones which are alternately arranged. Sometimes even the pits are flattened by mutual contact.' The pore of the bordered pit is usually circular, but sometimes elongated and oblique. In the latter case 'crossing' of the pores of superposed bordered pits on opposite walls of the tracheides was often observed. In a very few instances faint white lines were observed between the bordered pits, but for the most part no evidence of the presence of rims of Sanio could be detected.

A remarkable feature is the entire absence of resin-parenchyma or of

resin-canals. This is confirmed by the examination of transverse sections. On the other hand, what are probably resin plates or 'spools' are of common occurrence in many of the tracheides. It is interesting to notice that Thomson finds resin tracheides to be present in the cone-axes of species of *Pinus*, and he regards this as a retention of the primitive condition which is found in the Araucarineae and Cordaitales.

Trabeculae, or incomplete septations of the tracheides, occur in several places. They may, sometimes, be difficult to distinguish from the walls of the medullary ray cells, but are

usually thicker and better preserved. The medullary rays are not well preserved. They are usually several cells in height, but always uniseriate. In almost all cases, and large numbers are to be found in the radial sections from the Sedgwick Museum cone, the course of the medullary rays is markedly oblique to that of the tracheides. Owing to the poor state of preservation and to the thickness of the sections, the details of pitting are only observable with difficulty; where clearly seen the walls exhibit some indications of 'Abietinean pitting'. No definite ray tracheides were noted, but sometimes the shape of the marginal cells of the ray is suggestive in this connexion. The tracheide field is occupied by 1-2 large 'Eiporen'; these pits are most conspicuous in transverse sections of the cone-axis. The cambium and phloem, which are not always preserved, are composed of rather crushed, thin-walled cells filled with carbonaceous

TEXT-FIG. 1. *P. ovatus*. Radial longitudinal section of wood from base of cone, showing resin-spools, bordered pits, and walls of medullary ray cells. Cowderoy Collection, V 11003e. Diagram from a photograph.

matter. The cortical region consists of thick-walled cells circular in outline. It is marked by the presence of large, regularly disposed resin-canals arranged in a circle round the vascular cylinder. The canals are very large in the case of *P. ovatus*; in the Sedgwick Museum cone they are slightly smaller and less uniform. In all the transverse sections of *P. ovatus* the canals are exactly thirteen in number. The transverse section prepared from the Sedgwick Museum cone of *P. macrocephalus* is unfortunately not complete, but about three-quarters of the axis is present and is provided with nine resin-canals, so that, in this case also, the total number was probably thirteen.

Although such a strikingly large and regular set of canals is not to be found, as far as I am aware, in any other recent or fossil Conifer, a series of canals, varying in diameter and disposition, is of frequent occurrence in the cone-axes of many existing Abietineae. Moreover, Radais (12) has shown that in recent species the number of canals may be similarly constant, and represents the number of orthostichies; for the canals run vertically between the orthostichies, giving off branches which accompany the sporophyll traces. The latter, the 'canaux appendiculaires' of Radais, can be well seen in the transverse sections of these cones (Fig. 6, Pl. XV). Since we have thus every justification for assuming that the case here is exactly as in the recent species, we may conclude that the denominator of the phyllotaxis fraction is thirteen, and this number fits in with the ordinary Fibonacci series. Henslow made a diagram of the phyllotaxis of his specimen of *P. macrocephalus*, and concluded that the arrangement was represented by the fraction $\frac{1}{2}\frac{1}{3}$. Carruthers rightly points out that this is an anomalous arrangement, but from his examination of Mr. Dowker's specimen of *P. macrocephalus* he determined the ratio as $\frac{3}{8}$. From the considerations given above it is probable that the real value in both cones must be the next in the series, viz. $\frac{5}{13}$.

2. The Bract Scales.

Neither Carruthers nor any of the later writers makes any mention of the bract-scales. Yet evidence on this point is not lacking. In longitudinal sections of *P. macrocephalus* the bract-scale could sometimes be identified as a stout, pointed body inserted below the ovuliferous scale and occupying the space just above the micropyle of the ovule below. A similar structure was noted in a longitudinal section from the base of the cone of *P. ovatus*. A transverse section of such a scale can be seen in the tangential section from the same cone (see Fig. 4, Pl. XV). This is composed of compact, thick-walled tissue and possesses a row of small resin canals but no vascular bundle. In no case has it been possible to make any observations on the vascular supply of the bract-scale.

