

LOWER CARBONIFEROUS LYCOPODS FROM GHANA

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ABSTRACT. Two new species of lycopods, based on compression fossils with cuticles preserved, are described from the Takoradi Shales at Essipon on the coast of Ghana: *Archaeosigillaria essiponensis* sp. nov. and *Lepidodendropsis sekondiensis* sp. nov. This extends the record of the 'Lepidodendropsis Flora' further south into Africa than it was known hitherto; the Ghanaian fossils show closer similarity to the several Lower Carboniferous lycopod assemblages from North Africa than to the closest comparable species described from the Witteberg Series in the Cape.

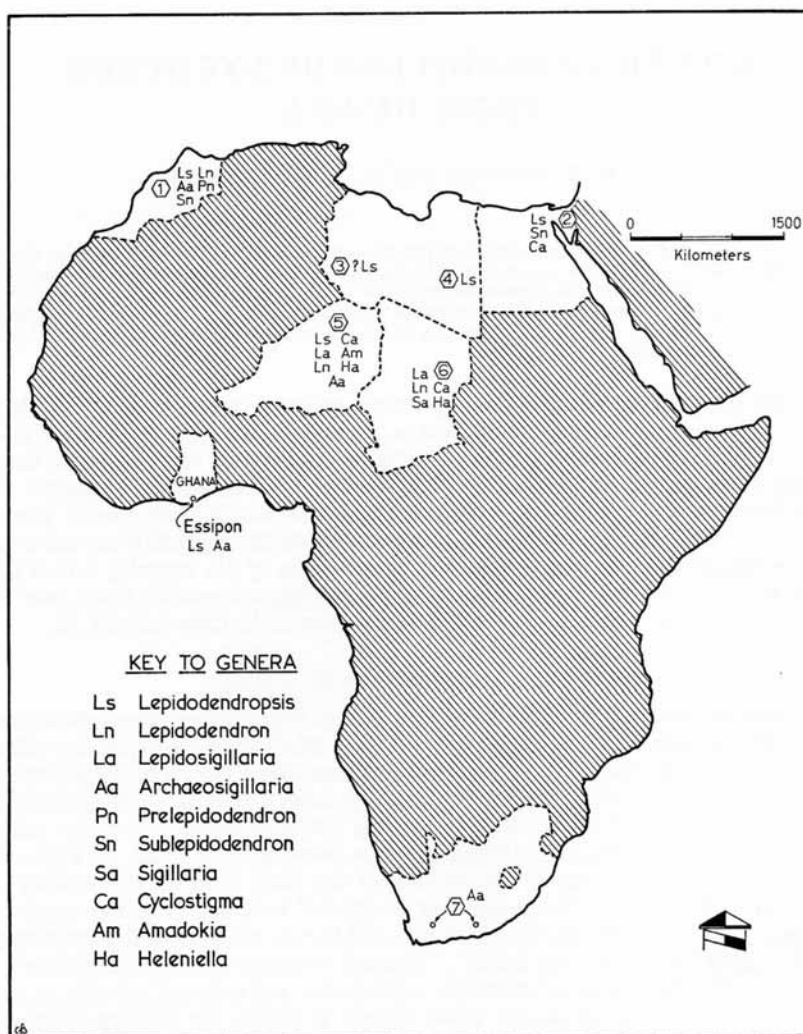
THE fossil lycopods described in this paper were collected by one of us (M. K. M.) in 1968 at Essipon on the coast of Ghana near to Sekondi, in rocks believed to be of Lower Carboniferous age. The preservation of some of the material has proved to be surprisingly good, and represents the first occurrence of pre-Permian fossil lycopods from Africa from which a cuticle has been prepared. Comparable lycopod-rich floras of similar age (the 'Lepidodendropsis flora' of Jongmans) are known from many other parts of the world. Aside from the good state of preservation of this material, it is of significance in its relative geographic isolation, lying between comparable floras over 1500 miles away in North Africa, and over 2500 miles away in the Cape (text-fig. 1).

SOURCE AND AGE OF MATERIAL

The fossil plants described here were collected from large boulders up to 40 cm across, lying at the foot of the cliff immediately below the United Africa Company Rest House, at Turtle Cove about one mile east of the Sekondi naval base. The Rest House is between the village of Essipon (also spelt Esupon) and the coast. The rocks forming the cliff at this point west of the Inchaban fault are of the Takoradi shales unit of the Sekondi Series, dipping gently to the west, where they are overlain by the Efiu Nkwanta beds in a down-faulted block about 100 yd west of the fossil locality. The boulders are undoubtedly derived from the *in situ* rock of the cliff itself, and probably come from the upper part of the unit described by Crow (1952) as 'a series of hard, grey-green grit bands . . . interbedded with the shales . . . exposed along the coast-line at Esupon'.

The plant fossils occur as compressions, impressions, and endocortical casts, in a grey to brownish micaceous sandstone, which cleaves to follow the bedding planes only rather irregularly. Individual pieces of the rock detached from the boulders may be more or less reddish brown or have an outer zone of brown coloration with a grey core. Some of the plant compressions retain abundant coaly material, from which cuticles have been prepared. Lack of coaly material is not simply correlated with oxidation and red coloration of the matrix, since in some cases coaly material is present on specimens showing strong red coloration.

