NON-VASCULAR LAND PLANTS FROM THE DEVONIAN OF GHANA

by W. G. CHALONER, M. K. MENSAH *and* M. D. CRANE

ABSTRACT. Two species of fossil plant (*Spongiophyton nanum* Kräusel, *S. lenticulare* (Barbosa) Kräusel) preserved as compression fossils with cuticles, are described from the ?Middle Devonian of Ghana. *S. nanum*, first described from the Devonian of Parana, Brazil, is a plant of dorsiventral thalloid organization, branching dichotomously, and with a series of large pores on the presumed upper surface. It has a cuticle far thicker than that of most vascular land plants. On its inner surface the outlines of cells of the underlying tissue may be seen. Nothing else is known of the inner tissue of the plant. Material of *S. lenticulare* is similar, but is only seen as small fragments. *Spongiophyton* combines an external morphology resembling that of some algae and liverworts, with a thick cuticle unknown in those groups. In this and its dorsiventral organization, it appears to show adaptation to a terrestrial environment. It may be compared with *Foerstia* (? = *Protosalvinia*) and with *Parka*, but shows significant differences from these and other genera of Devonian thalloid plants.

THIS paper is an account of two species of *Spongiophyton*, a thalloid plant, represented by compression fossils with 'cuticle', from the Takoradi Sandstone of Ghana. The material comes mainly from a horizon within the Sekondi Series lower than that which yielded lycopods believed to be Lower Carboniferous (Mensah and Chaloner 1971). The plants described here are preserved as compression fossils in a matrix of shaly sandstone and are believed to be of Middle Devonian age. This age is based on the identity of the plants themselves with specimens from Brazil dated as Middle Devonian on palynological evidence. The plants are in the form of fragments of branched tubes, representing the outer membrane of an originally more or less cylindrical structure. Two species are recognized, *Spongiophyton nanum* Kräusel and *S. lenticulare* (Barb.) Kräusel, which were described from the Middle Devonian of Parana, Brazil, by Kräusel (1960). Examination of these Ghanaian fossils and particularly the use of thin sections and scanning electron microscopy reveals new features not previously reported in the Brazilian material. These two species are redescribed on the basis of our observations of the Ghanaian specimens. Their bearing on the age of the Takoradi Sandstone is then considered, and the affinity of *Spongiophyton* and some comparable genera reviewed.

PREPARATION AND EXAMINATION OF SPECIMENS

The plants described here may be observed directly on the bedding surfaces and in the matrix of sandstone but all the material illustrated was extracted either by maceration, or by removing fragments with needles. Most of the specimens were obtained from bulk maceration, by treating hand specimens of sandstone with concentrated nitric acid for up to 24 hours, followed by decanting and repeated washing in water. The swelling effect of the nitric acid acting on the plant material effectively disaggregated the matrix, so that after washing, the plant fragments were sieved from the sand and clay fraction. The larger pieces were then examined under a binocular microscope with top illumination. Individual specimens were given further oxidative treatment with Schulze's solution (a saturated solution of potassium chlorate in nitric acid), for from 5 to 20 minutes, until the cuticular material became translucent. Subsequent treatment with ammonia, commonly used for coalified plant cuticles, was found to be unnecessary, and merely caused darkening of the

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plant material. The macerated fragments were then mounted directly in glycerine jelly, or were dehydrated in alcohol and mounted in Canada balsam for observation by transmitted light. Specimens used for SEM were mounted on stubs using either double-sided Sellotape or 'Durofix' cement, or occasionally by using silver dag as an adhesive. They were then coated with carbon followed by gold-palladium, using an SEM planetary specimen holder in an Edwards High Vacuum Coating Unit. Photographs were taken on both a Cambridge 'Stereoscan' Mark II and an S600 scanning microscope. In order to eliminate the possibility of artifacts of cuticle structure arising from the maceration procedure, some SEM observation was carried out on fragments of the plant removed from the matrix with a mounted needle, without further chemical treatment.

The structure of the plant was further studied by embedding and sectioning pieces of the cuticle. Portions of the plant were transferred to acetone after Schulze's solution, and were then embedded in Araldite resin in capsules. The resin-embedded material was then sectioned on a Reichert microtome and the sections mounted in Canada balsam.

DESCRIPTIONS

Spongiophyton nanum Kräusel (1960)

Plate 120, figs. 1–4, 7–9; Plate 121, figs. 1, 3–7; Plate 122, fig. 1; Plate 123, figs. 1–3; Plate 124, figs. 1–2; text-fig. 1

General features. This description, based on observation by light microscopy, SEM, and thin section of the new Ghanaian material, amplifies that given by Kräusel (1960). A formal emendation of his diagnosis is given below (p. 945).

The specimens here attributed to *S. nanum* consist of flattened tubes of cuticle, with rounded apices, sometimes branching once or twice. The flattened tubes range from 2 to 5 mm across, the majority of specimens being at the upper end of this range. The longest fragment found is 25 mm long. A few specimens show one or two successive more or less equal dichotomies, apparently in the same plane. The rounded apices, where seen, are of thinner cuticle than the remainder perhaps representing regions of growth; they are frequently damaged, or a branch is simply truncated, with the apex missing. No apparently intact basal end of any of the fragments was seen; all have a truncated (broken) base.

In a few specimens, a dome-like, or basally contracted globular lobe appears laterally on one branch of the thallus, representing a relatively short branch at right angles to those normally lying in the plane of compression (Pl. 120, figs. 8, 9). Each of the flattened tubes shows a differentiation in the morphology of its two surfaces; one, the 'poral surface', has the thickest cuticle, and shows a series of circular to oval

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EXPLANATION OF PLATE 120

Spongiophyton from Komenda, Ghana.

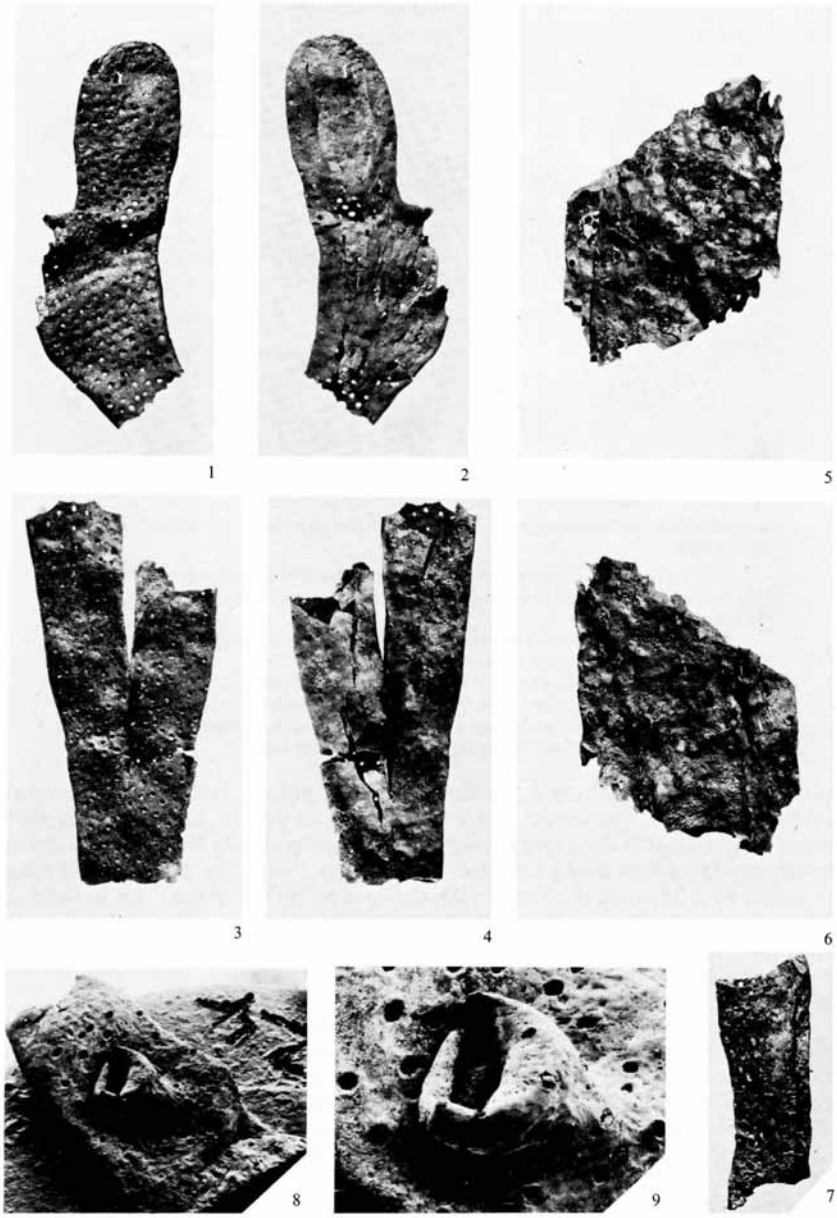
Figs. 1, 2. *Spongiophyton nanum*, apical portion of thallus extracted by maceration, × 5. 1, poral surface. Note broken edge of dichotomy at left. 2, aporal surface of same.