3. *The Ovuliferous Scales.*

The tissue of an ovuliferous scale consists chiefly of rather large, very thick-walled cells, often showing contents. In the surface layers the cells are smaller and more strongly sclerized. It is noticeable, however, that the scale as a whole, and particularly the basal region, as seen in transverse section, does not show such a large development of sclerotic tissue as seems to be usual in recent cones of a similar size. The difference in the thickening layers of the upper and lower surface is most clearly exhibited in the sections from the Sedgwick Museum cone. The lower layers of the scale consist of very narrow elongated sclereids appearing as fine wavy lines in a longitudinal section, and as crowded, circular areas with minute lumina in a transverse section of the scale. The layers of the upper surface consist of larger sclereids with polygonal outlines and frequently contain massive cells

TEXT-FIG. 2. *P. ovatus*. Transverse section of ovuliferous scale about half-way up, showing disposition and orientation of vascular bundles and chief resin-canals. *vb.*, vascular bundle; *xyl.*, xylem; *phl.*, phloem; *rc.*, resin-canal. Camera lucida drawing. $\times 6$. Cowderoy Collection, V 8309.

with peculiar irregularly elongated shapes, which may be compared to the idioblasts found in the cone-scales of the Araucarineae, &c. In the larger middle region the cells are only moderately thickened, and the whole tissue is permeated with a profusion of secretory canals. In *P. ovatus* the upper sclerized region is not so large, nor so clearly delimited from the middle region.

The seed-scale is supplied by two separate vascular strands arising independently from the sides of the gap in the main stele, just as Miss Aase (1) has recently shown to be the case among many recent conifers. Most transverse sections of the cone show the two bundles very clearly (Fig. 6, Pl. XV). The scale traces quickly broaden out and divide so as to form a single series of bundles with phloem uppermost. Text-fig. 2 shows the distribution of the bundles in a cross-section about half-way up the vertical part of the scale. The small size of the bundles and their frequent arrangement in pairs are noticeable features. In *P. macrocephalus* the bundles, though more numerous, seem to be even more minute than represented in

this figure. Some of the bundles have been cut obliquely longitudinally, and such sections show the tracheides of the xylem with uniseriate bordered pits on the walls appearing as oval black 'discs'. Protoxylem elements with spiral thickenings may be found at the edge farthest from the phloem. The bundles in the middle region of the scale are often inclined to one another at various angles, and in some cases are so grouped as to suggest the incipient formation of a second series: this is particularly the case in Mr. Edgell's specimen of *P. macrocephalus*. Dr. Stopes (13) records a similar condition in the case of *Pinostrobus sussexiensis*, Mantell., from the Lower Greensand, but in this cone the irregular orientation is more marked and a second series of bundles is definitely present.

4. *The Ovules.*

These form one of the chief features of interest. In a number of cases the contents of the ovules are comparatively well preserved and the relationships of the different structures can be made out with great clearness. The integument is thick and tapers at the apex to form a long blunt-ended micropylar tube, usually nearly or quite closed, and which is strikingly similar in appearance to that of certain Cycadean types. A transverse section in this region shows that it is composed almost entirely of heavily lignified tissue and has a narrow slit-like micropylar opening (see Fig. 4, Pl. XV). This, of course, is common in recent Gymnosperm ovules. Some of the ovules are flattened in the plane of the scale on which they lie, and in some seeds of *P. ovatus* the lateral edges are so distinctly ridged as to give a marked impression of bilateral symmetry. It is probable that the ridges are partly caused by the pincer-like extensions of the wings along the edges of the seeds from the base upwards. In the large transverse section of an ovule at the left of Fig. 4, Pl. XV, a crack appears to penetrate each of the lateral ridges, but, as a matter of fact, the opening is closed to the exterior. In the large ovule on the right-hand side of the same photograph the passage seen is actually complete, although the section seems to be quite transverse and much below the micropylar opening. The effect is probably due to external pressure. The base of the ovule frequently exhibits an extensive wing tissue at its point of attachment (see *W.*, Fig. 3, Pl. XV). Comparison may be made with Tubeuf's (15) figure of a longitudinal section of an ovule of *Pinus excelsa* which shows the large parenchyma developed by the wing in the same region. There seems no ground for Mr. Gardner's (5) statement that in *P. macrocephalus* the seeds are possibly wingless.