Crow discusses the fauna of the Takoradi shales, which consists of lamellibranchs, brachiopods, gastropods, and fish, and also mentions the occurrence at Essipon of



TEXT-FIG. 1. Map to show the localities of various records of Lower Carboniferous or uppermost Devonian lycopods in Africa. The localities 1-6 are believed to be of Lower Carboniferous age, as is that of Essipon dealt with here; the South African records (loc. 7) are believed to be of Upper Devonian age, but are shown here on account of the record of *Archaeosigillaria*. (1) Morocco (several localities); Danzé-Corsin (1960) and earlier references there cited. (2) Sinai; Jongmans and van der Heide (1955). (3) Fezzan, Libya; Chiarugi (1949); (see also Jongmans 1954a). (4) Kufra, Libya; Gothan (1933). (5) Djado; Danzé-Corsin (1965), Lejal (1968). (6) Ennedi; Danzé-Corsin (1965). (7) Cape Province, South Africa; Witteberg Series localities; Plumstead (1967).

'abundant poorly preserved and fragmentary remains of plant tissue and indeterminate carbonaceous matter'. He interprets the deposition of the upper part of the Takoradi shales as occurring during a phase of emergence, in which the estuary of a river flowing from the north-east was silting up with the formation of marine or deltaic swamps. The plants described here show no evidence of being in the position of growth, but they evidently had not been subjected to much transport.

The age of the Takoradi shales can be said to be either Devonian or Carboniferous, on the basis of the fauna (Crow 1952, summarizing the work of Cox, here quoted). Cox (1946) commenting on the faunal assemblage from the Takoradi shales says that 'the fossil evidence does not give clear confirmation of a Carboniferous age but is equally, perhaps slightly more, suggestive of the Devonian'.

The only readily recognizable plant fossils present in the boulders are the lycopods described here; a number of finely striated axes or leaves superficially resembling cordaitaleans were noted, but have not been studied further.

The specimens have been photographed dry (e.g. Pl. 66, fig. 4), and in some cases where a mould (i.e. an impression of the outer surface only) was present on the rock (ESSI 6, Pl. 66, fig. 1) a cast of this mould was prepared, using Revultex liquid rubber. This was then coated by sublimation of ammonium chloride vapour, and photographed in oblique illumination (Pl. 66, fig. 3). Some specimens with coaly material still present were photographed under xylene to increase the contrast (Pl. 64, fig. 1). In such cases attempts were made to prepare cuticles by the removal of the coaly material, followed by treatment for one hour with Schulze's solution (saturated solution of potassium chlorate in nitric acid) followed by ammonia solution. The cuticle was then mounted in glycerine jelly containing safranin, for examination and photography.

SYSTEMATIC DESCRIPTIONS

Class LYCOPSIDA

Order PROTOLEPIDODENDRALES

Family ARCHAEOSIGILLARIACEAE

Genus ARCHAEOSIGILLARIA Kidston 1901 *emend.* Lacey 1962, Grierson and Banks 1963

Type species. *Archaeosigillaria vanuxemi* (Göppert) Kidston 1901.

Discussion. Emended diagnoses of *Archaeosigillaria* were published independently by Lacey (1962) and Grierson and Banks (1963). Lacey's emendation is influenced by his discovery of a Welsh Lower Carboniferous species with cuticle preserved. Grierson and Banks's emendation is based largely on the 'rediscovered' holotype of the American Upper Devonian type species. We regard these two emendations as complementary, and the species here attributed to *Archaeosigillaria* is consistent both with Grierson and Banks's interpretation of morphology (e.g. in the persistent leaves) and in the general features of the cuticle described by Lacey.

Archaeosigillaria essiponensis sp. nov.

Plate 64, figs. 1-8; Plate 65, figs. 1-4

Diagnosis. Lycopod stem compressions with persistent leaves, known from fragments up to 2.7 cm in diameter and 3.5 cm in length; branching unknown. Leaves borne in



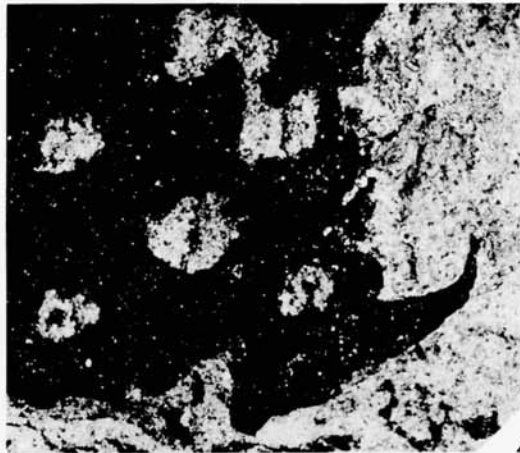
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MENSAH and CHALONER, Carboniferous lycopods

alternating whorls; leaf base decurrent, somewhat expanded to form a subdued cushion; vertical series of leaf bases more or less prominent on compressed stems. Distance between leaf bases in any vertical series 1.7–8 mm, and within a whorl (a horizontal series) 2.5–6 mm. Leaves approximately 1 mm in length, seen only in profile at the flattened stem margins; more or less sigmoid, with a flattened (lamine) apex, thickening to a decurrent base. Leaf about 0.5 mm thick at junction with stem. No evidence of leaf scar or ligule pit. Stem cuticle thick (c. 25 μm) showing elongated rectangular to fusiform epidermal cells, $150 \times 30 \mu\text{m}$ between the leaf bases, aligned more or less parallel to the axis, and in the immediate vicinity of the leaf bases, becoming shorter and aligned towards the leaf. The cuticle thins abruptly at the decurrent leaf base but continues on to the leaf surface; leaf cuticle beyond immediate leaf base not seen. No stomata present on stem cuticle.