Figs. 3, 4. *S. nanum*. Poral and aporal surfaces of thallus showing dichotomy, × 5.

Figs. 5, 6. *S. lenticulare*. Short length of intact cuticular tube (long axis upright, torn edges above and below), × 3. Pores are present on both surfaces, but are more abundant in fig. 5.

Fig. 7. Piece of *S. nanum* thallus flattened so that poral face appears at left side, aporal at right, × 5.

Figs. 8, 9. *S. nanum*, portion of thallus with short ?upright lateral branch, with its apex collapsed showing cellular reticulum on inner cuticle surface. (Fig. 8, × 20; fig. 9, × 50.) (Scanning electron micrograph.)



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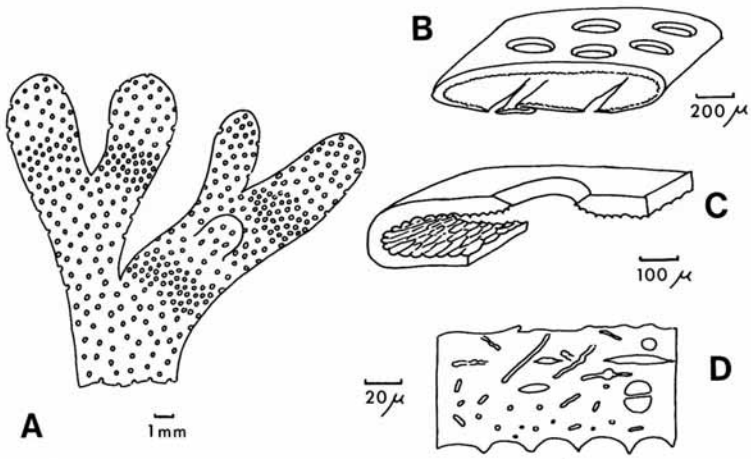


TEXT-FIG. 1. Diagrammatic reconstruction of the *Spongiophyton nanum* cuticle, at different magnifications, summarizing details revealed by light microscopy and scanning electron microscopy.

A, external detail, showing two successive unequal dichotomies and one additional small lobe on the poral surface. The density of distribution of pores varies along the length of the thallus.

B, reconstructed segment of thallus showing pores on thicker, supposedly upper, face and slits and folding of thinner aporal face.

C, section of pore showing bevelled edges, and cellular reticulum on inner face of cuticle. Cut edges of cellular reticulum are brought together, where the tube is folded at left.

D, section of cuticle shows borings in various orientations, fusiform and more or less spherical cavities, and ridges of cellular reticulum on inner face.

pores typically 200–300 μm in diameter scattered more or less irregularly over the surface. The other, the 'aporal surface', has a thinner cuticle, and commonly shows some longitudinal folding and tearing; this surface generally lacks pores, although a few may be present along the edges (Pl. 120, figs. 1–4). The 'poral' cuticle ranges from 24 μm to 84 μm in thickness, while the 'aporal' cuticle ranges from 24 to 36 μm. These measurements are based on ten specimens showing suitable more or less transverse fractures of the two surfaces. The ratio of poral to aporal cuticle thickness ranges typically between 2:1 and 3:1, although occasionally specimens are seen which show little difference in thickness between the two surfaces.

Where the aporal surface has longitudinal tears (Pl. 120, figs. 2, 4) these show matching edges, and appear to represent a simple physical splitting in the thinnest part of the cuticular tube. This may have occurred simply as a result of the mechanism of the collapse of the tube, with the thinner aporal surface coming under tension as the thicker poral surface became splayed out; or it may be as a result of greater vulnerability of the thinner cuticle to the maceration process, although this seems less likely.

In most cases the flattening of the cuticular tube on fossilization was such that the

poral and aporal surfaces coincided with the upper and lower faces of the flattened tube. This suggests that there was therefore some preferred orientation related to the poral/aporal differentiation. The simplest explanation would be that in life the tube was somewhat flattened in the poral/aporal plane. However, a few specimens show part of each flattened tubular cuticle surface with pores, and part without (Pl. 120, fig. 7).

Seventy-two fragments of *S. nanum* were picked from the Komenda material, showing clearly the flattened tube structure with both edges intact; of these, 56 showed the two surfaces to coincide with the poral/aporal faces, while 13 showed the poral/aporal boundary lying within the flattened face (cf. Pl. 120, fig. 7). This suggests some degree of preferred orientation, but clearly not such as would be shown by a flattened thallus as of, say, *Fucus* or a thalloid liverwort. The preferred plane of orientation in the sediment might have been simply the result of dichotomous branching of a more or less cylindrical thallus in the plane of the poral/aporal differentiation, as seen in the specimen of Plate 120, figs. 3–4. Of the total 72 specimens examined in this respect, only three showed pores more or less uniformly on both surfaces. These are considered further below.

The pores are typically about five diameters apart, but there is a good deal of variation. Along the length of a tube there are zones of relatively high concentration (with pores up to about one diameter apart) and others where they are more sparse. The resulting zonation of pore density (text-fig. 1) appears to show no consistent relationship with dichotomy of the thallus. Each pore is bevelled or countersunk as seen from the outer surface (Pl. 121, fig. 5; text-fig. 1*c*); from the inner surface it lies in a slight depression (i.e. the cuticle thins gradually towards the pore). While the pores are more or less randomly scattered, there are never large pore-free areas on the pore-bearing surface, nor are two pores ever closer than an average pore radius.

Cuticle structure. The cuticle forming the tubes superficially resembles fossil cuticle of vascular land plants (e.g. conifers) prepared by maceration. It is brown to black in colour, with a good deal of variation presumably due to vagaries of preservation history. The better-preserved fragments are relatively tough and even flexible to some extent. The outer surface is more or less smooth, although it may be marked with an irregular series of vermiform borings attributed to post-mortem microbial attack (see below).

We use the term 'cuticle' throughout this article in the broad sense of an outer resistant covering of what was evidently a cellular organism. Although its superficial appearance and behaviour under maceration are similar to fossil vascular plant cuticles we do not wish to press the implications that the covering of *Spongiophyton* is cuticle in this rather precise sense. We prefer this term, used broadly and variously in different biological contexts, to any alternative (e.g. meristoderm, used of the *Foerstia* 'cuticle') which has more specific implications of algal affinity.

The inner cuticle surface shows a cellular reticulum formed by cuticular ridges comparable to those left on the inner face of typical higher plant cuticles after maceration. The cellular reticulum shows rather elongated cells, typically 40 μm long and 20–30 μm broad, generally aligned more or less parallel to the long axis of the tube, except in the vicinity of pores where a more or less radiating orientation may be

