A SPECIES OF COMPRESSED LYCOPOD SPOROPHYLL FROM THE UPPER COAL MEASURES OF SOMERSET

by M. C. BOULTER

ABSTRACT. Compression fossils of a new species of Lycopod sporophyll, *Lepidostrobophyllum alatum*, are interpreted in terms of their compression history. Three superficially different types of fossil are assigned to the same species as a result of this interpretation. These, it is suggested, are determined by the original orientation of the sporophylls in the sediment prior to compression; either upright, inverted, or lateral. The species has an alated pedicel, and the evolutionary significance of this is discussed.

THE appearance of plant compression fossils, as seen on a broken rock surface, is governed by three factors. First, the orientation of the plant organ in the original sediment; second, the collapse of the fossil resulting from compaction of the matrix; and third, the actual face of the fossil which is revealed by cleavage of the sediment.

This paper is an account of some Carboniferous lycopod sporophylls, assigned to *Lepidostrobophyllum* Hirmer 1928, the varied appearance of which is interpreted in terms of these three factors.

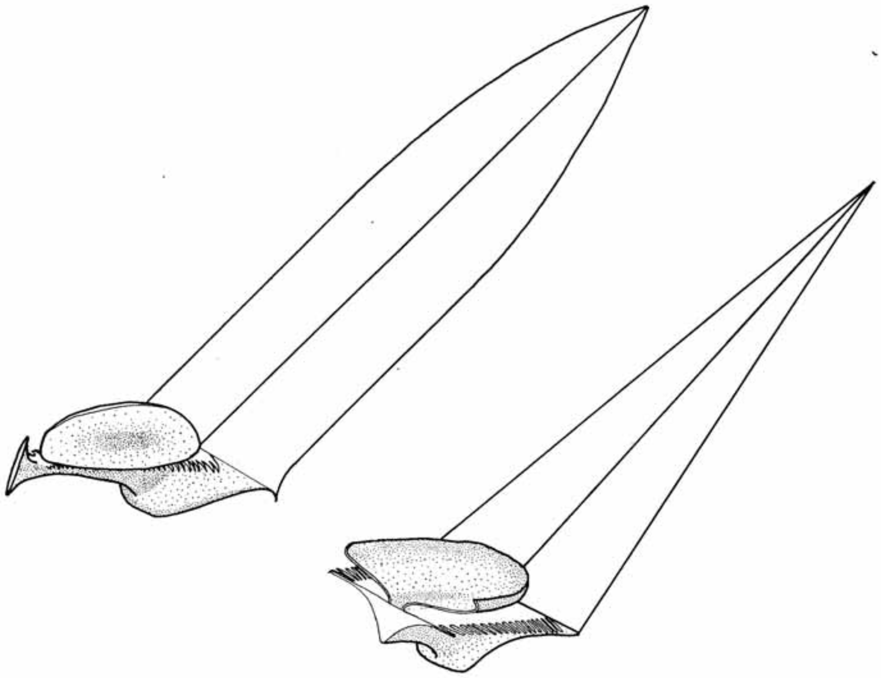
An interpretation of the original form of the sporophyll described here is shown in text-figs. 1 and 2. Its general character is that frequently demonstrated for petrified *Lepidostrobus* (Balbach 1966, Snigirevskaya 1964, Scott 1920) and for compressed sporophylls (Abbott 1963, Allen 1961) in which a distal leaf-like lamina extends from a shorter proximal region, called the pedicel. The end of this pedicel region was originally attached to the strobilar axis. Such a sporophyll could have fallen into the Carboniferous mud in three different orientations; in the first, the sporophyll remained more or less upright; in the second, it settled in an inverted position (the lower surface uppermost); in the third, it settled on its side so that the lamina of the sporophyll came to lie more or less on edge in the matrix. These three states are here described as upright, inverted, and lateral, respectively (text-fig. 3).

Walton (1936) suggests that the appearance of plant compression fossils is determined primarily by the original shape of the organ's undersurface in the matrix. On this basis, the present sporophylls, together with the matrix of mud, were subjected to vertical compression from the weight of overlying sediment, which compressed the vertical structure but left the horizontal outlines more or less unchanged. Accordingly, it is here suggested that the upright, inverted, and lateral states of orientation in the sediment resulted in the sporophylls being compressed in different ways, depending on the shape of the lower surface in the mud (text-fig. 3).

Splitting of the rock will roughly follow the bedding, and will expose the plant itself by cleaving along the plane of weakness represented by the coaly layer (or layers) of the fossil. The fossil is accordingly represented by an upper counterpart and a lower counter-

[Palaeontology, Vol. 11, Part 3, 1968, pp. 445–57, pls. 83–84.]

part. The three orientation states and these two counterparts mean that a sporophyll may be represented by six different possible states on an exposed rock surface (text-fig. 3). Even more fossil states can exist, due to there being two layers of coal in the collapsed proximal region of the sporophyll, one representing the collapsed pedicel, and the other the collapsed sporangium wall (text-fig. 2). The rock may cleave along either the coaly



TEXT-FIG. 1. TEXT-FIG. 2.

TEXT-FIG. 1. Reconstruction of *Lepidostrobophyllum alatum*. A large sporophyll which it is suggested would fall in an inverted position in the substratum.

TEXT-FIG. 2. Reconstruction of *Lepidostrobophyllum alatum*. A small sporophyll which would fall in an upright position in the substratum. The dehisced sporangium is shown in section at the proximal end. This line of section can be compared to Plate 84, fig. 6.

layers of the pedicel (Pl. 84, figs. 1 and 5) or along the coaly layers of the sporangium wall (Pl. 84, fig. 3), giving two quite different fossil forms to the pedicel region. Alternatively, the exposure of the fossil might have started by cleavage along the coaly layer of the pedicel surface, which then jumped across to cleave along the sporangium wall layer (Pl. 84, fig. 3). On this interpretation it can be seen that a single species of sporophyll can be represented by several fossilization states of rather different appearance.