Holotype. Specimen nos. ESSI 1 and ESSI 7 (part and counterpart), and slides (cuticle) ESSI 1 A–D, Plate 64, figs. 1, 2, 4–6. Geology Department collection, University of Ghana, Legon. From a beach boulder of Takoradi Shales, Turtle Cove, Essipon, 2 miles north-east of Sekondi naval base, Ghana. Age believed to be Lower Carboniferous (on the basis of the plants here described). Additional specimens: ESSI 4, 5, and 12 (all comparable to the holotype in size and state of preservation), and ESSI 13 (one of the broader axial fragments, with more widely spaced leaf bases).

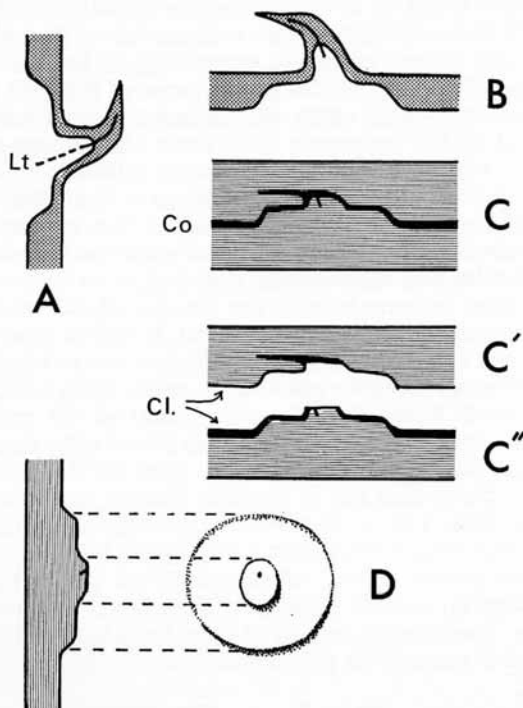
Description of specimens. The part and counterpart constituting the holotype represent a stem compression fossil exposed by a cleavage surface which has passed between the outside of the coaly material of the plant fossil and the matrix (text-fig. 2). This cleavage has left a stem compression with the cuticle on one surface, with underlying coalified cortical tissue (Pl. 64, fig. 1) but the tips of the leaves, now embedded in the matrix at the bases of depressions (corresponding to leaf cushions), remain embedded in the counterpart specimen (Pl. 64, fig. 2). A cuticle preparation from the one surface accordingly shows a series of holes (Pl. 65, fig. 1) which are not of course the site of abscission but of a breakage which occurred as the matrix was cleaved open to expose the fossil. This may be contrasted with the situation in *Eskdalia* Kidston (see Thomas 1968) where

EXPLANATION OF PLATE 64

Figs. 1–8. *Archaeosigillaria essiponensis* sp. nov. from the Takoradi shales, at Essipon, Ghana; believed to be of Lower Carboniferous age. 1, Holotype, photographed in xylene, $\times 2.5$; preservation state corresponding to text-fig. 2 c' (ESSI 1). 2, Counterpart of the same, also photographed in xylene, $\times 2.5$; preservation state corresponding to text-fig. 2 c' (ESSI 7). 3, Transfer preparation of a specimen similar to the holotype (ESSI 12), photographed dry, $\times 3.5$; this shows the original outer surface of the plant with the slightly decurrent leaf bases, and truncated tips of leaves left by breakage of the free leaf tip during transfer. 4, Part of holotype, in xylene, $\times 15$; showing a leaf seen in profile at the flattened stem margin (cf. text-fig. 2A). Note that this photo and the following two taken with the Zeiss Photomicroscope, are reversed with respect to the original specimen. 5, Part of the counterpart of the holotype (ESSI 7) in xylene, $\times 15$; note that the leaves, of which the truncated bases are seen at left buried in matrix, correspond to the gaps in coaly matter seen in fig. 4. 6, Part of holotype seen with top lighting, showing the low ridges encircling the leaf bases (see also figs. 7 and 8, and text-fig. 2D). 7, A cortical cast, corresponding with a decolified version of the holotype, showing vertical seriation of leaf bases and ridges around them simulating leaf cushions; $\times 2$; cf. text-fig. 2D (ESSI 2). 8, Part of the same, $\times 7$.