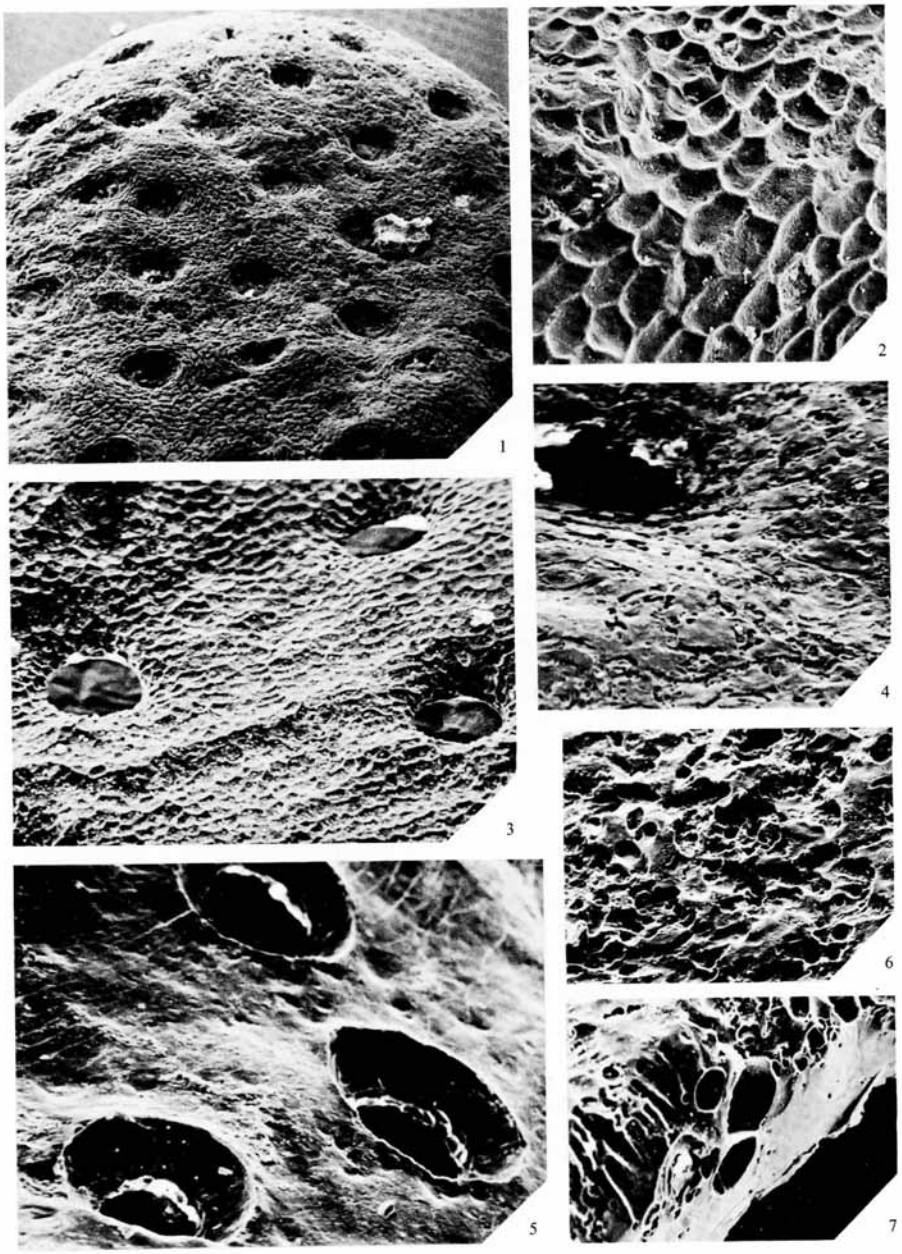
followed. These cell outlines show clearly by transmitted light. Scanning microscopy (Pl. 121, fig. 3) and thin sections (Pl. 124, figs. 1, 2) show that the ridges representing cell outlines are on the inner surface of the cuticle. The cellular outlines are less clear on the cuticle of the thin, aporal surface. They are there also of more markedly elongated shape and linear alignment. The extent to which the cuticular ridges appear pressed together at the edge of the flattened tube (Pl. 124, fig. 2) suggests that the flattening was not an original feature of the plant. This implies that the thallus might have been more or less elliptical in cross-section, but was not a flat ribbon-like structure in life. The cuticle shows no sign of having been compressed during compaction of the sediment; it appears equally thick where it lay horizontally, as at the folded edge. We can see no evident explanation for this, but note that Carboniferous megaspores seen in coal thin-sections, even when completely flattened, similarly show no reduction of exine thickness in the vertical dimension compared with that seen at the folded edge.

The cuticle was examined in thin section, following resin embedding, and broken faces were examined by SEM. The texture and colour of the cuticle is not uniform, being generally darker towards the outer surface. Within the cuticle there are a number of cavities giving it a locally spongy or foam-like texture (Pl. 121, fig. 7; Pl. 124, fig. 1), and this seems to become more pronounced in macerated material. These lacunae are largely enclosed within the cuticle although they may abut on the inner or outer surface. There are in addition occasional lens-shaped cavities in the cuticle perhaps associated with separation of layers of lamellated cuticular material. Independent of these, and more irregular in distribution, are a series of what are here referred to as 'borings', which abut mainly on the outer surface, apparently representing the site occupied by some micro-organism (Pl. 121, figs. 4, 6, and Pl. 124, fig. 1). They vary from 2 to 5 μm in diameter, and occasionally appear to divide. They appear to be concentrated particularly towards the outer surface of the cuticle. They show various orientations within the cuticle, and sometimes appear at the surface as grooves or gouges. It is possible that they represent the activity of some parasitic organism during the life of the *Spongiophyton*, but in view of their extensive occurrence they seem more likely to be a post-mortem (saprophytic) invasion of the plant. The resulting grooves in the surface may take the form of a 'negative reticulum' pattern, simulating that of the underlying cell outlines (and perhaps influenced by them?). This is seen in the outer cuticle surfaces shown in Plate 121, figs. 1 and 4.

EXPLANATION OF PLATE 121

Scanning electron micrographs of *Spongiophyton* from Komenda, Ghana.

Fig. 1. *S. nanum*, apex of thallus. Note irregular, cell-like pattern of borings, × 60.
Fig. 2. *S. lenticulare*. Inner surface of cuticle, × 300.
Fig. 3. *S. nanum*. Inner surface of cuticle, showing pores, × 100.
Fig. 4. *S. nanum*. Outer surface of cuticle, showing borings, × 100.
Fig. 5. *S. nanum*. Outer surface of cuticle of another specimen, showing bevelled edges of pores, × 150.
Fig. 6. *S. nanum*. Outer surface of cuticle showing borings simulating cellular pattern, × 75.
Fig. 7. *S. nanum*. Oblique view of fractured edge of cuticle, × 400; outer surface is at top left. (Compare text-fig. 1 and Pl. 5, fig. 1.)



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These borings are very similar to those described in Silurian arthropod cuticles as 'vermiform tubules' by Rolfe (1962) and as 'thallophyte borings' in the cuticle of Cretaceous decapods by Taylor (1971). We follow Taylor in believing that chitrids (a group of aquatic phycomycetes) are the most likely causal organisms, both in his structures and our own. Rolfe's description of 'haphazardly arranged, anastomosing, meandering and convoluted tubules' aptly describes the borings that we have observed in the *Spongiophyton* cuticles. Taylor's borings are unbranched, but branching is simulated by their intersection; their diameters range from 0·3 to 15 μm, which straddles the range of our observations. The only reservation that might be made concerns Taylor's suggestion that the chitinous content of the substrate may have been important in the metabolism of the invading chitrid. If, as we believe, our *Spongiophyton* cuticle was comparable to that of higher plants, and so largely of lipid composition, then the invading fungus cannot have been chitinophilic. It might also be observed that when fungal hyphae penetrate leaf cuticle they usually do so by a single direct passage of a hypha through the cuticle, in contrast to the meandering borings seen here. This adds to our uncertainty about the role of the cuticle as a metabolic substrate for the micro-organism. However, the size and character of the borings favours fungi, rather than any other group, as the most likely causal organisms.

Unmacerated specimens of *Spongiophyton nanum* removed from the rock matrix with a needle and embedded and sectioned, show only occasional patches of black structureless substance between the two cuticle layers. Presumably this represents a residue of the original internal tissue but its featureless appearance did not encourage us to attempt any further investigation.

Incorporation and fossilization. The conditions of deposition of the basal Takoradi Sandstone are regarded by Crow (1952) as representing a transition from estuarine to fluviatile conditions during a phase of emergence. There are no invertebrate fossils associated with the *Spongiophyton*. While the majority of specimens, as indicated, are flattened in the poral/aporal plane, they are not all oriented the same way in the sediment. Specimens from Komenda showed some tendency for the poral surface to lie uppermost in the sediment; of 30 fragments of *S. nanum* showing both faces, on five orientated rock hand-specimens, 22 (rather over 70%) had the poral surface facing upwards. From the coarse-grained, clastic nature of the sediment, and hence its presumably relative rapid rate of accumulation, it is assumed that these plant fossils were transported down the drainage system into the site of deposition, rather than representing marine organisms washed into a non-marine environment. This is also consistent with their fragmentary nature. The preferred orientation in the sediment is not very great and might be the result of some internal tissue differentiation associated with the poral surface (e.g. air cavities with trapped air or gas underlying the pores—cf. the liverwort *Marchantia*).