As might be supposed, the frequency of occurrence of the upright, inverted and lateral states is not random. The frequency of one orientation against another will be governed by the mechanical properties of the sporophyll (centre of gravity, hydrodynamic properties), the physical properties of the Carboniferous sediment (mud, sand, etc.), and by the environment of deposition (speed of deposition, current action). A sporophyll with a small lamina is most likely to fall upright, since the centre of gravity is at the lower part of the pedicel region. A sporophyll with a larger lamina will have its centre of gravity at the upper part of the pedicel region, and so will more readily fall either inverted or laterally. A sporophyll with a tall, narrow sporangium is more likely to fall in a lateral position.

Acknowledgement. I am indebted to Dr. W. G. Chaloner, University College London, for suggesting this topic, and for numerous discussions thereon.

METHODS

Specimens were photographed macroscopically under xylol. An adaptation to Walton's transfer technique (Walton 1923) prepared selected specimens for microscopic examination. A 4 mm. layer of Ceemar embedding resin was poured into a polythene mould. After about one hour, when the surface became tacky, the fossil was placed face downwards on the resin surface. A further 1 mm. layer of resin was immediately poured on to the tacky resin. When the absence of air bubbles was ensured, the block was left overnight to set, and then immersed in hydrofluoric acid in the usual way. This adapted technique yields results as good as Walton's original canada balsam method, and has the advantage that there is no problem of temperature control in the balsam 'cooking' process. A recent detailed description of plastic transfers of fossil plant compressions (Cridland and Williams 1966) is essentially similar to the method used here. In order to investigate parts of the fossils concealed in the matrix (e.g. the heel and sporangium wall), specimens were cut and smoothed in the relevant position at a surface perpendicular to the bedding plane. When viewed under xylol, these sections show considerable detail (Pl. 84, fig. 6). Selling (1944) used a similar procedure to examine Calamitean cone compressions, though he used a microtome to produce thin sections. Block sections such as were used in this investigation require no preliminary softening treatment, and produce results similar to those of Selling. Maceration was attempted, but did not reveal cuticle or spores in any specimen.

THE GENUS *LEPIDOSTROBOPHYLLUM*

Brongniart (1828) instituted the genera *Lepidostrobus* and *Lepidophyllum* to describe respectively the supposed cones and isolated leaves of *Lepidodendron*. Later authors used *Lepidostrobus* and *Lepidophyllum* rather indiscriminately for what were believed to be isolated cone scales (i.e. sporophylls) of *Lepidodendron*. Arber (1922) in a revision of British *Lepidostrobus* compressions referred many of the species based on isolated sporophylls to *Lepidostrobus*, arguing that they are not foliar leaves, as was at one time thought, but the sporophylls of a cone. Hirmer (1928) subsequently set up the genus

Lepidostrobophyllum for those species which were based on isolated sporophylls, using *L. major* as type species. He retained *Lepidophyllum* for what were believed (from lack of a basal sporangium) to be vegetative leaves. Snigirevskaya (1958) has recently pointed out that *Lepidophyllum* was invalid in its application to fossils (having previously been used for a living plant) and substituted the generic name *Lepidophylloides* for vegetative lepidodendroid leaves. Allen (1961) emended *Lepidostrobophyllum* to describe a species of sporophyll containing a number of large megaspores.

Abbott (1963) introduced two new genera to describe unisexual lycopod strobili and their isolated sporophylls, megasporangiate, or microsporangiate. *Lepidostrobopsis* has a horizontally alated pedicel, but otherwise is similar to *Lepidostrobus*. *Lepidocarpopsis* has a horizontal and upturned alation to the pedicel, much wider than the lamina, and bears *Cystosporites* type megaspores or *Lycospora* type microspores. Abbott regards *Lepidocarpopsis* as being 'closer to genus *Lepidocarpon* than *Lepidostrobus*'. A later section in this paper explains why the name *Lepidostrobophyllum* is used for the specimens described here.

SYSTEMATIC DESCRIPTION

Class LYCOPSIDA
Order LEPIDODENDRALES
Genus LEPIDOSTROBOPHYLLUM Hirmer 1928

Lepidostrobophyllum alatum sp. nov.

Plate 83, figs. 1–8; Plate 84, figs. 1–10

Diagnosis. Isolated sporophylls consisting of distal lamina and proximal pedicel. Lamina: 1·0–5·0 cm. long; 0·4–1·0 cm. wide at base, directed obliquely towards apex. Central mid-rib extending the whole length of the lamina. Pedicel: 0·4–1·2 cm. long, 0·4–1·0 cm. wide at edge joining lamina. Prominent keel on whole length of lower surface. Heel on lower surface at junction with lamina. Hairy alation at edges, hairs up to

EXPLANATION OF PLATE 83

Figs. 1–8. *Lepidostrobophyllum alatum* sp. nov., specimens compressed in the inverted state. All the specimens figured are in the Geological Survey collection, South Kensington, London. Specimens in figs. 1, 2, 3, 6, 7, and 8 were photographed under xylol, and figs. 4 and 5 in air. 1, Upper counterpart with hastate base to lamina, and prominent sporangium wall at pedicel region; RC 4829, ×5. 2, Syntype; upper counterpart specimen in which the coal layer of the pedicel has broken away, presumably on to the fossil's lower counterpart. The outer part of the sporangium wall remains on this specimen as can be seen at the right hand side of the figure; RC 4830, ×5. 3, Smallest specimen of the inverted type which was collected; lamina mid-rib is seen to protrude down into the shale, and pedicel region is at a lower level than lamina, therefore a specimen from a lower counterpart; RC 4831, ×5. 4, Transfer of pedicel region The hastate lamina and the mid-rib are seen on the right; the hairy pedicel alation leads to the heel, which protrudes upwards (transfer of upper counterpart); RC 4832, ×6. 5, Margin of lamina, showing teeth pointing towards apex; RC 4832, ×100. 6, longitudinal section of upper counterpart showing step between lamina (on left) and pedicel, and the heel embedded in the matrix; RC 4833, ×30. 7, Transverse section across pedicel region of a lower counterpart, showing one side of the sporangium wall extending just below the surface of the cleavage plane; RC 4834, ×12. 8, Transverse section across pedicel region as in fig. 7; RC 4835, ×12.