(i) *The Integument.*

The thick wall of the integument shows a differentiation into at least three layers. The structure, which can be studied to the best advantage in the well-preserved ovules of the Sedgwick Museum cone, is identical in all

three specimens. There is an outer layer which has usually been completely carbonized, though in some places the crushed remains of thin-walled cells adhere to the inner layers. From the manner of preservation it is clear that this represents the remains of an outer fleshy layer. Next comes a wide zone of well-preserved, thick-walled cells, obviously representing a 'stony layer'. As the photographs show, the outline of this towards the exterior is very irregular, indicating that the surface must have been marked by projecting ridges, which in some places are very prominent. The testa of the ovule of *Pinostrobus sussexiensis*, already referred to, appears to have possessed much the same structure. In reference to this Dr. Stopes remarks, 'In section, the stony layer of the testa is much indented and is irregularly star-shaped in outline, which appears to represent surface-corrugations. How far these are natural, and how far petrifact, the sections do not afford data to determine' (13, p. 127). In the less well preserved tissue of the integument of *P. ovatus* the interior of this stony layer has often been partly decomposed, leaving spaces filled with black, carbonaceous granules. This is especially common in the interior of the larger ridges.

Towards the inside the stony layer merges gradually into a less heavily sclerized zone, the cells of which are rendered conspicuous by their polygonal outlines and distinct lumen. These cells are more or less isodiametric, while those external to them are usually somewhat radially elongated. On the inside again there is a transition to small thick-walled cells, but their structure is not easily discernible and they appear to pass insensibly into the layer of crushed, fibrous-like cells which form the inner lining of the integument, and which has often become separated from the main part of the wall. This is very noticeable in the ovule seen in Fig. 9, Pl. XV, where the inner layer is only in connexion with the ovule at the very base.

(ii) *The Nucellus.*

Except in the apical region, only a thin layer of this tissue has been preserved. In the ovule mentioned above (Fig. 9, Pl. XV) it might appear at first sight as if the nucellus were free from the integument from the base upwards, but on a little closer examination it becomes evident that the nucellus is coalescent with the separated wall of the integument and only becomes free in the upper portion. In this ovule, moreover, the relations of the different structures are rendered perfectly clear by reason of the separate, distinct outline of the small crumpled prothallus which occupies the centre. Many of the other sections, however, are more difficult to interpret. A good example is the well-preserved ovule of Fig. 1, Pl. XV. In this ovule it would seem as if the cavity were nearly filled by a well-rounded prothallus which exhibits an extraordinary beak-like prolongation in its apical region. The rather shadowy surrounding tissue appears to be lifted up by the beak, so that the whole structure at once calls to mind the

way in which the 'tent-pole' of *Ginkgo* lifts up a cap formed by the remnant of the nucellus. The analogy, however, turns out to be quite false because from closer examination and comparison with other ovules it can be made out that the apical column or beak is composed of nucellar tissue, while the 'cap' forms part of the separated inner layer of the integument. In the first place it is not difficult to recognize that the thick layer surrounding the prothallus consists of much more than the megaspore membrane alone. Presumably the latter does line the interior, since the whole structure is filled with remains of prothallial tissue, but it is fairly certain that the nucellar membrane is responsible for much of the thickness. This view derives much support from the fact that at both shoulders of the large prothallial body, part of the membrane is seen to become fused with the inner integumentary tissue. Moreover, where the structure of this membrane can be determined, as, for instance, in the apical region, it is found to share all the characteristics of the nucellar tissue of other ovules. We may conclude, therefore, that we have to deal with an ovule, at a fairly advanced stage of development, in which the prothallial tissue has become much enlarged and the nucellus reduced to a mere lining layer, only part of the original prolongation being still preserved. The nature of this prolongation is discussed later on. Even in this ovule the nucellus has not altogether shrunk away from the integument. It is the inner layers of the latter which have separated from the main wall of the ovule, but yet adhere in several places to the nucellar tissue; thus also taking some part in the formation of the composite lining of the prothallus.

Turning now to other ovules for further verification, it may be noticed first that very similar conditions are to be found in one of the ovules directly below that just described. Here in one place, part of the rather delicate megaspore membrane has become separated from the thick surrounding layer, leaving no doubt that the latter is mainly of nucellar origin. In the other ovules shown in this longitudinal section of the cone, the prothallus, and consequently also the nucellus, has rarely such a well-rounded form as in two examples just cited; both nucellus and prothallus are usually much shrunken. On the other hand, in another longitudinal section which is taken from the same cone, there are some well-preserved ovules in which the nucellus is in contact with the integument for the greater part of its length (see Figs. 11, 12, Pl. XV). The nucellus lines the integument wall right up to the apical region, where it becomes free and extends across the cavity of the ovule. In both cases there is a large megaspore with a clearly defined membrane. In the ovule of Fig. 11, Pl. XV, the inner layer of the integument has separated somewhat at the apex of the ovule.