Spongiophyton lenticulare Kräusel (1960)

Plate 120, figs. 5–6; Plate 121, fig. 2; Plate 122, figs. 2–3

This species has been fully described by Kräusel (1960), and the Ghanaian material adds relatively little to our knowledge. As in his case, our specimens are much more fragmentary than those of *S. nanum*. The largest of the Ghanaian specimens is that in Plate 120, figs. 5–6, which shows part of a cuticular tube 12 mm in diameter, and irregularly broken at both ends. The fusiform pores are clearly seen, and show much the same range in size and density of distribution that he reports. The pores in the Ghanaian *S. lenticulare* have not the clearly defined circular to oval outline typical of *S. nanum* but rather fusiform slits, at the margin of which the edges of thin cuticle may be seen to curl back (Pl. 121, fig. 2). The cuticle itself is basically similar to that of *S. nanum*, but the cell outlines, showing as a reticulum on the inner face of the cuticle

are larger and narrower (Pl. 121, fig. 2) but also generally more obscure. They give a more markedly striate or longitudinally grained appearance to *S. lenticulare* (Pl. 122, fig. 2).

Kräusel has described vividly how prolonged maceration causes tears to appear and expand in the membrane, so forming 'pores' where they did not exist previously, except perhaps in the form of incipient lines of weakness. Although we have not repeated Kräusel's progressive maceration sequence, it is evident that his basic observations are applicable to our material; while fusiform pores are present in unmacerated cuticle, the formation and expansion of further slits takes place with prolonged oxidative maceration in Schulze's solution.

We accept Kräusel's interpretation that *S. lenticulare* is a distinct species of the genus *Spongiophyton*. However, the fragmentary nature of the material leaves uncertain the external form of the whole plant. We have seen no pieces indicating a clear dichotomy, so that we have direct evidence only that the thallus was covered with a (tubular) cuticular layer, showing pores and an internal cellular reticulum. We have not sufficient pieces of intact tube to establish a clear differentiation of poral and aporal surfaces; indeed, some pieces (e.g. Pl. 120, figs. 5, 6) show the pores distributed irregularly on both faces, while others suggest some differentiation of pore concentration between the two surfaces, as in *S. nanum*. We do not regard the supposed 'internal' structure of irregular wrinkles and depressions described and illustrated by Kräusel as representing original features of the cuticle; this is discussed further below.

LOCALITY DATA

The plants forming the basis of this study come principally from the base of the Takoradi Sandstone of the Sekondi Series close to its contact with the underlying Elmina Sandstone at Komenda, on the coast of Ghana about 28 miles east of Sekondi. The exposure (our locality 1) is in the beach below Komenda College (longitude 1° 29′ 30″ West, latitude 5° 2′ 40″ North) at the bottom of the cliff directly opposite the Principal's bungalow. Here, the basal part of the Takoradi Sandstone consists of 30 m of thin- to medium-bedded sandstone with shaly partings. The material was collected from the uppermost 10 m of this member which becomes exposed only at low tide.

More fragmentary material, typically fawn or yellow in colour as though 'naturally macerated' before being incorporated in the matrix, occurs (our locality 2) in grey fine-grained argillaceous sandstone from Essipon, 500 m east of the Coconut Beach Hotel, from the upper part of the Takoradi Shales on top of the shaly member which yielded the Essipon invertebrate fauna reviewed by Crow (1952, p. 32). This appears to be at a horizon above that yielding the plant macrofossils of *Archaeosigillaria* and *Lepidodendropsis* (Mensah and Chaloner 1971). In addition, a single specimen of *Spongiophyton nanum* has been identified on a single unlogged borehole core (our locality 3) from the Accra Shales near the UTC warehouse and wholesale stores on the High Street in Accra (over 150 km to the east of localities 1 and 2). Fragments of *Spongiophyton* sp. have also been seen in the Takoradi Sandstone (our locality 4) just above the Elmina Sandstone on the southern side of the hill on which Fort Convaadsborg (Fort St. Jago) is situated at Elmina (1° 21′ West, 5° 5′ North).

All the figured material, and that on which the descriptions are based, comes from locality 1. We believe that this (and probably that from locality 4) represents primary fossilized material, whereas the more fragmentary paler specimens from localities 2 and 3 could well be reworked. This supposition is based partly on the state of preservation, and the obvious facility with which this material would survive reworking, but also partly on our belief that the earlier (locality 1) occurrence is Middle Devonian, while the horizon represented by locality 2 is probably early Carboniferous in age.

All the figured and cited material of Ghanaian specimens has been deposited in the Geology Department, University of Ghana. Duplicate material is in the Department of Palaeontology, British Museum, Natural History.

DISCUSSION

Comparison of Ghanaian and Brazilian material. Our study of Kräusel's material of Brazilian *Spongiophyton* housed in the Forschungsinstitut Senckenberg at Frankfurt am Main was confined to light microscopy. We attempted to remount some specimens for observation by SEM, but were unable to free them sufficiently from the mounting medium, which appeared to be denatured glycerine jelly. Microscopic observation confirmed the identity of our two species with Kräusel's, with the exception of one of his specimens recorded as *S. lenticulare*, which was evidently *S. nanum* inadvertently mislabelled. Agreement extended to the presence of the 'borings' clearly recognizable in the Brazilian *S. nanum*.

Kräusel put much emphasis on an aspect of his cuticles which he regarded as representing a characteristic feature of *Spongiophyton*, namely a series of irregular anastomosing ridges or corrugations of the cuticle which he interpreted as remains of original structure. This he referred to as a spongy structure (Schwammstruktur) composed of irregular longitudinal ribs (Längsbalken). Having carefully examined Kräusel's specimens, we believe that these irregularities are an effect of preservation peculiar to his material, perhaps associated with imprinting of the angular matrix particles on the cuticle. This 'spongy structure' is evident only in some parts of his specimens and may appear (Pl. 123, fig. 3) in immediate juxtaposition to clearer areas of the cuticle showing a cellular reticulum agreeing closely with that seen in our Ghanaian material (Pl. 123, fig. 2). We therefore regard this supposedly original 'Schwammstruktur' of *Spongiophyton* as a product of a particular environment of preservation. We have seen no evidence of preservation of any internal tissue of either *Spongiophyton* species in Kräusel's material or our own. But the reticulum of elongated cell outlines on our cuticles of *S. nanum* strongly suggests the presence of an internal cellular tissue probably of parenchymatous organization as seen in typical higher plants, rather than the more or less rounded cells seen in the 'cuticle' of *Foerstia* (figured here on Pl. 124, fig. 3) or the meristoderm of a brown alga (Pl. 124, fig. 4).

We believe that the cellular fragments of early Devonian age figured by Mortimer and Chaloner (1972, Pl. III, figs. 1–3) from South Wales and boreholes in south-east England, referred to '*Spongiophyton* sp.' and 'cf. *Spongiophyton*' should probably not be referred to this genus. They might equally well be compared to *Foerstia* (?*Protosalvinia*) or *Orestovia* (see table 2). In the present state of our knowledge, such fragments are perhaps better left generically unassigned.

THE AGE OF *SPONGIOPHYTON* FROM GHANA AND BRAZIL

Kräusel (1960) originally described five species of *Spongiophyton* from Brazil (*S. lenticulare*, *S. nanum*, *S. minutissimum*, *S. articulatum*, and *S. hirsutum*). The last of these he later (Kräusel and Venkatachala 1966) removed from the genus, and assigned

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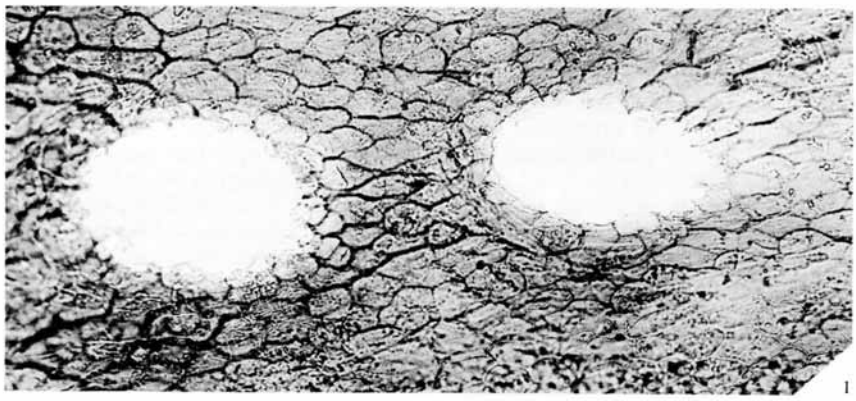
EXPLANATION OF PLATE 122

Fig. 1. Cuticle of *S. nanum* from Komenda, photographed by transmitted light, showing cellular reticulum, two pores, and borings (at left-hand margin), × 160.