3 mm. long. Sporangium wall extending laterally from pedicel, semi-rhomboidal in transverse section. No spores have been found.

Locality. Tip heap, Kilmersden Colliery, Radstock, Somerset. For the past twelve years, this colliery has been working the no. 10 seam, which occurs in the Farrington Group of the Upper Coal Measures, and represents Plant Zone H of Dix's divisions (Dix 1934). There is no doubt that the sporophylls described in this paper come from within this group.

Syntypes. RC 4830, Pl. 83, fig. 2; RC 4837, Pl. 84, fig. 2; Geological Survey, London.

Description of sporophylls oriented in the upright state. Detached sporophylls which are seen in this state consist of two parts, the distal part or lamina, and the proximal part which was originally attached to the strobilar axis, called the pedicel. The lamina is of variable size, 1·0–4·2 cm. long and 0·4–0·7 cm. wide at the base. The lateral margins are more or less straight, and have teeth about 0·2 mm. long, pointing towards the apex (Pl. 83, fig. 5). The mid-rib, which is about 0·7 mm. wide, passes from the base to the apex, and is made up of two parallel ridges (Pl. 84, figs. 1, 2).

The pedicel is of variable size, 0·4–1·0 cm. long, and 0·4–0·7 cm. wide at the edge joining the lamina, tapering down in nearly all specimens to 0·2 cm. wide at the proximal end. A hairy alation extends from each of the lateral margins, the hairs being up to 3 mm. long at the distal end (Pl. 84, fig. 4). These hairs are best seen in transfers, but in many of the specimens which were studied during this investigation they were not preserved. The keel extends for the whole length of the pedicel, and protrudes either upwards or downwards in upper or lower counterparts respectively. It develops into a heel at the juncture with the lamina, as can be seen in section (Pl. 84, fig. 7). The sporangium wall is preserved as two lobes, one on either side of the pedicel, and extending further than the pedicel alation (Pl. 84, fig. 4). Transverse sections across the pedicel reveal the sporangium wall embedded in the matrix (Pl. 84, fig. 6), though, as would be expected, this is only seen on the upper counterpart specimens.

Description of sporophylls oriented in the inverted state. The lamina is of variable size, 2·0–4·8 cm. long, 0·6–1·0 cm. wide at the base. The lateral margins are parallel for about the first two thirds of the length; then they curve to form an acuminate apex. Just as in the upright state specimens, these have a serrate edge and a mid-rib, though in the inverted state the lamina is hastate at the base (Pl. 83, figs. 1 and 4). The pedicel is of variable size, 0·7–1·2 cm. at the distal end. As in the upright state specimens, the pedicel has a hairy alation, though here the hairs are slightly thicker and less regular (Pl. 83, fig. 4). Collapse, during compression, has taken place into the (open) sporangium, and so the sporangium wall is more prominent in this type of preservation than in the upright orientation state. Transverse sections of some lower counterpart specimens show the embedded sporangium wall (Pl. 83, figs. 7, 8), though this is often absent when cleavage has occurred along the plane of the wall. There is a difference in level between the lamina and pedicel of up to 2 mm. On the lower counterpart the lamina is on a higher level than the pedicel, whilst on the upper counterpart the lamina is lower than the pedicel.

Description of sporophylls oriented in the lateral state. The lamina is from 1·0 to 3·0 cm. long. The distal end is often broken by cleavage or concealed in the rock. It is preserved so as to lie more or less perpendicular to the bedding plane, and so is preserved on the cleaved rock face only as a narrow line, or steeply dipping surface of about 3 mm. width. Such characters as the original width, the serrate margin, and the mid-rib cannot be seen. The pedicel proper is from 2 to 4 mm. high throughout its whole length (Pl. 84, fig. 8). On the lower edge the keel is about 3 mm. deep in the centre, becoming deeper at the proximal end for attachment to the strobilar axis. It is also deeper at the distal end where it forms the heel (Pl. 84, fig. 9). The sporangium wall extends from 0·5 to 1·0 cm. above the whole length of the upper surface of the pedicel (Pl. 84, figs. 8–10).

