A NEW BRITISH CARBONIFEROUS CALAMITE CONE, *PARACALAMOSTACHYS SPADICIFORMIS*

by B. A. THOMAS

ABSTRACT. *Paracalamostachys spadiciformis* is described as a new species of calamitean cone from the lower Westphalian of Northumberland, England, from which isolated cones, attached cones, and associated shoots were collected. The cones, which are up to 9 cm. long and about 1 cm. broad with whorls of about 16 bracts and 6 sporangiophores, are bisexual with spores referable to *Calamospora* cf. *laevigata* (Ibrahim) Schopf, Wilson, and Bentall sensu Smith and Butterworth, *C. perrugosa* (Loose) S. W. & B., *C. microrugosa* (Ibrahim) S. W. & B. and *C. pallida* (Loose) S. W. & B. The cones were borne in close whorls on broad stems which were themselves probably produced terminally on narrow shoots; this attachment of the cones is unusual and unlike previous descriptions.

MANY species of calamite cones have been described either as compressions or petrifactions and have often been found attached to parent shoots. The spore contents have frequently been described showing that there are both unisexual and bisexual cone species.

This account deals with a collection of compressions of isolated and attached cones, leafy and non-leafy shoots which were all found in close association. They all came from one shattered and weathered block of light grey shale about 70 cm. square and 30 cm. thick. The shale came from an old colliery tip which was being re-excavated near Bedlington, Northumberland (Grid reference AA 246815). The original stratigraphical horizon of the shale can only be given as Productive Coal Measures below the Ashington Marine Band (Westphalian A or B).

The specimens were examined dry and under xylol and several isolated cones were transfered on to glass slides by the Walton method, but with 'Lakeside' as the mounting medium. Spore samples were prepared by macerating small fragments of compression in Schulze solution and any small spore aggregates that remained were dispersed with ultrasonic vibrations.

The specimens and preparations have been deposited in the collections of the Geological Survey, London; nos. 77226–38 and PF4450,1.

DESCRIPTION

The cones. The isolated and attached cones are described together as one species. The only dissimilarity is one of length and this is not considered of specific importance in this instance.

Most of the detached cones are incomplete but all are longer than the 3 cm. length of the largest attached cone. The longest, no. 77229 (Pl. 44, fig. 2), is 9 cm., but even this one is incomplete at the apex. All are roughly 1 cm. broad except no. 77229 with sporophylls more widely spreading than in other cones. The cone axes are about 1·3 mm. diameter and have a basal swelling 3–4 mm. broad. There are whorls of bracts at 3–4 mm. distance on the axes with the lowest whorl 5 mm. from the basal swelling. There are about 16 bracts in each whorl although the exact number could not be seen in any

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whorl. Each bract is about 1 cm. long and 0·6 mm. broad near its base gradually tapering towards its apex. The bracts leave the cone axis at right angles but then turn upwards in varying amounts, becoming roughly parallel to the axis in some specimens. The basal three or four whorls are sterile, but the rest possess whorls of about six sporangiophores. The greatest number of fertile whorls observed was 21 on no. 77228. The alignment of the sporangia, especially in the longitudinally split cones, suggests that the sporangiophores were borne in the axils of the bracts. However, there is no visible attachment point to prove this. The sporangia are about 3 mm. long and 2 mm. broad but no details were seen of their attachment to a sporangiophore.

The attached cones are borne in close whorls on broad stems. Two portions of broad stem were found but unfortunately both were broken by shale fragmentation prior to collection. No. 77226a (Pl. 44, fig. 3) is the lower part of such a stem attached to a narrow articulated stem bearing whorls of small leaves at its nodes. The broad part of no. 77226a has round-polygonal areas with what appear to be bracts. The internodes of the narrow stem decrease in length acropetally from 12 mm. to 1·5 mm., with a rapid decrease in the size for the last two internodes below the abrupt increase in stem diameter. No. 77227 (Pl. 45, fig. 6) also appears to be the lower part of a swollen stem but is not attached to a narrow shoot. No. 77227, however, has rectangular areas and, unlike no. 77226a, has lost most of its compression. Both stems bore lateral leafy shoots but only no. 77227 is seen to have cones.

Maceration of part of the compression from the broad stem (no. 77227) gave only a very few spores and no cuticle. The spores were similar to the microspores described below and are, no doubt, merely liberated spores that have become trapped on the stem surface.