(All the specimen numbers cited here and on the following plate legends, prefixed by ESSI, relate to specimens in the collection of the Geology Department of the University of Ghana, Legon.)

leaf abscission has left comparable holes which are, however, outlined by a sharp, smooth, continuous margin. The fact that leaves were still in attachment in our fossil at the time of fossilization is made clear by their being seen in profile at the stem margin



TEXT-FIG. 2. Diagram to show the inter relationship of different preservation states of *Archaeosigillaria essiponensis* sp. nov. The stippled area represents robust tissue such as might have survived partial decomposition up to the time of cessation of microbial activity in fossilization. The shaded area represents compacted rock matrix. A, hypothetical radial section through the outer cortex and a leaf (cf. Pl. 64, fig. 4); Lt = leaf trace. B, the same, oriented as at the time of incorporation in sediment. C, the same after compaction of enclosing matrix and coalification of the plant material, Co. C', C'', part and counterpart separated by a fracture surface (Cl.) running over the outer surface of the coalified cortical tissue; this has left the bulk of the coaly matter with the cuticle on C'' (Pl. 64, fig. 4) but has removed the free tips of the leaves on C' (Pl. 64, fig. 5). D, a state comparable to C'' but with coaly matter removed, showing the leaf-cushion-like protrusion around the matrix infilling of the decurrent leaf base (cf. Pl. 64, figs. 7 and 8).

(Pl. 64, fig. 4). The leaf morphology is accordingly known only in this profile view, and the degree of tapering of the leaf as it would have been seen on the stem surface is unknown.

A specimen (ESSI 2) attributed to this species is interpreted as a compression similar to the holotype, but from which all coaly material is missing (as a result of sub-aerial weathering?), is shown in Plate 64, fig. 7. This shows the sites of leaf attachment on what amounts to a cast of the stem (or possibly, more correctly, to an endocortical cast). These leaf attachment areas show vertical and horizontal seriation, as in the holotype,

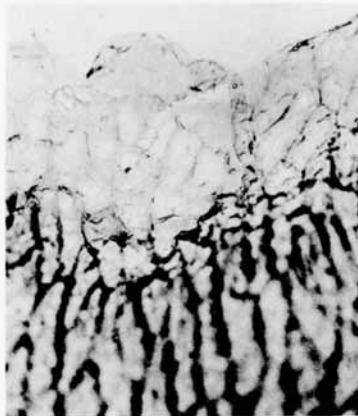
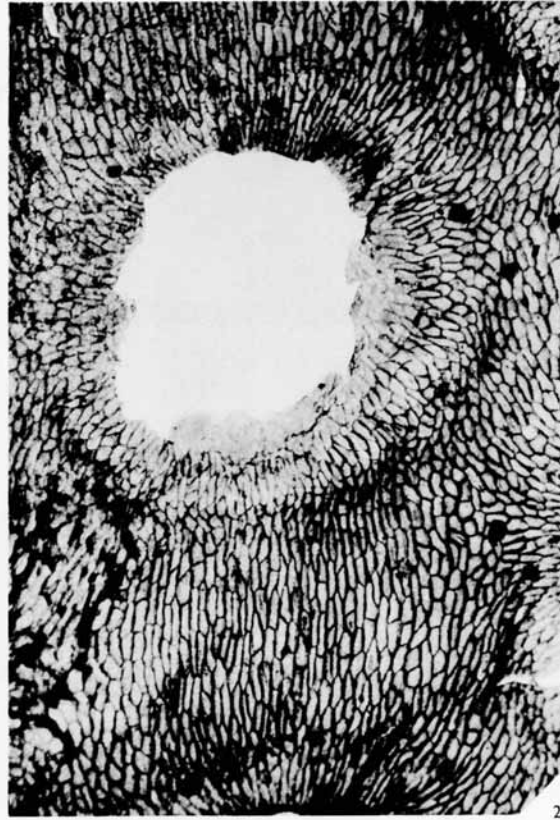
with each leaf base elevated as a more or less oval protrusion surrounded by an incomplete circular ridge, only just perceptible under low-angle illumination (Pl. 64, fig. 8). We suggest that these features may be related to collapse of matrix into the leaf cushion and leaf base, as shown in text-fig. 2, with the vascular strand (probably protruding into the cortical cavity in life) producing the central depression on the endocortical cast, as shown. Similar circular features are shown surrounding the leaf bases on the counterpart of the holotype (Pl. 64, fig. 6). The cuticle prepared from the holotype (Pl. 65, fig. 1) represents principally stem cuticle, but fragments of what evidently formed the cuticle of the base of the leaf are present at the lower edge of some of the 'leaf holes' (Pl. 65, figs. 2 and 3). Where the stem cuticle passed on to the leaf surface there is a still-perceptible change in angle of the surface (see change in focal plane in Pl. 65, fig. 3). The cuticle becomes abruptly thinner at the transition from stem to leaf surface, and there are small changes in the epidermal cell size and shape. No stomata were recognized either on the considerable area of stem cuticle examined, or on the few fragments of leaf cuticle seen. But it must be borne in mind that the area of leaf cuticle seen was very minute, and represents only the very base of the leaf. In its lack of stomata on the stem surface, *A. essiponensis* differs from those *Lepidodendron* species which have stomata on the leaf cushions (Thomas 1966) but resembles *A. stobsii* Lacey (1962) from the Lower Carboniferous of North Wales, the only other species of this genus for which the cuticle is known. Further attempts to prepare cuticle from the few exposed pieces of leaf failed, and it can only be concluded that (as in the basal leaf fragments mentioned) the leaf cuticle is much thinner than that of the stem. There is no sign of a ligule pit near the edge of the hole in the stem cuticle corresponding to the leaf adaxial surface (Pl. 65, fig. 2), such as is seen in *Porostrobus* and *Eskdalia* (Thomas 1968). It is of course possible that a ligule pit was present on the leaf surface beyond the level of fracture which detached the leaf from the stem on cleavage of the matrix; if so, it would not be seen on the stem cuticle. From our knowledge of other fossil ligulate lycopods this seems rather unlikely, and it can only be said that on present evidence it appears that our fossil was eligulate.