It is a significant fact that in the sections of *P. ovatus* those ovules which have been cut at all longitudinally exhibit very much the same

sort of internal structure as those of *P. macrocephalus*. The nucellus partly lines the integument and is partly free from it. It is always in connexion with the integument at the shoulders of the ovule, and there are nearly always indications of a well-developed apical column. Fig. 10, Pl. XV, which represents the upper part of a large ovule cut obliquely longitudinally, gives some idea of the stage of development shown in these sections. In this, as in many other examples, the structural features of the nucellar tissue are well preserved. They can easily be made out in the patch of tissue on the right-hand side of the photograph, especially when examined with a lens. The tissue is rarely more than one cell layer in thickness, and the thin walls of the separate cells have often been finely preserved. The cells are comparatively uniform in size, the whole structure forming a network of narrow elongated meshes. The characters just mentioned afford a criterion by means of which it is possible to recognize the nucellus in several cases which would otherwise be doubtful. Thus it often happens that by this means it is possible to distinguish both nucellar and integumentary tissue in a layer in which the double morphological origin is not immediately obvious. It, of course, affords decisive evidence of the nucellar nature of the tissue surrounding the prothallus in the ovule of Fig. 9, Pl. XV.

(iii) *The Nucellar Column.*

More or less definite evidence of the existence of this peculiar feature is to be found in almost every longitudinal section of an ovule. It is evident from the photographs (Figs. 7, 10, 11, 13) that this structure does not form a nucellar beak, but is rather a cylindrical column of parenchymatous or somewhat thick-walled cells which may exhibit the typical structure of the nucellar tissue as seen elsewhere. This parenchymatous structure is especially distinct at the base of the column where there is a shallow, moat-like depression (see Fig. 13, Pl. XV).

In the ovules of the Sedgwick Museum cone the structure of the nucellar apex is exhibited with exceptional clearness. The typical columnar form is usually represented, but the darker opaque portion appears irregularly broken into bands separated by clearer spaces, and is very suggestive of permeation by a number of pollen-tubes (see Fig. 15, Pl. XV). The cellular framework is also coarser than usual—the cells being elongated and the walls thicker and darker, though the characteristic fine meshwork tissue is often evident in the lower part of the column. There is one case in which only the thick outer wall of the column has been preserved, and this is not continuous across the apex, so that here the beak actually appears as a hollow open chamber with contorted sides.

In the thicker sections from the other cones where the whole of the beak is seen it almost invariably is dark-coloured and opaque or encloses an opaque

mass of substance, which makes it practically impossible to determine the nature of the tissue. The evidence is in favour of the view that the basal part, at least, is hollow. In the ovule seen in Fig. 10, Pl. XV, the opaque body appears to extend right into the tissue of the prothallus, but even here the bounding layer of the megaspore is found to be continuous round the intrusion. In some cases where the longitudinal section of the ovule is rather out of the median, the beak is not represented at all, but its position is indicated by a gap in the nucellar tissue which stretches across the apical region; the edges of the gap being somewhat upturned. This appearance (see *M.*, Fig. 3, Pl. XV) lends support to the view that the base of the beak was originally hollow. In one of the ovules from a small tangential longitudinal section there occurs a somewhat similar, but much narrower gap in the upper part of the nucellus, which is peculiar in being continued below through the megaspore-membrane as a sharply curved channel in the tissue of the prothallus. At the margins of the channel can be seen elongated cells somewhat like those of the nucellus, but larger and with more resemblance to the cells of the endosperm tissue, which, as a matter of fact, can only be made out in this particular slide. It is possible that the cavity has been formed by the invasion of the prothallus by a pollen-tube, although no trace of the pollen-grain can be found. It must, however, be remembered that the section is very oblique.

(iv) *The Female Gametophyte and Embryo.*

All the ovules seen in the larger sections contain prothallial tissue at about the same stage of development, but the actual state of preservation is somewhat different in different sections. An unusual condition is to be found in an ovule from the base of the cone of *P. ovatus* (Fig. 10, Pl. XV), the centre of the ovule being occupied by a small contracted megaspore with a much crumpled outline. In the majority of cases the prothallus is fairly large, though its membrane has often been somewhat contracted. Very often, especially in the Sedgwick Museum cone, there seems to have been little or no shrinkage, the outline being well rounded and closely surrounded by the nucellus (e. g. Fig. 9, Pl. XV).