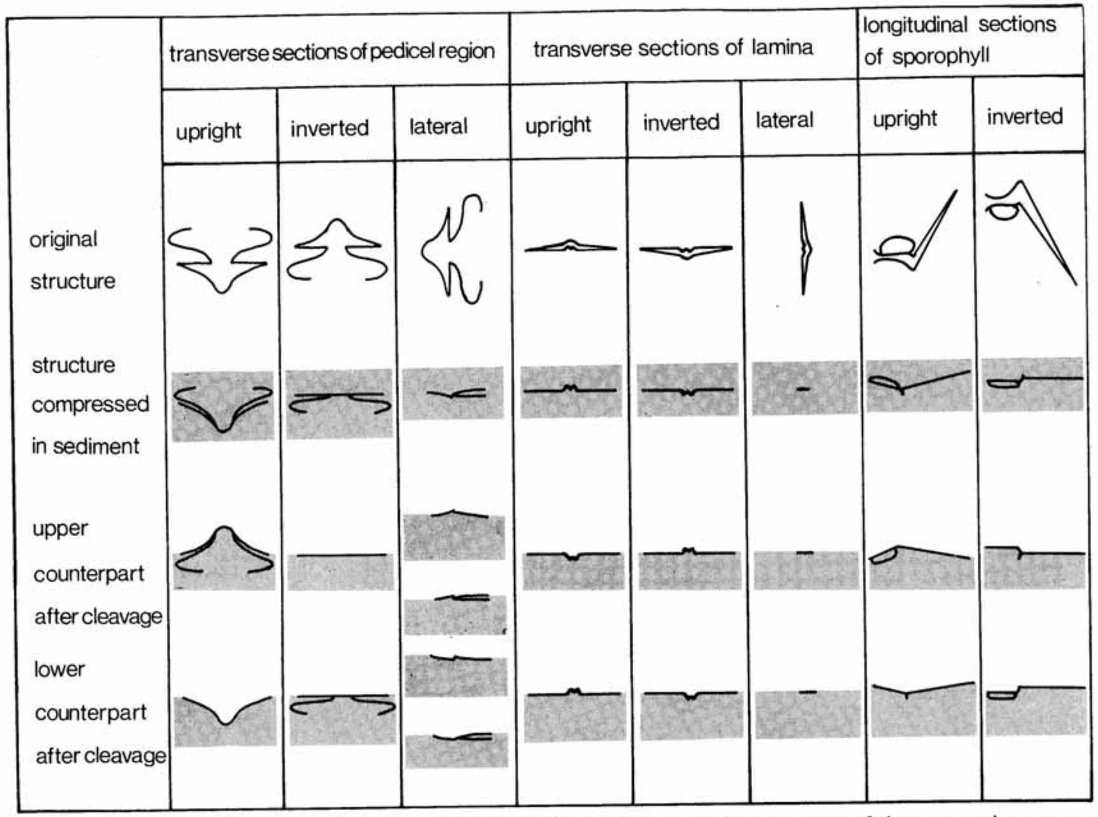
INTERPRETATION OF THE FOSSIL STRUCTURES

It was explained at the beginning of this paper that the appearance of the sporophyll fossils has been determined by the original shape of the undersurface in the mud. The sporophyll could have fallen in the mud in three principal orientations, each with a different undersurface, and these are correlated with the three different fossil states of the original structure which are found to occur.

Sporophylls falling into the mud in an upright position have the keel, heel, lower pedicel surface, pedicel alation, the outer extremity of the dehisced sporangium wall, and the entire lamina, making up the lower surface in the matrix. These structures have been preserved without distortion in the horizontal plane. The original upper surface of the pedicel and the inner parts of the sporangium wall will collapse to the level of the lower surface. But since the sporangium was semi-rhomboidal in transverse section, it became filled by, and separately enclosed in mud, and so is preserved as a separate extension from the upper surface of the pedicel (text-fig. 3). Thus, we would expect to see the sporangium buried in the matrix of the upper counterpart specimens (Pl. 84, fig. 6). The original adaxial lamina mid-rib is compressed to form a ridge protruding upwards in the matrix.

EXPLANATION OF PLATE 84

Figs. 1–10. *Lepidostrobophyllum alatum* sp. nov. All specimens figured are in the Geological Survey, London. All but figs. 2 and 4 were photographed under xylol. 1–7, Specimens fossilized in the upright state. 1, Upper counterpart in which the sporangium wall is not visible at the surface; it is suggested in this article that the sporangium wall is embedded in the shale; RC 4836, ×4. 2, Syntype. The lamina mid-rib protrudes into the matrix whilst the pedicel protrudes outwards, suggesting the specimens to be from the upper counterpart; the outer parts of the sporangium wall can be seen passing into the shale; RC 4837, ×4. 3, Upper counterpart. At top left of figure, the sporangium wall extends beyond the pedicel alation; the opposite part of the sporangium wall has not followed the cleavage plane and is embedded in the matrix of the counterpart; RC 4838, ×4. 4, Transfer showing hairy alation to pedicel and sporangium wall extending beyond this alation; RC 4839, ×4. 5, Small specimen from lower counterpart with no sporangium wall; RC 4840, ×4. 6, Transverse section of upper counterpart across pedicel region, showing the two lobes of the sporangium wall embedded in the matrix; RC 4841, ×20. 7, Longitudinal section of lower counterpart; heel prominent, and no step between lamina and pedicel; RC 4842, ×20. 8–10, Specimens fossilized in the lateral state. The lamina is broken off in three specimens (top left in 8 and 10, top right in 9). 8, Pedicel alation extends to half way up the sporangium wall; RC 4843, ×4. 9, Sporangium wall almost three times higher than the pedicel alation; heel (bottom right) and keel are prominent below the pedicel; RC 4844, ×4. 10, Specimen showing further variation in the size of the sporangium wall; RC 4845, ×4.



TEXT-FIG. 3. Diagrammatic sections of *Lepidostrobophyllum alatum* describing the consequences of the compression process. Sections across the matrix shown by stippling. Compression of the original sporophyll produces structures shown in the second horizontal row of drawings; for instance, the upper counterpart of upright state sporophylls have a protruding pedicel, a depressed (never protruding) lamina mid-rib, and no step between lamina and pedicel (see drawing of L.S. sporophyll). Again, the upper counterpart of inverted state sporophylls always have a flat pedicel region, a protruding lamina mid-rib, and a step down from the pedicel to the lamina. A specimen with a protruding pedicel (i.e. upright state, upper counterpart) never has a protruding lamina mid-rib, or a step between lamina and pedicel.

For sporophylls which fell in an inverted position, the dehisced sporangium wall and upper pedicel surface will form the lower compression surface. The pedicel and its hairy alation, together with the sporangium wall, will be preserved. But the position of the sporangium wall in the matrix will be influenced by the pedicel collapsing on top of it. The wall will thus be compressed close to the pedicel surface (Pl. 83, figs. 7, 8). The original lower surface of the pedicel and the keel will collapse on to the underlying pedicel surface and will not be preserved. The heel collapses to a more or less vertical position, but remains separated from the pedicel surface (Pl. 83, fig. 6). The originally adaxial lamina mid-rib collapses into its morphologically upper surface; that is, downwards in the matrix. It is suggested that the step between the lamina and pedicel in these inverted specimens is due to the original morphology at the juncture of lamina and pedicel. Petrified specimens (Arber 1914, pl. 22, fig. 9; pl. 24, fig. 20; pl. 26, fig. 43) show that the distal face of the heel is a straight continuation of the lower surface of the lamina, and that there is a slight depression on the upper surface at the distal end of the lamina, directly above the heel. This is likely to be preserved after compression, as a difference in level between lamina and pedicel (text-fig. 3).