A single transfer was prepared from a specimen comparable in size and state of preservation to the holotype. This was effected by cementing the specimen (representing the coalified outer surface of the stem) to a glass slide using Lakeside 70 cement, coating all of the specimen except the exposed matrix with wax, and immersing it in 60% hydrofluoric acid for six hours (see Walton 1940, and references there cited). This

EXPLANATION OF PLATE 65

Figs. 1-4. Cuticles of *Archaeosigillaria essiponensis* sp. nov. 1, Cuticle from the holotype of *A. essiponensis* photographed by transmitted light; the holes represent the sites of truncated leaf bases, the remainder of the leaf having been removed on the counterpart, $\times 18$ (ESSI 1e). 2, Detail of one leaf base from the same preparation, $\times 45$; note the changing alignment of the epidermal cells as the leaf base is approached. 3, Detail of the base of the leaf from the same preparation, $\times 180$; note the rather shorter epidermal cells in the upper part of the photo, from part of the cuticle which lies at an angle to the main stem surface; this presumably represents part of the rather thinner cuticle which covered the base of the abaxial leaf surface proper, rather than stem cuticle. 4, Stem cuticle from the holotype (ESSI 1e), $\times 80$, for comparison with the following.

Fig. 5. Fragment of stem cuticle from *Lepidodendropsis sekondiensis* sp. nov. (ESSI 24a), $\times 80$, showing elongated epidermal cells, rather smaller than those of *A. essiponensis*.



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MENSAH and CHALONER, Carboniferous lycopods

eventually revealed the outer surface of the flattened stem opposite to that cemented to the slide, with the remains of attached leaves (Pl. 64, fig. 3). This generally confirms the observations made on the fractured external surface and on the cortical casts. Unfortunately no completely intact leaves were obtained, since these broke away piecemeal as the matrix was disaggregated, presumably being more vulnerable and more fragile (with thinner cuticle) than the general stem surface. In some cases the outer surface of the decurrent leaf base also collapsed, confirming that the substance of the leaf here also was relatively insubstantial. Enough of the proximal part of several leaves remained to confirm that they were in fact still attached; but beyond demonstrating that the leaf does not taper immediately and rapidly above the base, they gave no further information about leaf shape.

Discussion. This species may be compared most closely with *Archaeosigillaria vanuxemi* Kidston (the type species) from the Frasnian of New York State (Grierson and Banks 1963), and also with *A. caespitosa* (Schwartz) Plumstead (1967) from the Witteberg Series, South Africa, and *A. subcostata* (Danzé-Corsin 1965) from the Lower Carboniferous of Djado, Niger. The preservation state of Dr. Plumstead's specimens appears to be similar to that of our specimen illustrated in Plate 64, fig. 7 (cf. her pl. 11, fig. 1) and it seems likely that the lack of leaves in her material may be due either to pre-fossilization attrition (i.e. decortication, as she suggests) or to their removal, embedded in the counterpart specimen. The lack of leaves and cuticle in her material and that from Niger greatly limits the scope of any comparison. There are of course differences in shape and surface markings on the truncated leaf cushions of the Ghanaian, Niger, and South African material, but these are no greater than differences observed between parts of large specimens of other fossil lycopods (e.g. *Lepidosigillaria whitei*, see White 1907). The information available for the present Ghanaian material concerning leaf morphology and cuticle characters makes it undesirable to assign these fossils to either the Niger or Cape species which are based on much less completely known material. The similarity of our species to the American *A. vanuxemi* is much closer, but the swellings constituting the enlarged leaf bases in that species (cushions of some authors, but not in the interpretation of Grierson and Banks) are pronouncedly hexagonal rather than rounded; as with the other African material, there is no information on cuticle characters for the American fossil.

The only species of *Archaeosigillaria* for which the cuticle is known is *A. stobbsi* Lacey from the Visean of North Wales (Lacey 1962). Our cuticle resembles Lacey's in being very thick, lacking stomata, and in thinning rapidly as the cuticle passes on to the leaf base; but the epidermal cell shape is entirely different in the Welsh and Ghanaian material.