The megaspore membrane consists of a comparatively thin brownish layer. Traces of prothallial tissue can nearly always be found within the megaspore; as a rule the individual cells are not distinguishable, though there is a close network of faint yellow lines and granules which is clear enough evidence of the nature of the tissue. The individual cell-walls could only be distinguished in one of the tangential sections where the ovule had been cut across transversely, and where at one side the prothallial tissue had contracted from the megaspore wall. In this region the outer part of the prothallus is seen to be composed of very thin-walled, more or less isodiametric, polygonal cells.

Very often the prothallus contains a large central cavity, or sometimes there may be more than one. In the Cowderoy specimen of *P. macrocephalus* these clear spaces are usually surrounded by an opaque black substance, largely of carbonaceous nature, which has probably been derived by the decay of the prothallial tissue that has shrunk away from the centre of the cavity.

The tissue of the gametophyte is remarkably homogeneous. With two exceptions not only are there no signs of an embryo, but there is not even evidence that, at the time of fossilization, differentiation of archegonia had taken place, even in the largest ovules. The two exceptional ovules were found in the cone of *P. macrocephalus* belonging to the Sedgwick Museum. In both the prothallus contains a body which undoubtedly represents a nearly mature embryo (Figs. 11, 12, Pl. XV). The better preserved of these is of typical cylindrical shape, tapering at the ends and contracted below the insertion of the cotyledons, and is surrounded by a tapetum-like jacket of endosperm cells which can be exactly matched in recent pine-seeds. The cells of the hypocotyl, though not individually preserved, have every appearance of being arranged in regular meristematic rows, but the cotyledonary apex is rather decomposed, so that neither the growing point nor the separate cotyledonary lobes can be distinguished. In this embryo the extremity of the radicle is very close to the base of the nucellar column, and it is interesting to notice that at the apex of the latter there are a number of structures which can only be interpreted as germinated pollen-grains (Fig. 15, Pl. XV). A suspensor could not be demonstrated; but in view of the age of the embryo this is not surprising.

In the other case the embryo exhibits at its apex a whorl of cotyledonary lobes with indications of a growing-point at their base; but otherwise it is less well preserved, and the middle region has become doubled up, presumably owing to the contraction of the apical region of the prothallus (Fig. 12, Pl. XV). No trace of pollen-grains or of pollen-tubes could be found in this ovule.

(v) *The Male Gametophyte.*

At the apex of the nucellar column of the ovule shown in Fig. 7, Pl. XV, there are two small rounded objects which most certainly represent two winged pollen-grains; they can be seen more clearly under the higher magnification of Figs. 13, 14, Pl. XV. The wing exhibits the characteristic reticulation seen in the pollen-grains of living pines, but this feature does not appear clearly in the photographs. These pollen-grains show no signs of germination.

On the other hand, it has already been remarked that structures which must be considered as germinated pollen-grains occur at the apex of the nucellar column of one of the fertile seeds. These form a small

collection of three or more grains, but the outlines are so indistinct that it is hardly possible to say whether a wing is present or not (see Fig. 15, Pl. XV).

No other examples have been found in any other ovule. Some much smaller spherical bodies, with a thin wall and filled with contents, have been observed in the neighbourhood of the nucellar apex; these seem to represent some sort of fungal spore. The nucellar apex often appears to have been perforated by pollen-tubes (this is evident in Fig. 15, Pl. XV), and a possible example of the invasion of the prothallus by a pollen-tube has been mentioned already.

THEORETICAL CONSIDERATIONS.

Before proceeding to discuss the significance of the special features associated with the cones just described, it will be as well to consider briefly the grounds on which it may be inferred that we are dealing with a single species only. The two species to which all the present material has been referred were founded entirely on differences in external appearances. Carruthers mentions only differences with respect to the form of the cone and the shape of the apophyses. His diagnoses read :

1. *Pinites macrocephalus*. Cone cylindrical, obtuse at both ends; scales with thick and flat, irregularly six-sided apophyses; basal scales largest.

2. *Pinites ovatus*. Cone ovate, with a truncate base and obtuse apex; scales with thickened, flat, sub-quadrangular apophyses; basal scales largest.

He states in his description of *Pinites ovatus* that this cone can be readily distinguished from that of *P. macrocephalus* 'by the form of the apophyses of the scales, which are longer than they are broad, and quadrangular or sub-quadrangular, the upper and lower angles being acute or but slightly truncate'. As to the general validity of this I am unable to judge, but some doubt has already been thrown on the value of this criterion in view of the intermediate character of the apophyses of the Sedgwick Museum cone.