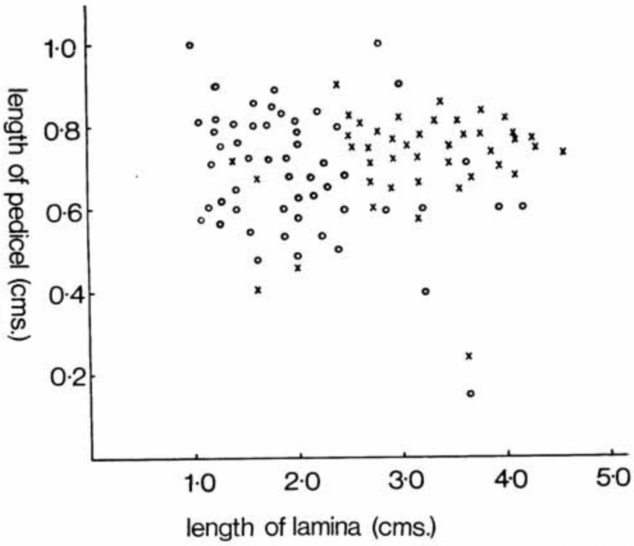
This interpretation is again consistent with the specimens studied. Specimens in which the lamina mid-rib is seen as a groove depressed into the matrix (i.e. in the lower counterpart) have no heel in section, though the sporangium wall can be seen in transverse section (Pl. 83, figs. 7, 8). This is never as well defined as in the upright specimens because, as is suggested above, the pedicel collapses on top of the sporangium wall during the process of compression. And when the mid-rib appears as a ridge projecting upwards from the cleaved fossil surface (i.e. in the upper counterpart) the heel is present in the matrix, as seen in section, and the sporangium wall is absent. The keel is never seen in either upper or lower counterpart fossils and the pedicel surface is always more or less flat.

Sporophylls which fell in the sediment in an upright position tend to have a smaller lamina length pedicel length ratio than those that fell inverted (text-fig. 4). This is presumably because the relatively greater lamina length favoured settling in the inverted position. The size of the sporophyll would probably be a function of its position on the strobilus; the larger sporophylls towards the base, the smaller ones towards the apex. This conclusion is evident from studies on petrified material (Arber 1914, pl. 23, fig. 13).

Specimens of sporophylls which have been compressed laterally show the original vertical aspect of the keel, heel, pedicel, sporangium wall, and lamina. The pedicel alation is preserved in most specimens (Pl. 84, figs. 8, 10) as a rugose margin above the pedicel, a very doubtful consequence of compression of the hairs which are seen in the upright and inverted states. From the evidence available in these compression fossils, it is not possible to ascertain the original morphology of the pedicel alation; whether it was horizontal, or upturned at the edges to protect (even partially) the sporangium. Indeed it must be accepted that the attribution of the laterally compressed specimens to this species (which is based primarily on upright and inverted specimens) is somewhat arbitrary. But at least all three states can be reconciled with a single reconstruction such as that offered in text-fig. 1. Until spores are found enclosed on the sporangium, or other indirect evidence is obtained, the correlation of the sideways compressed fossils with the other two states remains hypothetical.

COMPARISON WITH PREVIOUSLY DESCRIBED SPOROPHYLLS

The majority of specific, and indeed generic, diagnoses of detached lycopod sporophylls are concerned principally with the size and shape of the lamina and pedicel, and in some cases with the type of spore extracted. No spores have been found in the present study, and so the only comparable characters are size and shape. Both these have proved to be



TEXT-FIG. 4. Length of sporophyll lamina plotted against length of pedicel, for specimens of *Lepidostrobophyllum alatum* sp. nov. compressed in upright (*o*) and inverted (*x*) states. The distribution shows that the longer lamina give a preferred orientation towards the inverted state (clustering of symbol *x* at right of diagram).

extremely variable in *Lepidostrobophyllum alatum* and so the comparison with other sporophylls is limited by our ignorance of the details of sporangium and pedicel for most of the earlier described species.

Lepidostrobus triangularis Zeiller. The original description by Zeiller (1886) and subsequent descriptions (Arber 1922, Crookall 1966) show that this species is very similar in shape and size to the smaller specimens described in this paper as having been fossilized in the upright state. The pedicel resembles that in specimens of *L. alatum* which have cleaved across the layer of the pedicel and not along the sporangium wall (Pl. 84, fig. 5). But specimens labelled as *L. triangularis* in the Kidston Collection, Geological Survey, London (nos. 819a, 6249, 8196) show a clearly defined edge to the pedicel, which is too narrow to have alation. Also these specimens have a completely flat contour, and so their compression history cannot be compared to that of *L. alatum*.

Lepidostrobus goodei Jongmans (Jongmans 1931). In his recent review Crookall (1966) describes this species as having a wedge-shaped pedicel 5–7 mm. long and 2–3 mm. wide. This again could represent upright specimens of *L. alatum* in which the pedicel alation and sporangium wall are compressed in the matrix, if they are present at all; sporophylls at the extreme tip of the strobilus may not have had a well-developed alation or sporangium. The lamina of *L. goodei* is of a comparable size to upright specimens of *L. alatum*.

Lepidophyllum gracile Lesquereux. Lesquereux's type figure (Lesquereux 1884) has similar shape and size to upright specimens of *L. alatum* which have cleaved along the sporangium wall. The species has not been described from Britain.

Lepidostrobus brevifolius Lesquereux (Lesquereux 1857). This has a wedge-shaped, keeled pedicel, 0·8–1·0 cm. long, and a triangular lamina, 6–8 mm. long (Crookall 1966). This species can again be compared to small specimens of *L. alatum*.

Lepidostrobus lancifolius Lesquereux. The type figure of this species (Lesquereux 1870) shows identical features to the inverted state of *L. alatum*: acuminate apex to lamina, hastate base to lamina, prominent sporangium wall to pedicel, and similar dimensions. No details are available in the literature of the step between lamina and pedicel or whether the mid-rib formed a ridge or a groove.