Nine species of *Archaeosigillaria* are now known (excluding the new species under discussion). Eight of these are reviewed in Chaloner and Boureau (1967), and since that date Plumstead (1967) has reassigned Schwartz's species to the genus as *A. caespitosa*. The genus accordingly ranges from early Devonian to late Carboniferous in age. *A. vanuxemi* is the only securely dated (Middle and Upper) Devonian species. The South American *Archaeosigillaria conferta* (Frenguelli) Menendez, originally reported as Devonian is now believed to be Lower Carboniferous (Archangelsky 1970); this is one of the species in which persistent leaves have been clearly demonstrated; but they differ

from those of the present species in being linear-lanceolate and relatively much longer (cf. Archangelsky's fig. 16). The other South American species, *A. picosensis*, believed to be Devonian, is of more doubtful status. *A. caespitosa* (Schwartz) Plumstead cannot be securely attributed to the Devonian, although it is evidently within the range of late Devonian to early Carboniferous. All the other species are Lower Carboniferous (*A. kidstoni*, *A. stobbsi*, *A. nathorsti*, and *A. subcostata*) with a single rather problematical species occurring in the Stephanian. The present record, therefore, scarcely helps to add precision to the existing Upper Devonian/Lower Carboniferous age assignment of the Sekondi Series, but is consistent with it.

Family SUBLEPIDODENDRACEAE
Genus LEPIDODENDROPSIS Lutz

Type species. Lepidodendropsis hirmeri Lutz 1933.

Lepidodendropsis sekondiensis sp. nov.

Plate 66, figs. 1-4

Diagnosis. Stem impressions up to 7 cm in length and 17 mm in width, covered with narrow inverted pear-shaped leaf cushions, which taper basally, becoming flush with the stem surface before the converging edges meet; broad rounded upper edge of cushion formed by false leaf scar; slightly raised triangular area sometimes present above the false leaf scar, extending to complete fusiform outline of cushion. Leaf cushions on holotype 5 mm long by 1.5 mm wide. Leaf cushions showing unequally inclined secondary spirals, produced by a primary spiral phyllotaxis, that of the lowest inclination being only slightly inclined (c. 15°) to the horizontal ('low angle spiral arrangement'). Branching dichotomous, with 60° divergence seen in one specimen.

Holotype. ESSI 6 (Pl. 66, figs. 1, 2). Geology Department Collection, University of Ghana, Legon. From beach boulder of Takoradi Shales, Turtle Cove, Essipon, 2 miles north-east of Sekondi naval base, now believed to be of Lower Carboniferous age. Additional specimens: ESSI 8 and ESSI 20 (showing dichotomous branching) and ESSI 9 (slightly decorticated stem with more widely spaced leaf cushions).

Description of specimens. The holotype is in fine-grained matrix, and the detailed topography of the cushion surface can be seen by direct observation, and from the (positive) rubber casts made from the (negative) impression specimen (i.e. mould) (Pl. 66, figs.

EXPLANATION OF PLATE 66

Figs. 1-5. *Lepidodendropsis sekondiensis* and an unidentified plant, from the Takoradi shales at Essipon, Ghana, believed to be of Lower Carboniferous age. 1, *Lepidodendropsis sekondiensis* sp. nov., the holotype (an impression or natural mould of the stem outer surface) illuminated from the left, $\times 2.5$ (ESSI 6). 2, Detail of the same, showing decurrent leaf bases (leaf cushions) and the false leaf scar at the apex of each; illuminated from the right, $\times 15$. 3, Part of a rubber cast prepared from the same specimen (ESSI 6A), coated with ammonium chloride and illuminated from the lower right to show the outline of the decurrent leaf bases, $\times 15$. 4, Specimen of the same species showing a small dichotomosing axis, $\times 1$ (ESSI 8). 5, Slightly tapering, finely striated unidentified axis or leaf rachis, $\times 1$ (ESSI 18).



MENSAH and CHALONER, Carboniferous lycopods

1-3). No leaves are seen in attachment at the stem margin, but this is not clearly revealed in any of the specimens; the evidence offered by the leaf cushions themselves is that their upper margin represents a false leaf scar (Chaloner and Boureau 1967, p. 533), in the form of an arc (*arc foliare* of Danzé-Corsin) where the cleavage surface has passed through the junction of the cushion with the leaf (or the remains of a partially eroded leaf). The rubber cast of the holotype brings out the fact that the base of the leaf cushion is not closed but that the cushion surface merges with that of the stem at the narrowed base of the cushion (Pl. 66, fig. 3). The area of the cushion immediately below the false leaf scar is often somewhat irregularly protruding (Pl. 66, fig. 2), giving a suggestion of a leaf scar; however, this area is quite irregular in definition (outline) and in occurrence and we do not regard it as a scar of leaf abscission. The leaf cushion has no evident sculpture, and has a more or less flat outer surface rather than a rounded or keeled one. There is no evidence of a ligule pit. The leaf arrangement is spiral, so as to produce two evident 'secondary spirals', both unequally inclined to the vertical and to the horizontal; one of these is steeply inclined, and the other only slightly so, producing the so-called low-angle spiral characteristic of the phyllotaxis of many late Devonian/early Carboniferous lycopods (see for example, Alvin 1965). On the narrowest axes (e.g. ESSI 8) the spaces between the leaf cushions are less than their own width, and fine striations are visible on the stem surface; broader axes (e.g. ESSI 6) have a horizontal spacing of the cushions about equal to their width, but with only a very faint indication of striations on the stem surface; larger axes, with the cushions spaced horizontally at a distance about equal to their length (ESSI 9, ESSI 25) show clear longitudinal striation. Fragments of stem cuticle were prepared from two specimens. The material which yielded them showed a stem surface covered with a thin coaly layer, in which the cleat was so strongly developed that the plant material was extensively fractured. As a result, maceration yielded only minute fragments of cuticle, each less than 1 mm square, without evident orientation or indication of their position with respect to the leaf bases. These fragments show elongated cells, typically about $100 \times 20 \mu\text{m}$ not unlike those of *Archaeosigillaria essiponensis*, but somewhat smaller (Pl. 65, fig. 5) and lacking in any distinctive characters. No large fragments were obtained from any specimen, so that little significance can be attached to the lack of stomata, except that none were seen on the small number of fragments that were carefully examined.