A conspicuous difference in the appearance of the slides examined is to be found in the darker colour of those of *P. macrocephalus*. This is particularly noticeable in the Cowderoy specimens. It is partly due to the greater thickness of the sections, but largely also to their siliceous matrix being actually darker and containing a larger proportion of black carbonaceous matter. In all cases, however, the actual tissues preserved are exceedingly alike in form, structure, and arrangement. In both forms the scales possess the same general shape, with a nearly horizontal proximal portion, and, according to Carruthers, both possess the long basal scales which form so distinctive a feature of these cones. Another characteristic

feature shared by both forms is the very slender cone-axis with its surrounding ring of uniform resin-canals. As far as can be judged the number of these canals does not vary in the different forms, and the consequent identity in phyllotaxis ratio constitutes another point of agreement between the cones.

With regard to the ovules, the similarities are equally well marked. The integument, the nucellus, and the prothallus are conspicuously alike in structure and in state of preservation. Mr. Gardner's view that in *P. ovata* 'the seeds seem rounder' is not borne out by any of the slides examined. It is especially noticeable that the characteristic nucellar column and the well-developed gametophytic tissue are to be found in all the preparations. On the whole it seems justifiable to state that there are no important anatomical differences between the two so-called species. Taking this into account it seems probable that the differences in external character will turn out to be of less than specific value. At any rate it will be seen from what has been said that we can proceed with our discussion as if we were dealing with a single uniform type.

We may now turn to the consideration of some features of the cone which seem to distinguish it from existing species of *Pinus*. In the first place must be mentioned the very long and often fertile basal scales. Assuming that this is a real feature and not due to the base of the cone being broken off, it would seem that Carruthers is quite right in saying that it is a structure peculiar to these cones but not sufficient to separate them from the fossil genus *Pinites*. The very slender cone-axis is a character of some importance. This is accompanied by a very weak development of the vascular tissue as a whole, which thus does not appear to show any correspondence with the demands which must be made upon it by the reproductive organs. The wood of the very narrow xylem cylinder, often separated into distinct bundles, is always of a very homogeneous character, the simple uniseriate medullary rays and the absence of resin-canals being particularly noticeable. If we regard the cone-axis as a seat of ancestral characters, it would seem that the presence of resin tracheides in the place of the usual ducts must be considered as a primitive feature. It is in accordance with the general weak development of the conducting tissue as a whole that we find that the sporophyll-traces are very small, and that the scale strands to which they give rise are also small and comparatively widely separated even in the basal region. In the nearly ripe cones of recent species of *Pinus* that I have examined the fairly thick vascular cylinder becomes markedly angular in the region of insertion of the large scale supply, and the latter divides up almost immediately to give a row of bundles nearly touching each other and with a considerable development of secondary xylem. Although, however, it has not been found possible to match in the recent species the extreme reduction of the vascular tissue that

we find in this case, there is no doubt that this feature is of no more generic value than the fact that the resin-canals surrounding the axis are more uniform in size and more regularly distributed than appears to be the case among the present-day representatives.

The same thing really applies to the peculiar ovular characters, however difficult their interpretation.

The large size of the ovules, the detached seed-wing, the lignified integument, with closed or almost closed micropyle, and the shrunken nucellar layer, all seem to favour the view that the cone is well on its way to maturity. This is borne out by the appearance of well-developed embryos in two of the ovules. On the other hand, there is generally no indication of either archegonium or embryo, in spite of the large prothallus, and prima facie it would be natural to conclude that the cone is really much more unripe than its size and general structure would appear to indicate. The presence of ungerminated pollen-grains would appear to support this conclusion and suggests the inference that the cone may have become detached from the tree very shortly after pollination, and its development checked before fertilization was possible. On the other hand, in view of the comparatively advanced stage of development of the two fertile seeds, the prevalent absence of both pollination and fertilization can hardly be ascribed to immaturity.

The ovules are rendered still more striking by the presence of the peculiar nucellar beak. This is a cylindrical structure and does not appear to have been open at the top, so we have no grounds for supposing that it could possibly have functioned as a pollen-chamber. This is confirmed by the peculiar position of the pollen-grains. From examination of the old slides I was inclined to regard the columnar appearance as having resulted from the shrinkage of what was originally a massive apical region to the nucellus. A parallel might then be drawn with the massive free upper part of the nucellus that Dr. Stopes records as occurring in an immature ovule of *Pinostrobus Benstedii* from the Lower Greensand. There, however, the nucellar apex is conical in shape, and the attenuated tip engages with the base of the micropyle. The ovule, also, is so young that the comparison is of doubtful value. Moreover, the appearance as seen in the new slides of *P. macrocephalus* is so definite and constant that it is difficult not to conclude that the structure is a normal and characteristic feature of these ovules.