Fig. 2. Cuticle of *S. lenticulare* from Komenda showing pore and cellular reticulum, × 64.

Fig. 3. Cuticle of *S. lenticulare* from the Ponta Grossa Formation, Parana, Brazil (Kräusel Collection), × 64. (Forschungsinstitut Senckenberg, slide no. FO 258/1.)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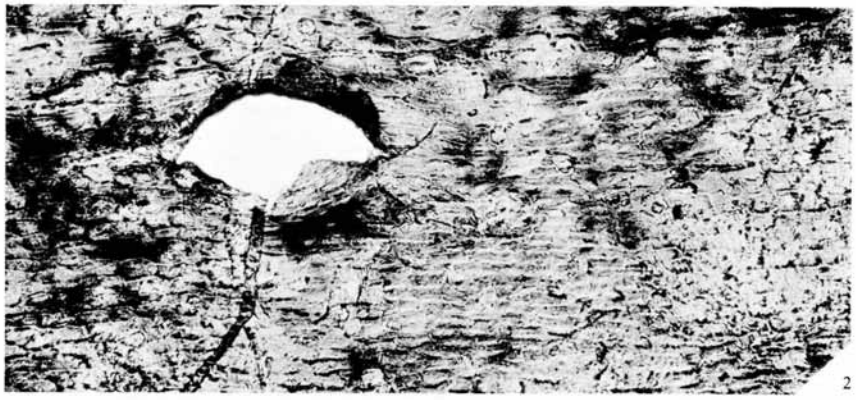
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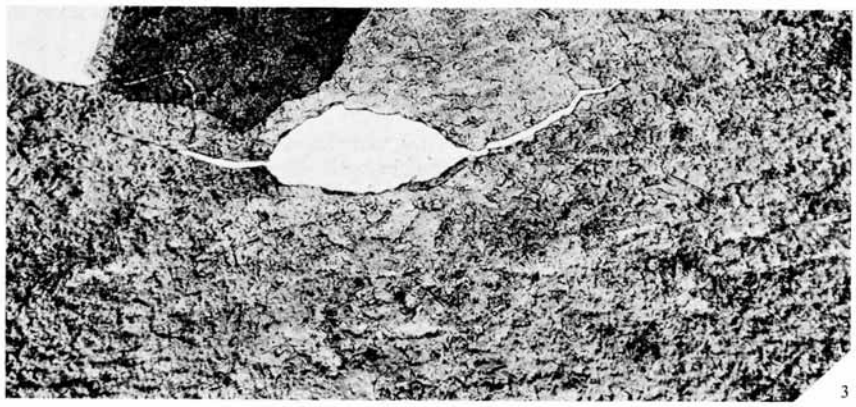
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CHALONER *et al.*, *Spongiophyton* cuticle

to a new genus *Aculeophyton* based on a Siberian Devonian species. Of Kräusel's four remaining species of *Spongiophyton* we have found only two in Ghana—*S. lenticulare* and *S. nanum*. Kräusel believed his material from Brazil to be of early Devonian age, but subsequent work by Lange and Petri (1967) taking account of palynology and marine faunas favours a Middle or Upper Devonian assignment. Lange and Petri (1967, p. 25) state that 'all the six localities from which Kräusel, 1954, described different species of *Spongiophyton* belong to the Middle Devonian Sao Domingo Member' (of the Ponta Grossa Formation, Parana Group). The Sao Domingo Member actually transgresses two palynologically based zones ('biostratigraphic intervals' of those authors, p. 26). These are the D4 and D5 Zones of Daemon *et al.* (1967) which are on well-documented palynological evidence equated approximately with the Givetian (Middle Devonian) and Frasnian (Late Devonian) respectively. However, this Frasnian palynological zone is recognized only in subsurface rock in Parana. The best approximation for the age of the Brazilian *Spongiophyton* is therefore, on available palynological evidence, Givetian (late Middle Devonian). This suggests that the Takoradi Beds (Takoradi Shales plus Takoradi Sandstone) probably span an interval from approximately Givetian to early Carboniferous age. This and other stratigraphic implications of the occurrence of *Spongiophyton* in the Sekondi Series are considered further by one of us in a paper now in press (Mensah 1973).

THE NATURE OF *SPONGIOPHYTON*

Kräusel (1960) and Kräusel and Venkatachala (1966) have discussed the possible affinity of *Spongiophyton*. The Brazilian species of that genus, and in particular *S. lenticulare*, were at first thought to be cuticle remains of a lycopod. They were indeed initially assigned to a genus of Devonian lycopod, as *Haplostigma lenticularis* Barbosa (1949). Kräusel (1960) subsequently showed that this assignment was unacceptable. On Barbosa's interpretation the holes (pores) in the cuticular tube were interpreted as the sites of (abscissed) leaves of a lycopod, of which the cuticle represented the stem surface (compare, for example, Pl. 122, fig. 1 with the lycopod stem cuticle of *Archaeosigillaria essiponensis*; Mensah and Chaloner 1971, Pl. 65, fig. 1). When we first encountered fragments of *Spongiophyton nanum*, we tried to interpret them as lycopod cuticles just as Barbosa had done, before realizing their identity with Kräusel's genus.

Two principal features of *Spongiophyton* 'cuticles' weigh against their representing stem surfaces of lycopods or other vascular plants. Firstly the dorsiventral nature of

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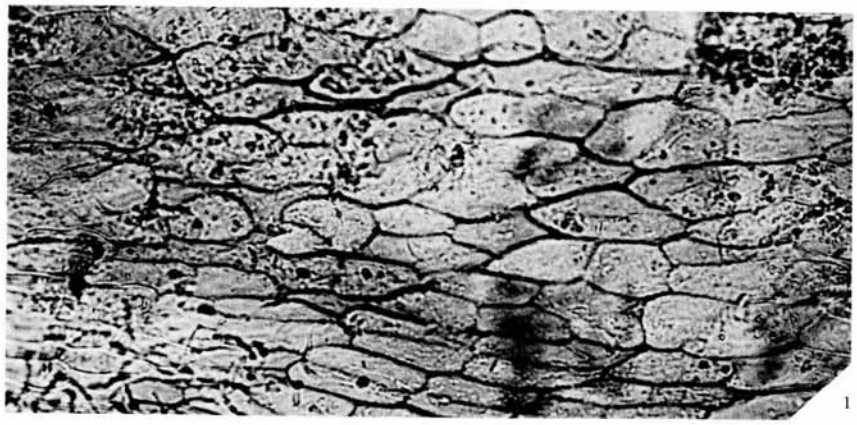
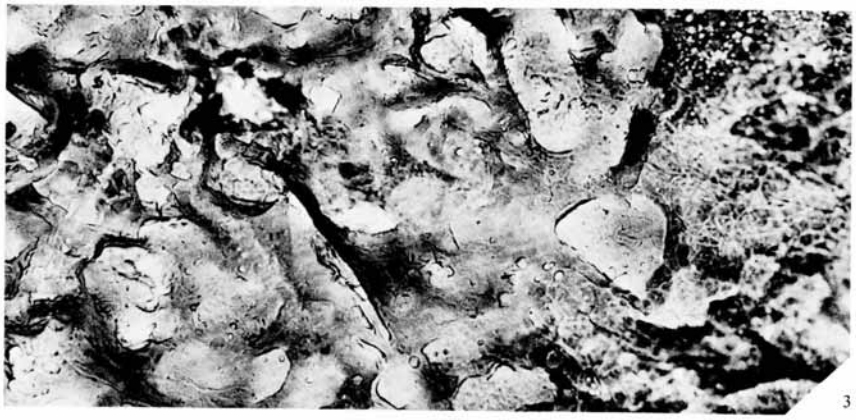
EXPLANATION OF PLATE 123

Figs. 1–3. Cuticle of *Spongiophyton nanum* photographed by transmitted light. 1, from poral surface of a specimen from Komenda, × 250. 2, 3, from poral surface of a specimen from Parana, Brazil (Forschungs Institut Senckenberg, slide no. TO 265), × 160. 2, shows the cellular reticulum, abundant trace of borings, and the irregularity of cuticular surface which grades into the condition seen in the following figure. 3, part of the same cuticle, showing the irregularity (due to preservation?) referred to by Kräusel as 'spongy structure'.