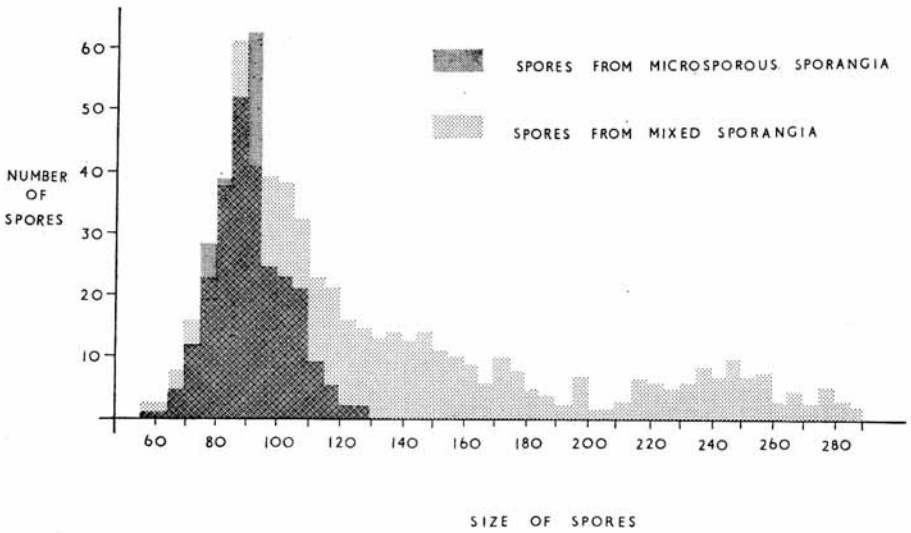
The spores. Spores were obtained by macerating small fragments of compression from various positions on the cones. Microspores and megaspores were recovered showing the cones to be hermaphrodite.

All the spores were probably roughly spherical before compression as their walls show numerous folds, but in the compressed condition they appear oval or round. Distinct trilete rays are shown, often with raised lips, and the contact areas are visible in most spores. The spore exines are translucent and laevigate or minutely granular. All the spores would be included in the genus *Calamospora* Schopf, Wilson, and Bentall (1944) if found in the dispersed state. The range of spore size is shown in text-fig. 1 and the spores are interpreted as microspores (55–130 μ) and megaspores (*c.* 100–350 μ). The macerations usually gave only microspores but occasionally microspores and megaspores were obtained. Megaspores were never prepared alone suggesting that the megasporangia were few and dispersed. The larger number of spores in the size range 100–30 μ in the mixed spore populations suggests that some of these are small megaspores and not microspores. The recovery of both microspores and megaspores from single macerations could be taken as evidence of bisexual sporangia but it is more likely that the spores were from adjacent but adhering sporangia. No definite arrangement of the two kinds of sporangia was discovered except that megaspores were only recovered from the basal areas of the cones.

Microspores. The microspores are normally 65–130 μ in diameter with the occasional spore as small as 55 μ. The mean diameter is 93 μ and the standard deviation 7·6 μ.

The trilete rays are straight or slightly flexuose and have small lips about 1 μ high. They are about one quarter to one third of the spore radius. The spore exine is structureless and slightly less than 1 μ thick.

Most of these spores are very similar to the dispersed spores known as *Calamospora microrugosa* (Ibrahim) Schopf, Wilson, and Bentall 1944. Imgrund (1960) and Playford (1962) stated the trilete rays to be up to two thirds the spore radius but no such lengths



TEXT-FIG. 1. Histograms of spore size distribution in *Paracalamostachys spadiciformis* sp. nov.; slides PF 4450, 1.

have been found in the spores studied here. Smith and Butterworth (1967) have described some spores as *C.* cf. *microrugosa* distinguishing them by their oval shape and greater size range (57–97 μ against 62–104 μ for their *C. microrugosa* sensu stricto) and because their trilete marks are mostly hidden by folds. However as such variations are shown within the present spore population this distinction would no longer appear necessary. The smallest forms (below 80 μ) are indistinguishable from *C. pallida* (Loose) Schopf, Wilson, and Bentall which is itself similar to *C. microrugosa* in all but size. Smith and Butterworth separated these two species by size alone using 75 μ diameter as the dividing measurement.