Lepidophylloides acuminatus (Lesquereux) Crookall (Crookall, 1966). Although no specimens of *L. alatum* as large as those described for this species have been collected, the shape and proportions of the two species are identical.

Lepidocarpon mazonensis Schopf. Schopf (1938) described a side-compressed sporophyll containing a seed megaspore which has a rugose texture on the margin of the integuments. The comparable structure in laterally compressed specimens of *L. alatum* is what is here regarded as the pedicel alation. Except for the megaspore in Schopf's specimens, the two types seem identical.

If the lateral states of *L. alatum* had a single functional seed megaspore and an integument, rather than the alated pedicel which is suggested in this paper, then they should be reassigned to *Lepidocarpon* sp.

Alternatively the interpretation of the lateral state of *L. alatum* given above could be correct. And if the specimens described by Schopf are equivalent (i.e. they have an alated pedicel rather than an integument), both Schopf's *Lepidocarpon mazonensis* and the specimens described here as *Lepidostrobophyllum alatum* must be reassigned to a different genus, describing sporophylls with a single functional megaspore and no integument, namely *Achlamydocarpon* Schumacker-Lambry (see below).

Thirdly, *L. alatum* may not have contained a single functional megaspore, in which case the present separation of *Lepidostrobophyllum alatum* from *Lepidocarpon* sp. holds good.

Cantheliophorus spp. Bassler. This genus (Bassler 1919), described as a 'sporangiophoric lepidophyte', has a similar appearance to the lateral states of *L. alatum*. Schopf (in Janssen 1940) refers Bassler's genus to *Lepidocarpon* by reinterpreting the structure. This was supported later (Schopf 1941, p. 559) by the identification of single megaspores from the illustrations in Bassler's paper. Photographs of *Lepidophyllum waldenburgensis* in Nathorst (1914), refigured by Bassler (1919), have a similar character to the specimens of *L. alatum* which were laterally compressed.

All the above-mentioned species are defined principally in terms of size and shape, factors which are variable in *L. alatum*. It is therefore suggested that the specimens described in this paper should not be assigned to any previously described species, unless characters of the pedicel structure and the compression process are investigated for these established species. Unfortunately, it is not possible to transfer or develop type specimens to obtain this information, and so full descriptions of species described over forty years ago are unlikely ever to be obtained. Inevitably, new species must be made which may overlap the ill-defined limits of other species.

GENERIC ATTRIBUTION OF *L. ALATUM*

The assignation of the species here described to *Lepidostrobophyllum* is uncertain, due to the absence of spores in all specimens. If the sporangium is ever found to have contained one or several tetrads of functional megaspores, or numerous microspores, then the assignation is correct. But if the sporangium contained only one functional megaspore, with three aborted spores (i.e. a *Cystosporites* type megaspore), then the sporophylls belong to a genus in the Lepidocarpaceae (Schopf 1941).

In all specimens of *L. alatum* the sporangium wall extends beyond the pedicel alation (Pl. 83, fig. 4; Pl. 84, fig. 4); the alation could never have completely enclosed the sporangium. Therefore the genus *Lepidocarpon* is not applicable to any of the specimens dealt with here.

Schumacker-Lambry (1966) describes a new genus of petrified lepidocarps as *Achlamydocarpon*. The pedicel alation is not developed into an integument, rather, it is as in the species described here, or absent. The single functional megaspore is completely protected by a sporangium wall four layers thick. If a single functional megaspore is ever found in any *L. alatum* specimens, the generic assignation might be changed to *Achlamydocarpon*, though the identification of a thick sporangium wall in compression fossils presents a severe difficulty. It is evidence that Schumacker-Lambry's genus *Achlamydocarpon* may be partially synonymous with Abbott's genus *Lepidocarpopsis*; they both represent 'unintegumented lepidocarps', although the evidence for lack of integument is clearer in Schumacker-Lambry's petrified material than in Abbott's compressions.

In his reinterpretation of Bassler's *Cantheliophorus*, Schopf refers it to the genus *Lepidocarpon*. He did not differentiate between the structures of an alated pedicel and a thick sporangium wall, so it is possible that some, if not all of the specimens described by Bassler are members of *Achlamydocarpon*. In this case, 'the surface rugosity of the sclerotic cells on the integument surface' (Schopf 1941, p. 560) would be cells of the thick sporangium wall, or of the pedicel alation.

EVOLUTIONARY SIGNIFICANCE

The structure of the pedicel in *L. alatum* represents an intermediate stage in the evolutionary change from the unprotected sporangium of many species of *Lepidostrobus* sporophylls to the integumented *Lepdidocarpon*. Abbott (1963) has instituted a new genus for such an intermediate, *Lepidocarpopsis*, whilst Balbach (1966) suggests that the morphological changes involved are only of specific importance.

The evolutionary tendencies towards specialization of the pedicel and sporangium structure in arborescent lycopod sporophylls seems to be more diverse than was previously thought. The simplest Carboniferous *Lepidostrobus* had completely unprotected sporangia containing microspores and megaspores. *Lepidostrobus takhtajanii*, *L. masleni*, and *Achlamydocarpon belgicum* seem to represent one extreme in the evolutionary development with a single fertile megaspore protected by a thick sporangium wall and no integument, whilst *Lepidocarpon*, with a single fertile megaspore protected by an integument around the sporangium, represents another.

The broad extent of the hairy alation in *Lepidostrobophyllum alatum* is in some degree morphologically intermediate between *Lepidostrobus* and *Lepidocarpon*. The lack of information concerning the thickness of the sporangium wall and the type of spores in these specimens make it impossible for us to appreciate the significance of the species, at the present.

REFERENCES

ABBOTT, M. L. 1963. Lycopod fructifications from the upper Freeport (no. 7) coal in southeastern Ohio. *Palaeontographica*, **B 112**, 93–118.

ALLEN, K. C. 1961. *Lepidostrobophyllum fimbriatum* (Kidston 1883) from the Drybrook Sandstone (Lower Carboniferous). *Geol. Mag.* **98**, 225–9.