1

2



3

CHALONER *et al.*, *Spongiophyton* cuticle

the tubes both in the distribution of the pores and in cuticle thickness. This lack of pores (putative sites of leaf attachments) on one surface is unknown in any lycopod, living or fossil. Secondly, and related to this, the pore arrangement is apparently random on the poral surface, and does not show the regular whorled or spiral configuration characteristic of all known lycopods. These two features taken together seem to rule out their attribution to any known vascular plant.

Once we dismiss a relationship of these cuticular tubes to a particular group of plants, their affinity must be reconsidered; even the possibility of animal versus plant origin must be entertained. *Spongiophyton nanum* could be compared superficially with at least three groups of colonial animal; the graptolites (in the broadest sense), the sponges, and the bryozoa. Several specimens and SEMs were examined by Dr. Adrian Rushton and Dr. Dennis White (Institute of Geological Sciences) who reject the possibility of graptolite affinity. Miss P. L. Cook (Department of Zoology, British Museum, Natural History) and Dr. P. Sandberg (Department of Geology, University of Illinois) examined specimens as possible bryozoa. They set aside this possibility emphasizing particularly that no known Palaeozoic bryozoa have an organic outer membrane of the considerable thickness of *Spongiophyton nanum*. They also suggest that the lack of any demarcation between the pores (if these were to be construed as the zoecia) is entirely unlike any bryozoan. Dr. R. P. S. Jefferies (British Museum, Natural History) also examined material, and expressed the opinion that its structure could not be interpreted in terms of any animal group known to him. We should like to thank these colleagues for their help, and permission to record their opinions here.

An attempt to postulate the systematic position of a fossil known only from its cuticular covering, must be both tentative and hazardous. In the case of *Spongiophyton nanum* the principal features on which such speculation can be based are as follows:

(1) It has a thalloid body, known to dichotomize at least twice successively, with rounded apices to the lobes.

(2) The whole organism has a very thick resistant cuticle, far thicker than most land plant cuticles, with an elongate-cellular reticulum on the inner surface.

(3) The cuticle is penetrated by pores mainly on one surface only; this, and differentiation in cuticle thickness, demonstrates a dorsiventral organization.

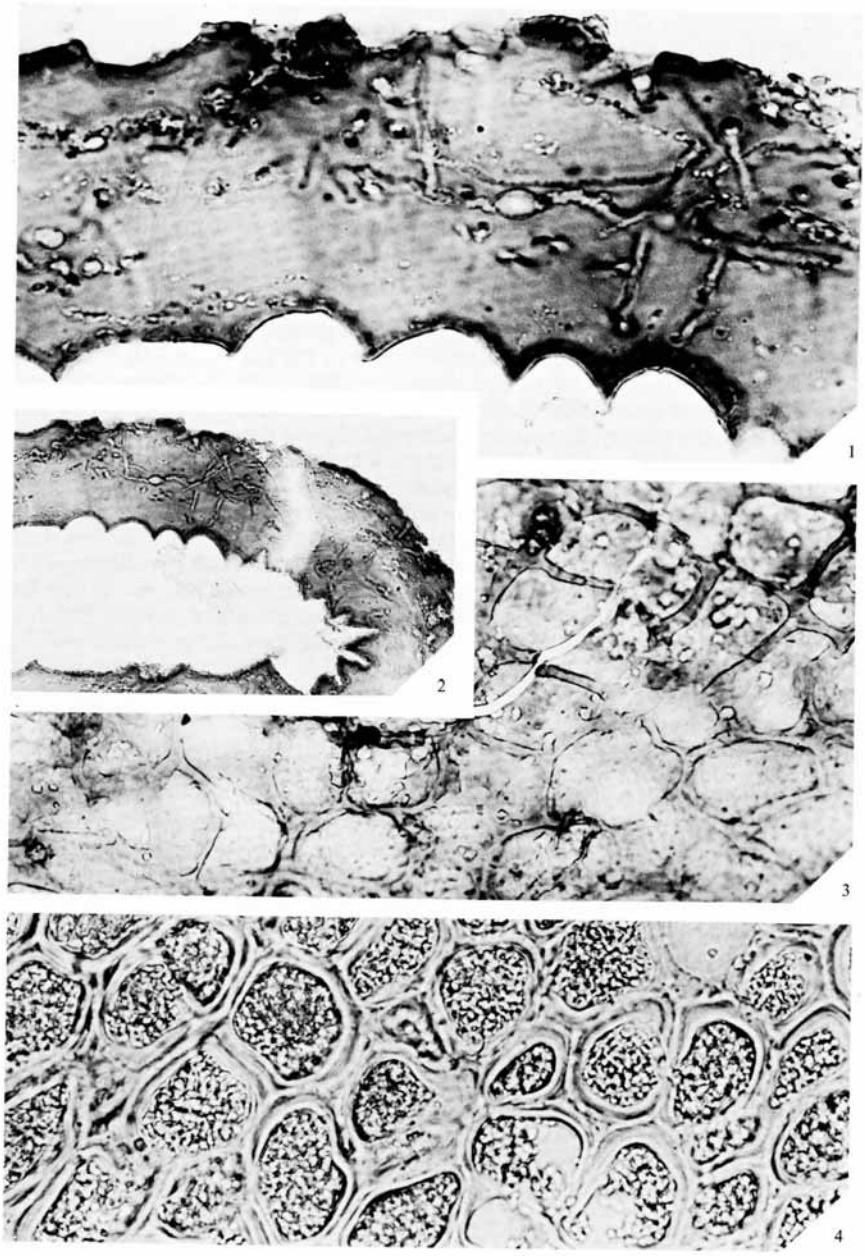
EXPLANATION OF PLATE 124

Figs. 1, 2. Vertical section of cuticle of *Spongiophyton nanum* transverse to thallus long axis, from Komenda, photographed by transmitted light. 1, the inner face of the cuticle is below, showing the ridges corresponding with underlying cells of the plant, in life. Note borings, and the various small lacunae (cavities) within the cuticle, × 250. 2, the same specimen, showing the folding of the cuticle (right) at one edge of the flattened cuticular tube, where the ridges on the inner cuticle surface are brought into juxtaposition at the fold, × 85.

Fig. 3. 'Cuticle' (outer surface of meristoderm?) of *Foerstia* (?*Protosalvinia*) *ohioensis* from the Upper Devonian of Ohio, U.S.A., photographed by transmitted light, × 250.

Fig. 4. Paradermal section through the meristoderm of *Fucus vesiculosus*, photographed by transmitted light, × 640.

These two figures show the characteristically rounded appearance of the cellular reticulum of *Foerstia* and *Fucus* which contrasts with the elongated cells of *Spongiophyton* (cf. Pl. 123, fig. 1).



CHALONER *et al.*, *Spongiophyton*, *Foerstia*, and *Fucus* cuticles

(4) The fossilized (coalified) substance of the *Spongiophyton* cuticle shows neither the laminar units nor the fibrous elements demonstrated for some invertebrate cuticles, e.g. the Eurypterid cuticles of Dalingwater (1973).

The conclusion that *Spongiophyton* is a plant is based on consideration of the four items above taken collectively, plus the rejection of the organism from each of the three plausible animal phyla cited earlier. It has to be conceded that there is no basis for totally rejecting animal affinity. Accepting a plant affinity on this tentative basis the character of the original organism can be considered.