Some of the broader axes with more widely spaced leaf bases (e.g. ESSI 9 and 26) resemble the plant identified by Gothan (1933) as '?*Porodendron*' from the Lower Carboniferous of Kufra in Libya, and which Jongmans (1952) has suggested might more properly be assigned to *Lepidodendropsis*. A single specimen (ESSI 3) shows a highly striated stem surface with irregular remains of fusiform leaf cushions probably in a somewhat decorticated state; it seems likely that this represents part of one of the larger axes of our species, but it can only be assigned as 'cf. *Lepidodendropsis sekondiensis*'.

Two axes (ESSI 10 and ESSI 19), both about 3 cm wide, showing widely spaced leaf attachments but virtually no evidence of a leaf cushion, may belong to this species. Both are impressions (i.e. moulds of the outer surface), and although they show some detail of surface topography they do not show clearly the status of the leaf base (scar or false scar?). They show some similarity to Chiarugi's (1949) *Sigillaria fezzanensis* from Libya; it is significant that Jongmans (1954a) has suggested that this species, also, should be assigned to *Lepidodendropsis*. Without more intermediate material linking

these two Essipon specimens with the holotype of *Lepidodendropsis sekondiensis* we regard their relationship to this species as problematical.

Discussion. Although several species of *Lepidodendropsis* are now known bearing reproductive structures (Chaloner and Boureau 1967), the type species is based on vegetative material only, so that the generic concept is perforce based on the rather limited number of characters offered by such material. Recent (and somewhat divergent) interpretations of this genus are given by Danzé-Corsin (1958), Lacey (1962), Chaloner and Boureau (1967), and Lejal (1969). We regard this genus as being limited to lycopods with narrow, fusiform leaf cushions arranged in a low-angle spiral, bearing false leaf scars, lacking leaf abscission (and hence true leaf scars), and any evidence of a ligule pit.

Lepidodendropsis is separated from *Sublepidodendron* Hirmer and *Prelepidodendron* Danzé-Corsin only on rather arbitrary criteria. It differs from *Sublepidodendron* in having a continuation of the tapered base of each leaf cushion linking it with the apex of the cushion below. But as Jongmans (in Jongmans and van der Heide 1955) remarks, this latter feature is evident only in well-preserved material. *Lepidodendropsis* differs from *Prelepidodendron* in the latter having true leaf abscission, leaving a clearly defined scar.

More than twenty species of *Lepidodendropsis* are now known (see Chaloner and Boureau 1967; Lejal 1969). *Lepidodendropsis sekondiensis* sp. nov. closely resembles the type species *L. hirmeri* (see especially the American material of Jongmans, Gothan, and Darrah 1937, pl. 48, fig. 22), and to a lesser extent, *L. fenestrata* Jongmans (see figures in Jongmans and van der Heide 1955). Both these species differ from the Ghanaian in having an elongated feature in the central upper part of the leaf cushion, attributed to a leaf trace by Jongmans, Gothan, and Darrah (1937), and to the presence of an elongated leaf scar by Lejal (1969).

ADDITIONAL PLANT FOSSILS

Many pieces of finely striated coalified plant tissue (axes, linear leaves or rachides?) occur together with the lycopods described above. One of the larger of these fossils is shown at natural size on Plate 66, fig. 5. The finely striate surface is reminiscent of the leaves of *Cordaites* s.l. (i.e. including the Gondwana forms assigned to *Noeggerathiopsis*; see Meyen 1969). The lack of nodes on any of the specimens makes the possibility of their being sphenopsid axes most unlikely. The slight taper shown by several specimens (including that figured) would be consistent with a spatulate form of leaf such as is shown by *Noeggerathiopsis* (cf. figures in Pant and Verma 1964); but equally with the possibility that they represent rachides of pteridosperms or fern fronds. There is evidence from the thickness of coal matter of some of these fossils, and from their surface topography, that some may represent compressions of fairly robust organs rather than a flat lamina; this marginally favours a rachis interpretation against a *Cordaites*-like leaf. Unfortunately, attempts to prepare cuticles from these fossils failed. On the present evidence we accordingly prefer to regard them as plant fossils (leaf or axis) *incertae sedis*.