Megaspores. Text-fig. 1 shows that the megaspores have a very wide size range and that they can be arbitrarily divided into two groups at 210 μ, with roughly one quarter of the spores belonging to the larger-sized group. Both groups are closely comparable to different species of dispersed spore.

The larger spores have a mean diameter of 246 μ and a standard deviation of 15·4 μ. The trilete rays vary in length from about 25–40 μ and have lips which are about 3 μ thick near the centre but which gradually thin further out and often disappear before the

end of the ray. The spore exine is about 2 μ thick and scabrate. The contact area is normally clearly visible due to denser granulation of the exine in this region.

These spores are almost identical with those described by Smith and Butterworth (1967) as *Calamospora* cf. *laevigata* (Ibrahim) Schopf, Wilson, and Bentall 1944. The only difference being their quoted size range of 150–260 μ. No spores were recovered from the cones which fully agreed with *C. laevigata* sensu stricto. Although some came within the size range of 250–500 μ all possess visible contact areas, which *C. laevigata* does not, and all have exines thinner than the 4–7 μ quoted for the species.

The smaller megaspores are intermediate in character between the microspores and the larger megaspores. The trilete rays are straight, about one-third of the spore radius, and have lips about 1 μ high. The mean diameter is about 135 μ but neither this nor the standard deviation can be given accurately as the smallest megaspores are indistinguishable from the largest microspores.

The closest dispersed spore species is *Calamospora perrugosa* (Loose) Schopf, Wilson, and Bentall, which differs from the spores described here only in its narrower size range (130–60 μ). Horst (1955) and Potonié and Kremp (1955) have compared *C. perrugosa* to a large form of *C. microrugosa* while Smith and Butterworth have distinguished these two species merely on size. It is therefore interesting to find spores resembling these two dispersed spore species within a single cone.

Associated shoots and stems. Leafy shoots, that would be included in *Asterophyllites* Brongniart, and leafless stems, that would be included in *Calamites* Suckow, were found in close association with the cones. The leafy shoots are either terminal as in Plate 44, fig. 4 or larger but non-terminal as in Plate 44, fig. 5. There are 12–16 leaves in each whorl; individual leaves being linear and broadest at their base. In the terminal shoots they are attached at near right-angles but in the larger shoots they depart at more acute angles. The largest specimen had leaves 2 cm. long and internodes 9 mm. long. The leafless stems possess ridge and furrow markings, alternating at the nodes, and fine longitudinal striations. All these stems are about 1–1·5 cm. broad with internodes 3·5–5 cm. long.

Generic attribution. The cones have the typical calamite arrangement of alternating whorls of sporangiophores and bracts and the spores clearly belong to the genus *Calamospora* which has often been described from such cones.