A flattened, thalloid dichotomizing habit occurs in three groups of living plants—algae (principally red, Rhodophyceae, and brown, Phaeophyceae); in liverworts (Hepaticae), and in lichens. Within these several groups, two situations may be contrasted. Large thalloid algae, adapted to live in the sea as anchored, submerged organisms, normally of more or less upright habit, show no differentiation of the two surfaces of the thallus. These contrast with the thalloid liverworts and lichens (both basically terrestrial organisms, although a few of the former are aquatic) which typically grow with one face applied to a rock or soil surface and show in varying degree both internal and external dorsiventral differentiation. The thalloid liverwort *Marchantia*, for example, shows gas-exchange pores in its upper surface only, with rhizoids and scales on the lower surface. It is worth noting that those few thalloid brown algae (e.g. *Fucus vesiculosus*, *Pelvetia canaliculata*) which have developed free-living growth forms adapted to a mud-flats environment in salt marsh (see Baker 1912) show no external differentiation of an upper and lower surface. This is presumably because as free-living (non-attached) forms they can be turned over freely with each rising tide, although they remain more or less safely 'trapped' within the marsh-pan environment. There are marine algae with a more or less thalloid habit which grow encrusting or appressed to rocky substrates, and which show some associated dorsiventrality of internal organization (e.g. *Ralfsia*, *Zanardinia*, and the *Aglaozonia* (sporophyte) stage of *Cutleria*, all in the Phaeophyceae; and *Peysonnelia*, *Hildenbrandia*, and *Rhizophyllis* among Rhodophyceae; see Fritsch 1952). The dorsiventral character of *S. nanum* taken on its own should therefore not perhaps be construed unequivocally as an adaptation to a terrestrial habit. But its enormously thick cuticle certainly suggests an environment in which it was necessary for the plant to drastically restrict water loss. The so-called cuticle of the Fucales is said by Fritsch to be of a mucilaginous composition, while that of the red algae is said to be 'probably of a pectic nature'. The labile character of both these groups of substances makes the preservation of a cuticle of such composition extremely unlikely in the sedimentary environment in which *Spongiophyton* occurs.

Among living vascular plants it may fairly be said that there is a broad correlation between cuticle thickness and aridity of the environment. However, nearly all conifers—regardless of habit—have relatively thick cuticles, as do many flowering plants of saline habitats. But the cuticle of *S. nanum*, over 80 μm in thickness, exceeds by a factor of four times what is rated as a 'thick cuticle' in fossil gymnosperm leaves (cf. 6–8 μm in *Pagiophyllum*, Kendall 1948; 10–20 μm in *Pachypteris*, Harris 1964). This cuticle thickness, alone, is perhaps one of the most remarkable features of *Spongiophyton*.

It must be conceded that a thick waxy covering could confer flotation on the *Spongiophyton* plant, much as the waxy cell walls of *Botryococcus* may be associated with its floating habit. One could then visualize a growth habit such as that of the water fern *Azolla*, or the liverwort *Riccia natans*, free-floating on a freshwater surface. However, we feel that a more plausible habitat for the plant, suggested by its thick cuticular covering and dorsiventral organization, is a terrestrial soil surface. This would also account for the few specimens which, while showing dorsiventral organization and branching in the assumed horizontal plane, occasionally have an upwardly directed lobe of quite limited growth (Pl. 120, figs. 8, 9 and text-fig. 1). It is possible that such lobes (and indeed the rounded apices, as in Pl. 120, figs. 1 and 2) represent reproductive regions comparable to the receptacles of living brown algae such as *Fucus*. The density of pores in such regions appears to be equivalent to that seen elsewhere, and does not particularly encourage this hypothesis. The specimen of Plate 120, figs. 8 and 9 shows such a lobe, of which the apex (probably with an originally thinner cuticle) has collapsed, revealing the cellular reticulum on its inner face. The few specimens of *S. nanum* with pores on all faces of a short cuticular tube may also represent such upright lobes of the generally dorsiventral thallus.

Further speculations about the life form of *Spongiophyton* devolve on the role of the pores. Despite Kräusel's suggestion of a doubtful—and ambiguous—group of dark bodies in one pore in *Spongiophyton*, we have seen no evidence in our material of spores being formed beneath the pores, as are regularly seen in *Foerstia*. None the less, it is possible that the pores represent such sites of release of reproductive bodies —either spores (presumably without any exine, as none are preserved) or motile propagules (cf. the osteole of the conceptacle of *Fucus*). Other possibilities are pores for secretion of mucilage (cf. various brown algae), or apertures leading to internal, aeration tissue (cf. stomata of vascular plants, or the barrel-shaped pores of *Marchantia*). There are doubtless many other possibilities; we merely suggest here that *Spongiophyton* (or, at least, the species *S. nanum*) was a dorsiventral, terrestrial plant, dichotomizing in the plane of the surface on which it grew, with the pores on the upper surface, from which occasional upright lobes developed.

The systematic assignment of *Spongiophyton* will be further considered after a note on the composition of the cuticle, and a review of other comparable plant fossils.

Composition of Spongiophyton *cuticle*. In an attempt to get further evidence on the nature of the *Spongiophyton* organism, an elemental analysis for carbon, hydrogen, nitrogen, and oxygen of fragments of *S. nanum* was carried out.

For comparison, similar analyses of two other types of fossil plant material were made. These were of *Foerstia ohioensis* White, from the Upper Devonian Ohio Shale of Ohio, U.S.A. (material kindly supplied by Professor J. M. Schopf), and leaf material of *Ptilophyllum pecten* (a gymnosperm) from the middle Jurassic of Cloughton, Yorkshire. These were both prepared in the same way. The relevance of the *Foerstia* is that it represents a plant perhaps closer in its structure (and affinity?) to *Spongiophyton* than any other available fossil material. The *Ptilophyllum*, in contrast, is perhaps adequately representative of coalified tissue of a land plant leaf with a rather thick cuticle. While the *Spongiophyton* and *Foerstia* specimens consisted of more or less coal-free 'cuticle' material which had to some extent been naturally

macerated during fossilization, the *Ptilophyllum* leaves certainly contained some coalified leaf mesophyll tissue.

The specimens used for the analysis were extracted from the matrix with cold 40% hydrofluoric acid, washed repeatedly with distilled water, and then dried at 100 °C. The analyses were carried out on duplicate samples, made (in the case of *Spongiophyton*) by splitting individual 'tubes' of the plant into more or less equivalent halves ('matched pairs'). It was hoped in this way to eliminate minor differences in original composition and effects of the microenvironment at the site of incorporation in the sediment. The resulting samples, composed of several individual fragments, weighed about 1 mg. The analysis was carried out in the Chemistry Department of University College, London, through the kindness of Dr. A. J. Layton, using a routine analysis procedure. This basically involves heating a weighed sample of fossil material in a furnace at 900 °C, flushing initially with helium, followed by a stream of oxygen. Metallic copper removes excess oxygen from the resulting gas mixture, and the carbon, hydrogen, and nitrogen are assayed as CO_2, H_2O, and N_2 by means of a detector measuring the thermal conductivity of the gas.

The results are given in table 1. In addition, comparable data are given for a bituminous coal and for two graptolites. These results are obviously only a very general guide to the original composition of the organic material at the time of fossilization. The coalification process, of course, alters the elemental ratios; and the three samples have had rather different histories of incorporation and subsequent diagenesis. Even so, some guarded conclusions may be drawn.

TABLE 1. Elemental composition of *Spongiophyton nanum* and other coalified fossil plant material. For the first three plants, the figures given are the means of duplicate analyses. Carbon (C), hydrogen (H), and nitrogen (N) are determined directly, and the oxygen is obtained by difference. The figures for an average bituminous coal are from Swain (1970); the nitrogen:carbon ratios for the two graptolites are means of 3 and 2 determinations respectively, and are from Wiman 1902.

	C	H	N	O	H/C %	N/C %
Spongiophyton nanum	78·4	8·4	2·7	10·5	10·7	3·4
Foerstia ohioensis	63·5	5·5	1·7	29·3	8·6	2·7
Ptilophyllum pecten	67·2	6·2	1·6	25·0	9·2	2·4
Bituminous coal	79	5·4	1·6	14	6·9	2·0
Desmograptus						5·0
Gothograptus						6·7

Kräusel has placed emphasis on the significance of the nitrogen fraction in such analyses as implying the presence of chitin in the original organic material. In his analysis of *Foerstia ohioensis* (Kräusel 1941) he obtained 2·5% nitrogen, for which he invokes an original 35% of chitin in that plant. This he used as a basis for suggesting fungal affinity for *Foerstia*, and hence for the recognition of a new group of plants, the 'Algomycetes' based on that genus. The danger of ascribing organic nitrogen in fossil material directly and solely to chitin as its source is well illustrated by recent work on graptolites. Many early workers regarded the carbonaceous substance of graptolites as chitinous (e.g. Kraft 1926; see also Wiman 1902, whose analyses are quoted in table 1). But it has now been shown that a major nitrogenous constituent of fossil graptolite organic matter (perhaps all) is scleroprotein, which on hydrolysis yields a range of amino-acids (see Florkin's 1969 discussion of the earlier work of Foucart). Kräusel's supposition that *Foerstia* contained chitin is perhaps no better founded than in the case of the graptolites.