The presence of the beak, coupled with the general absence of any embryonal structures, suggests a comparison with Pteridosperms, which, however, is perhaps more interesting than profitable. Oliver and Scott (10 a), speaking of *Lagenostoma Lomaxi*, say, 'The seed of *Lyginodendron* differed from recent seeds in the early maturing of its tissues. Already before fertilization has taken place they appear to have reached the limits of

their development and would appear to be incapable of further stretching.' It is just possible that something of the same sort may have occurred in these cones.

Oliver and Scott (10 a) also speak of 'the well-preserved tissues of the nucellar base'. In our ovule the nucellus is reduced to a thin layer, while the endosperm seems more developed than in *Lagenostoma*. If then the absence of an embryo is striking in the latter instance, it should be quite as much or more so in the case of *P. macrocephalus*.

Coming finally to the consideration of the affinities of the present specimen, it will hardly be necessary after what has been said to enumerate the features which make it more closely allied to the modern *Pinus* than to any other genus of the Abietineae. The general shape and size of the cone, the two sorts of scales and their relative importance, the two reversed ovules on each scale, the winged seed, all make it certain that the cone is in every essential character identical with the living genus. Special peculiarities there are, but we have already seen that none of these can be considered to be of generic value.

It is not at all so easy to make sure of its relations within the genus *Pinus* itself. Carruthers instituted a comparison of the internal structure with that of *Pinus Pinaster*, while from the apophyses he concluded that the affinities were with *Pinus pinea*. Of the latter feature he says, '(The apophyses) scarcely differ from those of *Pinus pinea*. . . . Indeed in the form, size and arrangement of the apophyses, this recent pine remarkably resembles the fossil cone.' But, as Carruthers admits, the form of the cone and the internal structure are very different, and it seems to me that there can be no comparison between the two cones. Nor has our cone much in common with *Pinus Pinaster*. There is some general resemblance in the form of the scales, but the pyramidal shape of the cone, the very stout axis, and the small pointed apophyses make the recent species a quite different type. It is unfortunate that information is lacking as to the crucial feature of the position of the umbo on the apophysis. Carruthers would have us believe that the apophysis was a large flat surface with possibly a small central umbo. At any rate, all his suggestions of affinity refer to the *Pinaster* section of the genus. But, as already pointed out, one cannot place a great deal of reliance on his restorations, and it seems more probable that the umbo was terminal on the apophysis, as in the section *Strobus*. The general features of the cone, such as the very slender axis, are in accordance with this view of its affinities. It is interesting to note also that there appear to be many resemblances between this cone and that of *Pinothrobus sussexiensis*, Mantell., from the Lower Greensand, which is generally agreed to be closely related to *Pinus Strobus*, L. The pitting of the medullary ray field agrees with that in the recent *Strobus* section, and denticulate ray tracheides are, at least apparently,

absent. It may be noted, also, that Radais, speaking of the anatomical distinctions between the two sections of *Pinus*, remarks the absence of resin-canals from the vascular system of the scales, and apparently also from the wood of the axis in the section *Strobilus* (12, p. 278). Resin-canals are, however, present in the wood of the cone-axis of the species *Pinus excelsa*. On the whole, the anatomical characters of *P. macrocephalus* agree with those of species belonging to the *Strobilus* section, and, while there is no very close agreement with any of them, the fossil seems to have more in common with *Pinus excelsa*, L., than with any of the others.

The following diagnosis is based on the cones here considered :

Pityostrobus macrocephalus, L. and H. Cone ovoid-cylindrical, apex obtuse. Length 15 cm. or less. Breadth 5 cm. Axis very slender, surrounded by a conspicuous ring of resin-canals. Scales leave axis almost horizontally and then ascend sharply beyond the seeds, which are borne in pairs in hollows on the upper surface near the base. Apophyses thick, flat, quadrangular or irregularly hexagonal. Basal scales with large apophyses. Short bract-scale. Ovules, two on each scale, 1 cm. long by 0.6 cm. in breadth. Stone layer corrugated. Seeds usually barren.

SUMMARY.

The paper gives a detailed description and comparison of the internal anatomy of two forms of cone occurring in the Lower Eocene of the London Basin.

Two separate species, *Pinites macrocephalus*, Carr., and *Pinites ovatus*, Carr., have been founded on the slight differences in external appearance, but the close resemblance in internal structure justifies the conclusion that they are specifically identical.

The new aggregate species has been called *Pityostrobus macrocephalus*, L. and H.