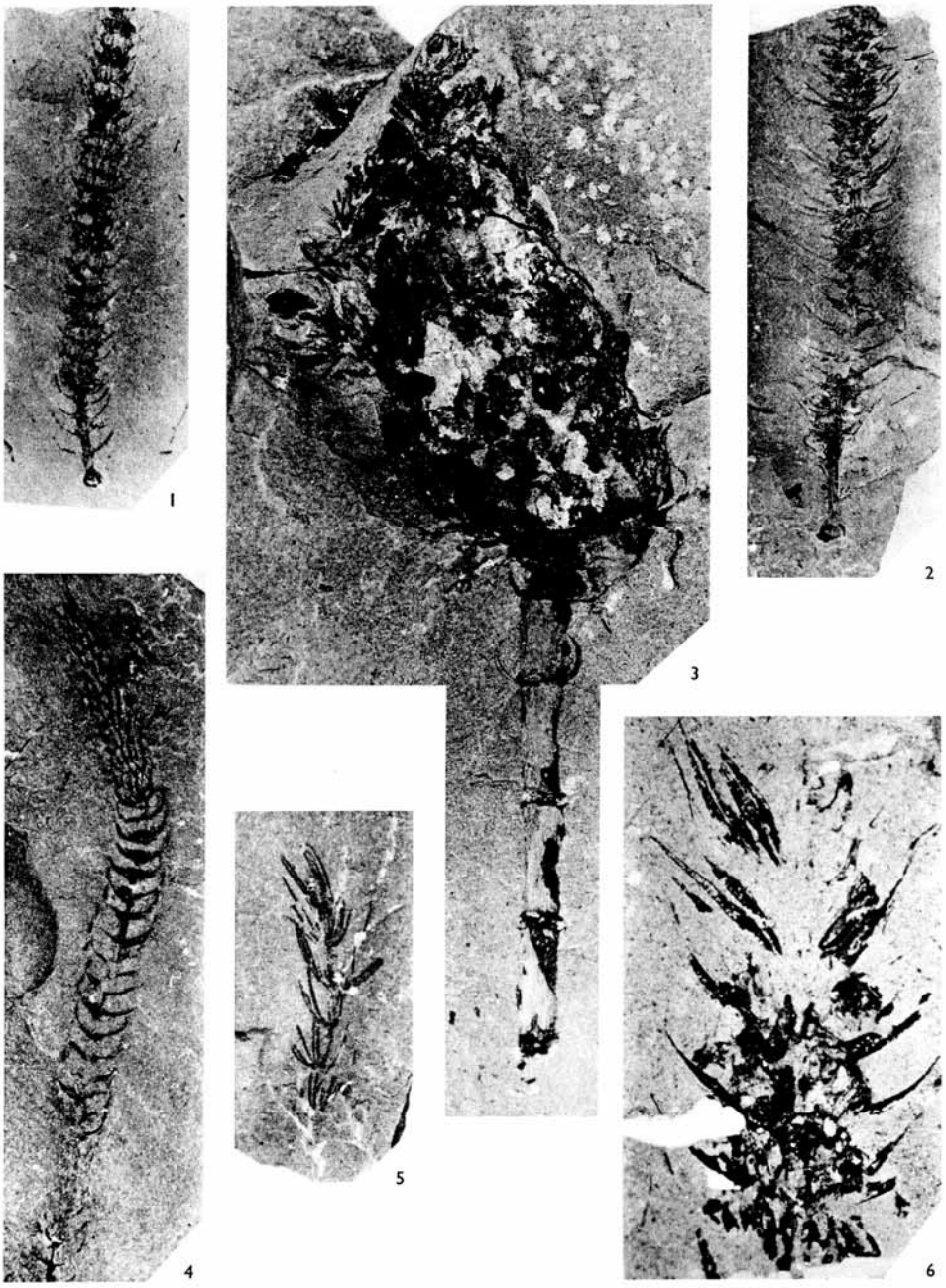
The lack of knowledge about the attachment positions of the sporangiophores prevents the specimens being included within the better-defined genera *Calamostachys* Schimper, in which the sporangiophores are attached to the cone axis half-way between the bract whorls, and *Palaeostachya* Weiss where they are attached in, or a little above, the axils of the bract whorls. Although the orientation of the sporangia suggests *Palaeostachya* to be the more likely genus, the present cones are included in *Paracalamostachys* which was instituted for such generically indeterminable specimens.

EXPLANATION OF PLATE 44

Figs. 1, 2, 6. *Paracalamostachys spadiciformis* sp. nov. 1, no. 77228, ×1. 2, no. 77229, ×1. 6, portion of split cone, no. 77230, ×4.

Fig. 3. Swollen shoot bearing leafy shoots, no. 77226a, ×2.

Figs. 4, 5. Associated leafy shoots, no. 77231, ×1.



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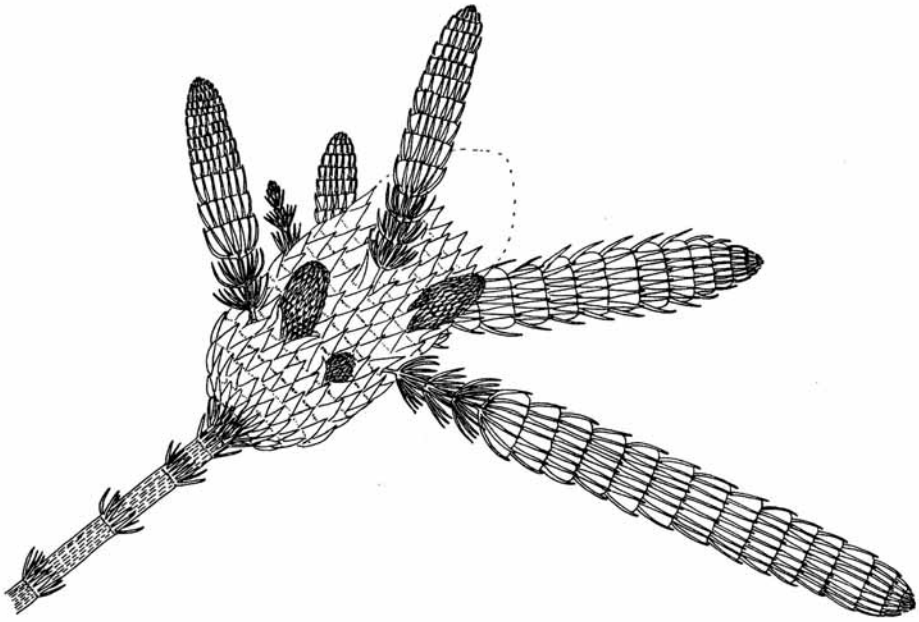
Genus PARACALAMOSTACHYS Weiss