ARBER, A. 1914. An anatomical study of the Palaeozoic cone-genus *Lepidostrobus. Trans. Linn. Soc.* ser. 2, **B 8**, 205–38.

ARBER, E. A. N. 1922. Critical studies of Coal-measure Plant-impressions. *J. Linn. Soc.* **B 46**, 171–217.

BALBACH, M. K. 1966. Paleozoic Lycopsid fructifications. II. *Lepidostrobus takhtajanii* in North America and Great Britain. *Amer. J. Bot.* **53**, 275–83.

BASSLER, H. 1919. A Sporangiophoric Lepidophyte from the Carboniferous. *Bot. Gaz.* **68**, 73–108.

BRONGNIART, A. 1828. *Prodrome d'un Histoire des Vegetaux Fossiles*, p. 87. Paris.

CRIDLAND, A. C., and WILLIAMS, J. L. 1966. Plastic and epoxy transfers of fossil plant compressions. *Bull. Torrey Bot. Club*, **93**, 311–22.

CROOKALL, R. 1966. Fossil plants of the Carboniferous of Great Britain. *Mem. Geol. Surv.*, Palaeontology, IV, part 4.

DIX, E. 1934. The sequence of floras in the Upper Carboniferous, with special reference to South Wales. *Phil. Trans. Roy. Soc. Edin.* **57**, 789–838.

HIRMER, M. 1927. *Handbuch der Paläobotanik*. R. Oldenbourg, Munich.

JANSSEN, R. E. 1940. Some fossil plant types of Illinois. *Illinois State Museum, Sci. Pap.* **1**. Springfield, Illinois.

JONGMANS, W. 1931. '*Namenänderung bei Lepidostrobus*' Jaarverslag over 1930, p. 91. Geol. Bureau, Heerlen.

LESQUEREUX, L. 1857. Fossil Plant Coalfields Pennsylvania. *Boston J. Nat. Hist.* **6**, 4, 430.

—— 1870. Fossil Plants of Illinois. *Geol. Surv. of Illinois*, **4**, 2, 442.

—— 1884. Description of the coal flora of the Carboniferous formation in Pennsylvania, vol. III. *2nd Geol. Surv. Pennsylvania, Report of Progress.*

NATHORST, A. G. 1914. Zur fossilien Flora der Polarländer, I. 4. *Nachträge zur Paläozoischen Flora Spitzbergen*, 110 pp. Stockholm.

SCHOPF, J. M. 1938. Two new Lycopod seeds from the Illinois Pennsylvanian. *Trans. Ill. State Acad. Sci.* **30**, 139–46.

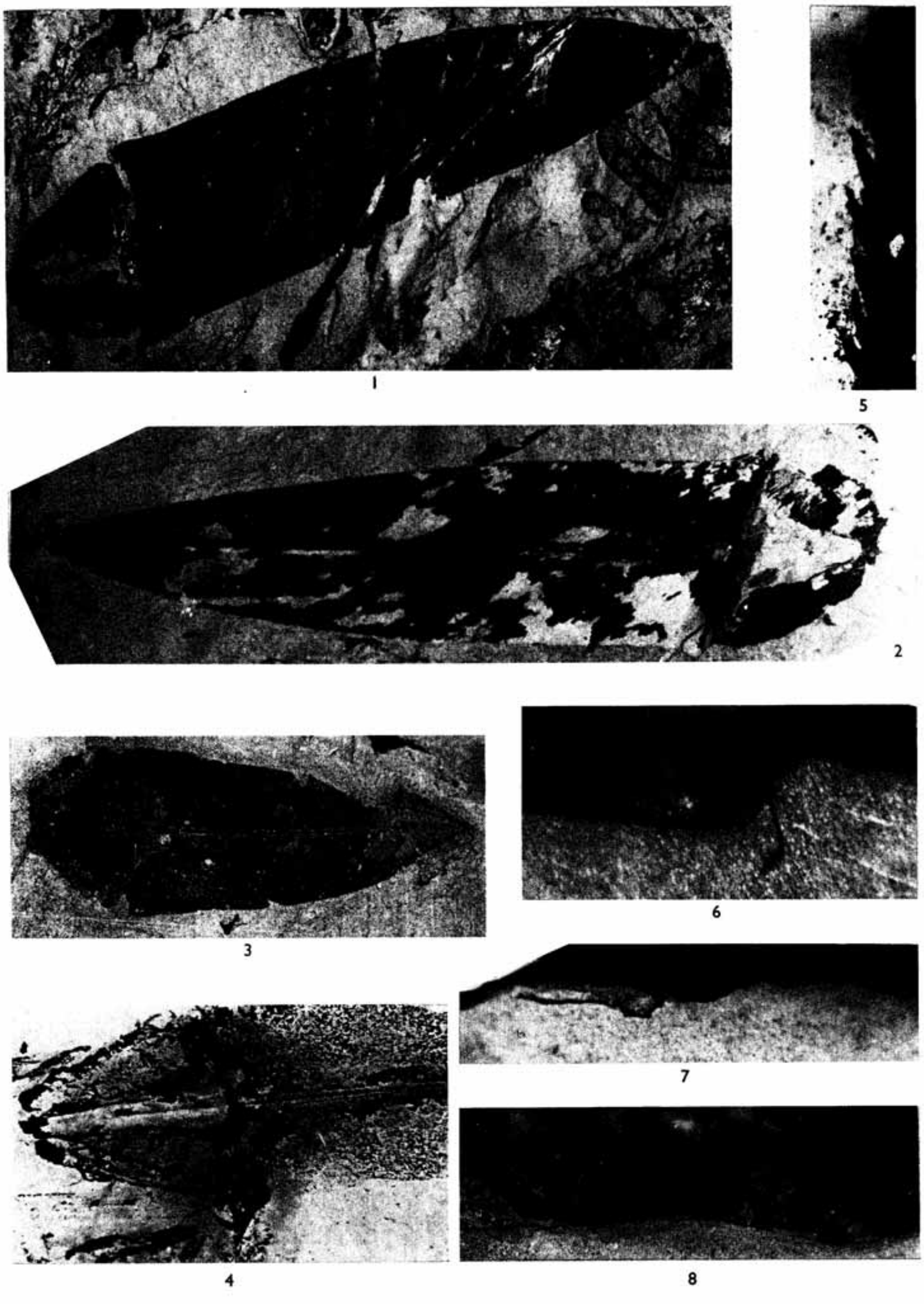
—— 1941. Notes on the Lepidocarpaceae. *Am. Midl. Nat.* **25**, 548–63.