Our interpretation of the data in table 1 may be summarized as follows:

(1) The N/C ratio in *Spongiophyton* is 25% greater than in *Foerstia*. This is at

variance with Kräusel's (1960) results for *Spongiophyton*, which showed a very low (unstated) nitrogen content, which he interpreted as equivalent to a chitin content of less than 1%.

(2) The N/C ratio in *Spongiophyton* is also appreciably higher than in the *Ptilophyllum* leaf material.

(3) The nitrogen content of all the plant specimens (expressed as a nitrogen to carbon ratio) is considerably less (2:3·4) than that shown by the graptolite analyses of Wiman (5:6·7).

Other Palaeozoic fossil plants comparable to Spongiophyton. We now know of a number of Devonian plants which, while lacking evidence that they were tracheophytes, show one or more attributes of land plants (e.g. a thick cuticle, spores with an exine). Four of these—*Prototaxites*, *Parka*, *Foerstia* (?*Protosalvinia*) and *Nematothallus* are thoroughly discussed by Lang (1945). *Foerstia* (of the Upper Devonian of the United States) and its relationship to the Brazilian *Protosalvinia*, has been extensively reviewed by Kräusel (1941), Arnold (1954), Schopf and Schwietering (1970), and Phillips *et al.* (1972). Kräusel and Venkatachala (1966) have also reviewed *Spongiophyton*, *Aculeophyton*, and *Orestovia*.

Excluding the relatively massive tree-sized *Prototaxites* and the probably related thalloid *Nematothallus*, the remaining genera show one or more significant features of comparison with *Spongiophyton*. The main features of these five Devonian genera are listed in table 2. Of the genera there listed, three are based on plants known only as a tubular cuticular covering of a more or less cylindrical plant body: *Spongiophyton*; the similar genus *Aculeophyton* (Lower Devonian of Western Siberia and possibly from Brazil); and the enigmatic Russian genus *Orestovia*. These three genera, of which the internal structure and reproductive organs are unknown, are grouped by Kräusel and Venkatachala in a family, the Spongiophytaceae. But the status of the family remains obscure; Kräusel and Venkatachala leave it unassigned, but make guarded comparison with the Rhodophyceae. The state of uncertainty of our knowledge of these plants is reflected in the fact that one of them, *Orestovia*, is treated by Ananiev and Senkevitch (1963) as a psilopsid (a vascular plant).

Views on *Foerstia* (?*Protosalvinia*) are equally diverse; Kräusel (1941) regarded *Foerstia* as a member of a new class of Thallophytes, the 'Algomycetes', while Schopf and Schwietering believe that the *Protosalvinia*/*Foerstia* complex 'probably should be assigned to the Fucales' (Phaeophyta, brown algae). We remain doubtful of this assignment, since the thick cuticle-like covering and resistant spore tetrads have no close counterpart in any living member of that order.

The essential features of the early Devonian plant *Parka decipiens* were demonstrated by Don and Hickling (1917) and it is a great tribute to the thoroughness of their work that no substantially new information on the plant has been forthcoming since that time. *Parka* may be compared to a limited extent with both *Foerstia* and *Spongiophyton*. It resembles both these genera in having been a somewhat flattened thalloid plant with a cuticular covering. Like *Foerstia*, *Parka* had large spore-containing cavities in the thallus, which gave the whole plant a rather net-like appearance. But although the spores of *Parka* have a resistant covering, as in *Foerstia*, they were not formed in tetrads as in that genus. There are several other poorly known

TABLE 2

Genus	Age	Geographical location	External morphology	Cuticle	Reproductive bodies	Systematic position	Important references
SPONGIOPHYTON Kräusel	Middle Devonian	Parana, Brazil (Kräusel) Ghana (this work)	Flattened, cylindrical dorsiventral dichotomizing thallus	Thick, with pores (on one face only?) inner reticulum of elongated cells	None seen	'Thallophyte'—Spongiophytaceae (Kräusel and Venkatachala 1966)	Kräusel 1960 Kräusel and Venkatachala 1966
ACULEOPHYTON Kräusel and Venkatachala	Lower Devonian (and ?Middle Devonian)	Kuznetzk Basin ?Parana, Brazil	Unknown; perhaps similar to *Spongiophyton*	Thin, with conical to spine-like papillae, and cellular reticulum	None seen	'Thallophyte'—Spongiophytaceae (Kräusel and Venkatachala 1966)	Kräusel and Venkatachala 1966
ORESTOVIA Zalessky *ex* Ergolskaya, *emend.* Kräusel and Venkatachala	Lower Devonian	Kuznetzk Basin Yunnan, China	?Cylindrical thallus with pseudo-monopodial branching	Thin, with cellular reticulum, pores of two sizes ('large and small')	None seen	'Thallophyte'—Spongiophytaceae (Kräusel and Venkatachala 1966) *or* Psilopsida (Ananiev and Senkevitch 1963)	Kräusel and Venkatachala 1966 Ananiev and Senkevitch 1963 Snigirevskaya 1971
FOERSTIA White (? *Protosalvinia* Dawson)	Upper Devonian	Mid-western U.S.A. Brazil	Flattened, disc-like or upright club-shaped or dichotomizing pincer-shaped thallus	Thick, with inner reticulum of isobilateral cells	Tetrads of large (200 mμ) triradiate spores in depressions in thallus	'Algomycetes', Foerstiales (Kräusel) *or* Phaeophyta, Fucales (Schopf and Schwietering 1970)	Kräusel 1941 Schopf and Schwietering 1970 Phillips *et al.* 1972
PARKA Fleming	Lower Devonian Upper Silurian	England Wales Scotland	Flattened, rounded to irregularly lobed dorsiventral thallus	Very thin, with cellular reticulum	Masses of small (30 μ) spores in cavities in thallus, not in tetrads	Anomalous plants of ?algal affinity	Don and Hickling 1917 Lang 1945

fossil plants, to which comparison with *Spongiophyton* may be guardedly extended. They include the thalloid fossil *Thallomia* Heard, and *Eohostimella* Schopf. *Thallomia* is an enigmatic genus in which modern plant material (leaf tissue) may have been erroneously linked with an undoubted fossil organism (see Heard and Jones 1931; Lang 1937, p. 247; and Kräusel and Venkatachala 1966, p. 222). Although its thalloid form might invite comparison with *Spongiophyton*, its putative internal structure and cuticle need reinvestigation. *Eohostimella* Schopf *et al.*, 1966 (from the Silurian of Maine, U.S.A.), consists of upright tubes of coalified tissue (?cuticle or cortex) of what were apparently plants, but we know nothing of their microscopic structure or internal organization.

We believe that systematic assignment of any of the genera of table 2 must be tentative, but this does not diminish their biological interest. Their greatest significance is that although they are not apparently tracheophytes, and cannot be closely matched in any extant plant group, they share adaptations to terrestrial life (a cuticle, resistant spores) which are now seen only in tracheophytes and the sporophytes of bryophytes. In these attributes they may be thought of as showing parallel development to the early vascular plants.

EMENDED DIAGNOSES OF TAXA

Genus SPONGIOPHYTON Kräusel 1954

Type species. S. lenticulare (Barbosa) Kräusel 1954, p. 206. (See also Kräusel 1960.)

Emended diagnosis. Tubular thallus with cuticular covering, branching dichotomously or subdichotomously with rounded apices; base unknown. Cuticle with internal cellular reticulum and circular to fusiform pores, largely confined to one surface of the thallus.

Spongiophyton nanum Kräusel 1960, p. 32

Emended diagnosis. Thallus cylindrical, of originally circular or elliptical cross-section, dichotomizing several times, with rounded apices. Branches typically 2–5 mm wide by up to 25 mm long (incomplete). Cuticle penetrated by numerous circular to elliptical pores 200–300 μm in largest diameter, with edges bevelled on the outer face. Pores principally confined to one face, this poral surface having the thicker cuticle (typically 60 μm); cuticle of aporal face, typically 30 μm thick. Inner face of cuticle with ridges forming a cellular reticulum, cells typically 40 μm long by 20–30 μm broad, oriented with the longer axis parallel to the length of the thallus.

Spongiophyton lenticulare (Barbosa) Kräusel 1954

Emended diagnosis. Thallus cylindrical, its cuticular covering forming a tube up to 12 mm diameter. Lenticular pores of various sizes present, up to 0·8 mm in longest dimension, elongated parallel to long axis of thallus; pores of greater concentration on one surface of cuticular tube. Inner surface of cuticle with cellular reticulum, cells typically 50 μm wide by 100 μm long, with pronounced arrangement in longitudinal series.

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