Paracalamostachys spadiciformis sp. nov.

Plate 44, figs. 1–3, 6; Plate 45, figs. 1–6

Diagnosis. Cone up to 9 cm. long and 1·3 cm. diameter; borne in close whorls on stems about 2·5 cm. broad. Cone axes 1·3 mm. diameter, with basal swellings 3–4 mm. broad. Whorls of about 16 bracts, 3–4 mm. apart, on cone axis; bracts about 1 cm. long, 0·6 mm. broad. Sporangiophore whorls between all bract whorls except the



TEXT-FIG. 2. Suggested reconstruction of fertile shoot of *Paracalamostachys spadiciformis* sp. nov.

basal three or four which are barren; about six sporangiophores in a whorl. Sporangia 3 mm. long, 2 mm. broad. Cones hermaphrodite; microspores, 55–130 μ diameter, similar to *Calamospora microrugosa* (Ibrahim) Schopf, Wilson, and Bentall and *C. pallida* (Loose) S. W. & B; megaspores, 100–350 μ diameter, similar to *C.* cf. *laevigata* (Ibrahim) S. W. & B. sensu Smith and Butterworth and *C. perrugosa* (Loose) S. W. & B

Holotype. No. 77227, Geological Survey Museum, London.
Name derivation. From spadix, being a spike with a fleshy axis.

Stratigraphical occurrence. Productive coal measures, below the Ashington Marine Band. Northumberland (Westphalian A or B).

DISCUSSION

Cone production. Calamite cones have previously been described as occurring individually at the nodes, in terminal groups or infructescences, or on specialized branches (Andrews 1961). The cones described here are unusual in being borne in close whorls on broad stems. How many cones were produced is not known, but possibly all the round polygonal areas on the broad stems represent positions of former cone attachment.

The fact that the detached cones are larger than those still attached need not be regarded as evidence for species distinction; it could also suggest that those cones still attached had not grown to their full length and being smaller were less likely to be detached during fossilization. The lowest whorls of bracts and sporophylls on the attached cones are like those of the detached cones while their upper whorls are more compact. This is comparable with the cones of the extant *Equisetum* which expand to full size from the base upwards. The calamites and Equisetales possibly had different rates of cone expansion, which could be taken as a reflection of growth habit of the plant as a whole. *Equisetum*, although having annual aerial shoots, still expands its cones quickly at the beginning of the growing season. This it is able to do by developing its cones to maturity, in everything but size, during the preceeding season and allowing them to overwinter on the perennial rhizome (Manton 1950). *Calamites*, in contrast, had perennial aerial shoots and would not have had the same need to produce cones quickly and simultaneously as there would not have been such distinct growing seasons. The swollen bases of the cone axes of *P. spadiciformis* probably represent abscission zones where the cones were themselves shed after spore liberation had ceased. After cone production and spore liberation had ended the swollen stems may have been shed or withered.

This method of cone production has not been described before and the only known specimens similar to these broad shoots were figured by Weiss (1844, pl. 10, figs. 2, 3) as *Asterophyllites longifolius* Sternberg. They are both articulated leafy shoots being in part narrow and in part swollen. Suggestions of leafy lateral shoots are shown but neither bears cones. They differ further in having a gradual stem expansion, quite unlike the abrupt increase shown by no. 77226a, and in having equally spaced nodes along their lengths. This, together with the fact that Weiss' figures show a narrow stem width above the broad part, suggests that his specimens were not homologous with those described here.