SCHUMACKER-LAMBRY, J. 1966. Étude d'un cône de Lepidocarpaceae du houiller belge: *Achlamydocarpon belgicum* g. et sp. nov. *Acad. Roy. Belgique Mémoires*, Coll. 4°, Deuxième séries, **17**, 1.

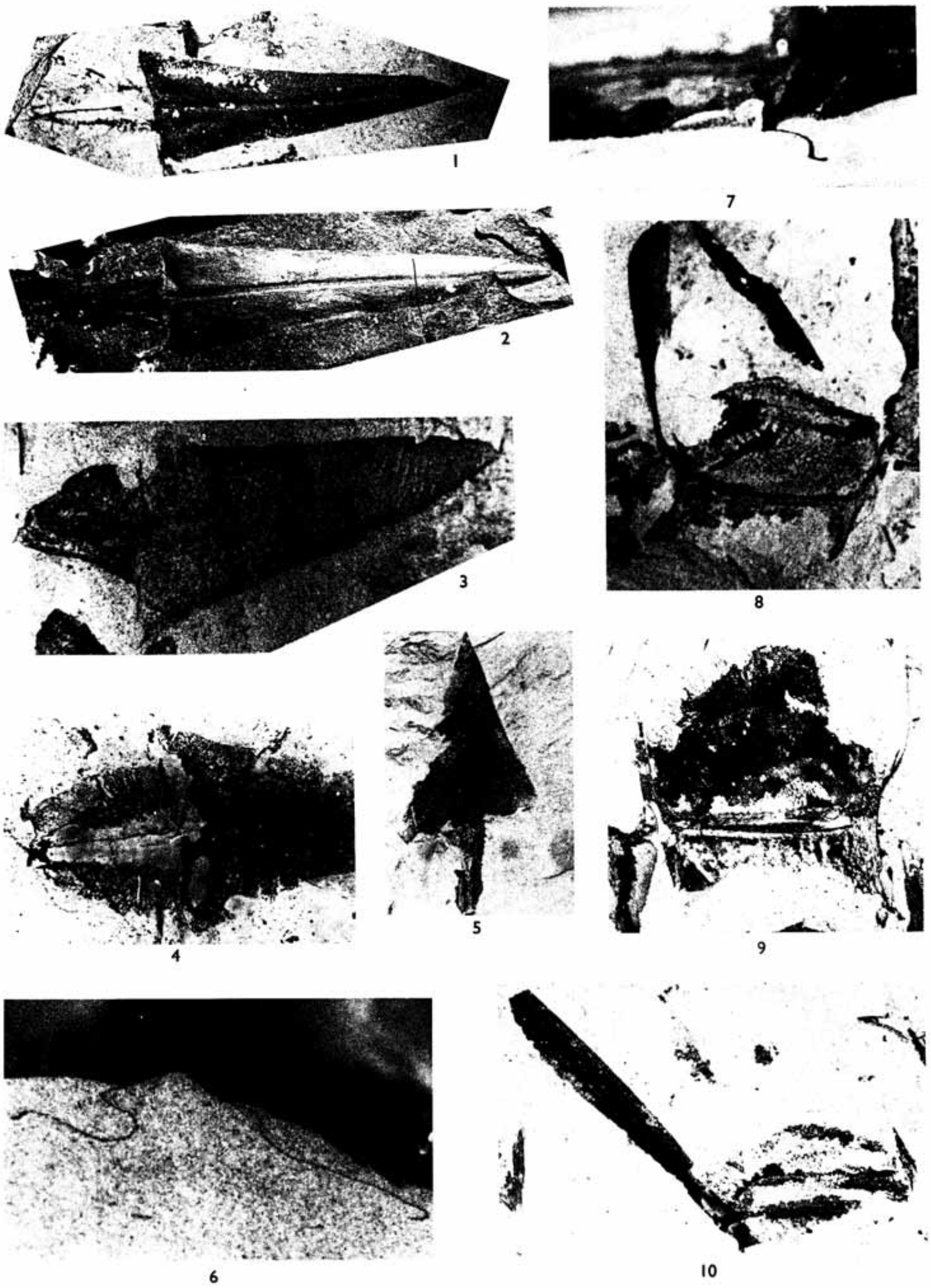
SCOTT, D. H. 1920. *Studies in Fossil Botany*. Part 1. Black, London.
SELLING, O. H. 1944. Studies on Calamitean Cone Compressions by means of serial sections. *Svensk Botanisk Tidskrift*, **38**, 295–330.
SNIGIREVSKAYA, N. S. 1964. An anatomical study of the plant remains from the Donets coalballs. I. Lepidodendraceae. *Paleobotanika Akad. Nauk., U.S.S.R. Trudy*, Ser. 8, Pt. 5, 1–36. [In Russian.]
WALTON, J. 1923. On a new method of investigating fossil plant impressions or incrustations. *Ann. Bot.* **37**, 379–91.
—— 1936. On the factors which influence the external form of fossil plants; with descriptions of the foliage of some species of the Palaeozoic Equisitalian genus *Annularia*, Sternberg. *Phil. Trans. Roy. Soc. Lond.* **B 226,** 218–37.
ZEILLER, R. 1886. 'Bassin houil. de Valenciennes.' Études Gîtes Min. France, 508 pp. (1888); Atlas (1886).

M. C. BOULTER
Department of Biology
West Ham College of Technology
Romford Road, London E. 15

Manuscript received 16 June 1967



BOULTER, Carboniferous lycopod sporophyll



BOULTER, Carboniferous lycopod sporophyll