The cone exhibits several interesting anatomical features. The cone-axis is very slender and has a weakly-developed xylem cylinder which contains neither resin-canals nor resin-parenchyma, but resin 'spools' are present in ordinary tracheides. A conspicuous circle of resin-canals surrounds the axis, and from their number an accurate determination of the phyllotaxis of the cone can be deduced.

The cone-scales are of the normal *Pinus* type, a short bract-scale being present. The cone is, however, peculiar in the large size of the lowermost seed-scales.

The most important observations have reference to ovular structures. The ovules are provided with a thick, differentiated integument with a long, almost closed micropyle. They represent nearly mature, winged seeds, but are usually barren and with the contents little shrunken.

The nucellus is marked by a peculiar apical column of tissue. Winged

pollen-grains, both germinated and ungerminated, have been found collected at the tip on the external surface.

The prothallus is large and well rounded, but from only two of the ovules were fossil embryos recorded. These were large and, apparently, of a normal polycotyledonous type.

It is concluded that the cone has closer affinities with *Pinus excelsa*, L., than with any other existing Conifer.

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EXPLANATION OF PLATE XV.

Illustrating Mr. C. P. Dutt's paper on *Pityostrobus macrocephalus*.

The specific names are those attached to the original specimens.

Fig. 1. *P. macrocephalus*. External appearance of cone in the Sedgwick Museum, Cambridge. About nat. size.

Fig. 2. *P. macrocephalus*. Nearly median longitudinal section of cone in the Cowderoy Collection. Basal scales with large apophyses. A, Ovule seen in Fig. 7, V 11001 b. About nat. size.

Fig. 3. *P. macrocephalus*. Median longitudinal section of same cone as in Fig. 2. B, Ovule seen in Fig. 8. W., base of seed wing; M., megaspore. Cowderoy Collection, V 11001 c. $\times$ about $1\frac{1}{2}$.

Fig. 4. *P. ovatus*. Tangential longitudinal section near base of cone. Ovuliferous scales bearing paired ovules; b.s., bract-scale. Cowderoy Collection, V 11003 d.

Fig. 5. *P. ovatus*. Transverse section of cone. Cowderoy Collection, V 8309. Nat. size.

Fig. 6. *P. ovatus*. Part of transverse section (Fig. 5) showing double nature of scale-trace supply; *r.c.*, resin-canals; *app.r.c.*, appendicular resin-canals accompanying the scale-traces. Cowderoy Collection, V 8309.

Fig. 7. *P. macrocephalus*. Ovule A, Fig. 2, more highly magnified; *n.c.*, nucellar column. Cowderoy Collection, V 11001 b.

Fig. 8. *P. macrocephalus*. Upper part of ovule B, Fig. 3. Not quite median section; *Int.*, part of integument separated from main wall; *Nuc.*, nucellus; *m.m.*, megaspore membrane; *End.*, endosperm tissue; *c.c.*, central cavity.

Fig. 9. *P. ovatus*. Longitudinal section of an ovule from the base of the cone, not quite median; *N.I.*, double layer of nucellus and integument tissue shrunk from wall; *Nuc.*, nucellar tissue alone, with indication of beak; *Mg.*, small contracted megaspore. Cowderoy Collection, V 11001 e.

Fig. 10. *P. ovatus*. Upper part of ovule showing peculiar nucellar apex; *n.c.*, nucellar column which appears to penetrate endosperm; *Nuc.*, nucellar tissue showing cellular structure clearly; *m.m.*, megaspore membrane. Cowderoy Collection, V 11003 c.

Fig. 11. *P. macrocephalus*. Longitudinal section of ovule showing large embryo and nucellar column. Sedgwick Museum.

Fig. 12. *P. macrocephalus*. Another ovule from the same cone also showing an embryo. A whorl of cotyledons (*cot.*) is present with a growing point at the base.

Fig. 13. *P. macrocephalus*. Nucellar column of ovule seen in Fig. 7, more highly magnified; *pg.*, pollen-grains. Cowderoy Collection.

Fig. 14. *P. macrocephalus*. Tip of same nucellar column still more highly magnified, showing two winged pollen-grains.

Fig. 15. *P. macrocephalus*. Tip of nucellar column of ovule seen in Fig. 11, showing germinated pollen-grains and nucellar tissue perforated by pollen-tubes.

C.P. Dutt et W. Tams phot.

DUTT—PITYOSTROBUS MACROCEPHALUS.

C.P. Dutt et W. Tams phot.

DUTT—PTYOSTROBUS MACROCEPHALUS.

Huth coll.

Dutt, C. P. 1916. "Pityostrobus macrocephalus, L. and H. A tertiary cone showing ovular structures." *Annals of botany* 30, 529–549.

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