Spore variation. The spore contents of many calamite cones have been described on several occasions and the fact that spores from one cone may be recorded as more than one species of dispersed spore has been often noted. Schopf, Wilson, and Bentall mentioned this possibility when they instituted the genus *Calamospora*. The present work

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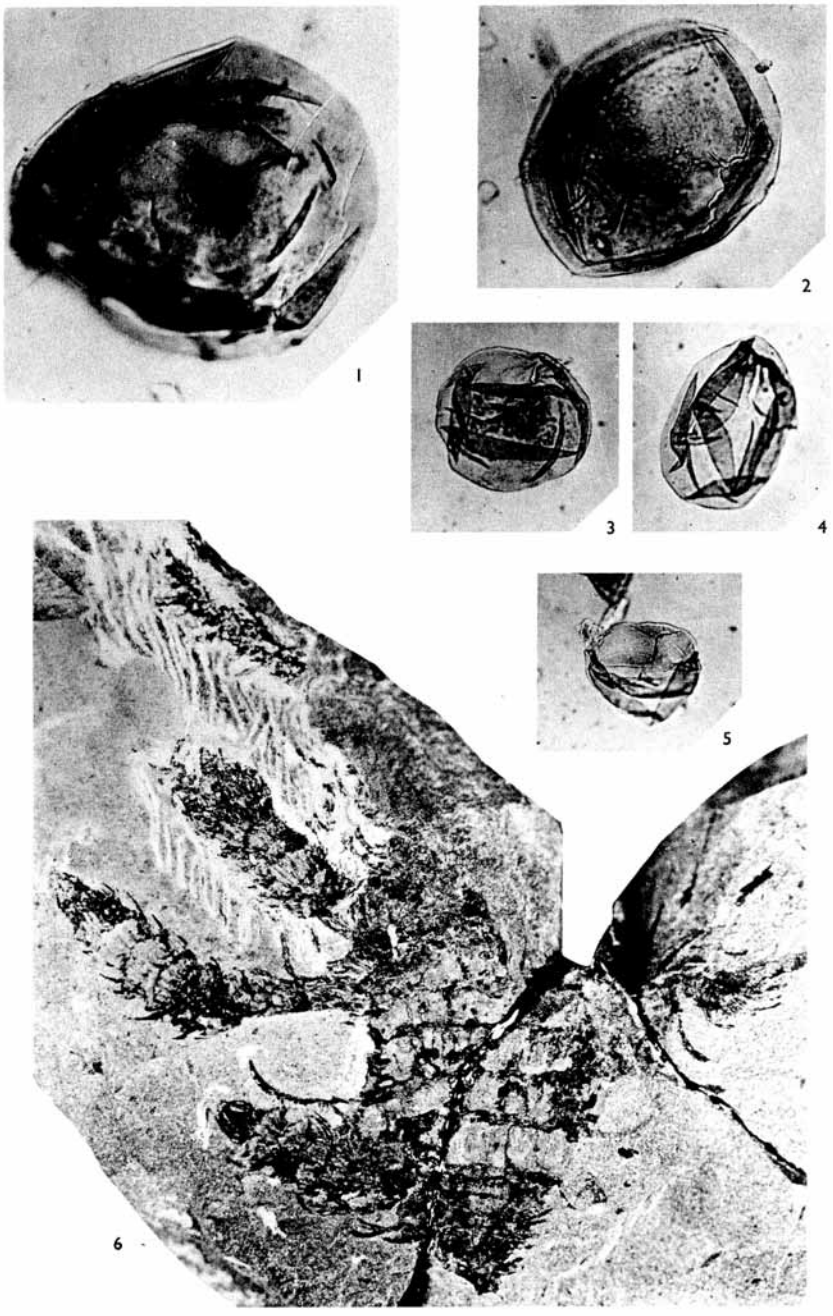
EXPLANATION OF PLATE 45

Figs. 1–5. Isolated spores from *Paracalamostachys spadiciformis* sp. nov.; slide PF 4450, ×250. 1, Megaspore comparable to *Calamospora* cf. *laevigata* (Ibrahim) Schopf, Wilson, and Bentall. 2, Small megaspore comparable to *C. perrugosa* (Loose) S. W. & B. 3, Microspore comparable to *C. microrugosa* (Ibrahim) S. W. & B. 4, Microspore comparable to *C.* cf. *microrugosa* (Ibrahim) Smith and Butterworth. 5, Microspore comparable to *C. pallida* (Loose) S. W. & B.

Fig. 6. Swollen stem bearing leafy shoots and cones, no. 77227, ×2.



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shows that spores resembling four species and one extra form of dispersed spores can be found within a single cone. This would suggest that many more spore species have been recorded than cone species. However, Crookall (1968) lists 19 British species of calamite cones while Smith and Butterworth (1967) give only 12 species and forms of *Calamospora*, although this latter number is lower than it might have been because they were recognizing a limited selection for practical purposes. *Calamospora* has also been recovered from fructifications of Eleutherophyllaceae, Sphenophyllaceae, Equisetaceae, Noeggerathiineae (Potonié 1962, 1965), and Protopityales (Walton 1957). There must be therefore a great number of botanical spore species which differ in only the minutest details making their recognition extremely difficult when separated from their parent fructifications. A comparison can be made with some groups of extant plants in which several species produce similar pollen grains. For example, the 13 North American pines have pollen grains which intergrade morphologically and can be distinguished only by detailed statistical analysis relying on measurement ratios (Ting 1966). Previous less detailed studies failed to separate the pollen species.

The ratio of one large to three small megaspores suggests that one member of each megaspore tetrad may have developed at the partial expense of the others. It is not suggested that the smaller megaspores are abortive as they are still relatively large and greater in size than the microspores. No complete tetrads could be found but small groups of spores showed this one to three size ratio.

COMPARISON

The main difficulty in palaeontologic taxonomy is deciding how much variation can be reasonably allowed within one species. If the cones of the extant *Equisetum* are examined large variation of both cone size and number of sporangiophores per whorl can be found and it is difficult to distinguish the species by isolated cones. A corresponding variation can be expected within the calamite cone species and slight differences in cone size and number of parts must be regarded cautiously. Spores recovered from the cones can be of value in species comparison but, as shown above, difficulties exist because of variation within a population and overlap of characters of species. A comparison of the parental shoots can be useful but this is often impossible as many specimens are found isolated.

Hermaphrodite species of *Paracalamostachys* and *Calamostachys* are known and the incomplete specimens of *Palaeostachya andrewsii* Baxter have spores, 270–320 μ in diameter, which are probably megaspores. Including this last species the known hermaphrodite cones are *Calamostachys casheana* Williamson (1887 and 1894), *C. solmsi* Weiss (1876), *C. americana* Arnold (1958), *Palaeostachya andrewsii* Baxter (1958), *Paracalamostachys heterospora* Remy and Remy (1958), and *P. striata* Weiss (1884). The hermaphrodite genus *Calamocarpon* Baxter (1963) differs in having only one megaspore in each sporangium and also in bract details and need not be considered further.

Paracalamostachys striata Weiss is the most similar species, being closely comparable with the Bedlington cones in diameter, number of bracts and sporangiophores per whorl, and in having similar-sized spores. The type specimens of this species were only 4–5 cm. long which is half the length of the Bedlington cones, but as shown above size alone should not be used for species differentiation. Other differences do however support their

distinction. The spores have a close resemblance although the megaspores described by Hartung (1933) have relatively longer trilete rays and the contact areas were not visible. These spores are thus closer to *Calamospora laevigata* (Ibrahim) Schopf, Wilson, and Bentall than those described from *P. spadiciformis*. The spore size ranges are also slightly different as in *P. striata* there is no overlap of size between the microspores and the smaller megaspores. The two species also differ in the way they were borne on the parent shoots. *P. striata* was borne terminally or in a panicle where *P. spadiciformis* was borne on specialized broad shoots.

Calamostachys solmsi is distinguished by its megasporangia being above its microsporangia. *C. americana* can be distinguished by its larger size (up to 4 cm. diameter), its correspondingly larger number of bracts and sporangiophores and because the relative number of bracts to sporangiophores is less than 2:1. *C. casheana* is only 5 mm. in diameter, being slightly less than half the size of the Bedlington cones, and has smaller microspores. *Palaeostachya andrewsii* and *Paracalamostachys heterospora* have slightly larger diameters (*c.* 1·5 cm.), relatively more bracts and sporangiophores per whorl and spores with larger size ranges than have the Bedlington cones. *P. andrewsii* also has a thicker axis compared with its 'complete' diameter. None of these four species has been found attached to a parent shoot, so no comparison can be made about the way they were borne.

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