Danzé-Corsin (1960) notes the occurrence of indeterminable rachides in the Moroccan Lower Carboniferous, associated with the abundant lycopods, and regards them as evidence of the presence of 'filicoid' plants (i.e. ferns or pteridosperms) in that flora. As in the present material, the Moroccan plant fossils had apparently been subjected to some attrition before fossilization, as is evidenced by the coarse lithology in which

they commonly occur. This could explain (as Danzé-Corsin suggests) the survival of the rachides without the more delicate part of the frond; the same mechanism may be invoked for the Sekondi material as for the Moroccan.

GENERAL DISCUSSION

The age of the Sekondi Series. The lycopods described here offer some basis for attempting to resolve between the suggested Upper Devonian or Lower Carboniferous age suggested for the Sekondi Series (Crow 1952). This aspect of the *Archaeosigillaria* has been dealt with above. Almost all of the known species of *Lepidodendropsis* are Lower Carboniferous; only two, from China (*L. arborescens* Sze and *L. dzungariensis* Sze) are reported to be of Devonian age. In fact the genus is so ubiquitous in plant-bearing rocks of Lower Carboniferous age, and so rare in the Devonian, that we would follow Danzé-Corsin (1960) in regarding *Lepidodendropsis* as characteristic of that interval ('*Lepidodendropsis* . . . a en effet été signalé au Carbonifère inférieur'). The occurrence of this genus in the Sekondi Series strongly favours a Lower Carboniferous rather than a Devonian age.

The Lepidodendropsis flora. Jongmans first described the flora of the Devonian/Lower Carboniferous transition as the '*Lepidodendropsis* flora' in a paper given to the Heerlen Congress in 1951 (Jongmans 1952, p. 300). In a paper delivered in Nova Scotia the following year (Jongmans 1954b) he somewhat expanded the geographic and conceptual range of the flora designating it the '*Lepidodendropsis-Cyclostigma-Triphylopteris* flora', emphasizing its worldwide extent—Peru, U.S.A., Europe, Egypt, China, and elsewhere. In addition, his map (1954b, fig. 4) indicated localities for the flora in European Russia and Kazakhstan, north to Spitsbergen, and in Gondwanaland into India and eastern Australia. Since the publication of Jongmans's paper, *Lepidodendropsis* has also been reported in Britain (Lacey 1962), from a number of new Russian localities (Vakhrameev *et al.* 1970) and from several new sites in North Africa. The work of Danzé-Corsin (1965) and Lejal (1968, 1969) building on that of earlier French palaeobotanists has extended our knowledge of the several lycopod-rich floras of Dinantian age from North Africa, beyond Jongmans's original records from Egypt. A good review of these floras is given in Danzé-Corsin (1960) (which gives extensive references to earlier French North African work) and a later account of new material from French West Africa is given in Danzé-Corsin (1965) and Lejal (1968, 1969). It is appropriate in the light of this later work to add to the two lycopod genera which Jongmans regarded as characterizing the flora (*Lepidodendropsis* and *Cyclostigma*) the several other lycopod genera that commonly occur in association with them in the Lower Carboniferous. These are *Prelepidodendron* Danzé-Corsin, *Sublepidodendron* Hirmer, *Lepidosigillaria* Krausel and Weyland, and *Archaeosigillaria* Kidston. Recent reviews of the systematic status of these genera and their principle species are given in Lejal (1969), Danzé-Corsin (1962), and Chaloner and Boureau (1967). The African occurrences of these genera in several floras of either confirmed Dinantian age, or of the supposed Devonian/Lower Carboniferous transition are shown in text-fig. 1. Two records from Libya may well represent further occurrences of *Lepidodendropsis* as Jongmans (1952) has pointed out. The first is Gothan's (1933) '*Porodendron* sp.' from Kufra (text-figs. 1: 4) which shows a general similarity to some of the larger axes of *Lepidodendropsis sekondiensis*. The other is

Chiarugi's (1949) *Sigillaria fezzanensis* from the Fezzan (text-fig. 1:3) which resembles some of the (indeterminable) axes from Sekondi. It is worth noting that in both these North African occurrences, as at Sekondi, the plants occur in the rather unusual matrix of red or limonite-rich sandstones. In addition to those mentioned above, the South African occurrence of *Archaeosigillaria* in the Witteberg Series (Plumstead 1967) is also shown; this is of particular interest in view of the similarity of *A. caespitosa* to the species described here, and the fact that that genus ranges in age from Middle Devonian to Upper Carboniferous.

Sullivan (1967) has recently discussed the palynological evidence for the existence and position of Lower Carboniferous floral provinces in relation to the contemporaneous palaeolatitude configurations. On his world map (1967, fig. 1) the African continent is conspicuous as an area with a paucity of palynological data, in which the postulated palaeolatitudes range from a South African polar position to a latitude of about 50° in Morocco. The similarity of the several small floras of Lower Carboniferous age now known between Ghana and the Mediterranean are hard to reconcile with a strong climatic gradient across this region. It is difficult to assess the degree of climatic similarity implied by the extent of the *Lepidodendropsis* flora, ranging in present-day latitude from Ghana to Spitsbergen. The genus may represent a group of lycopods corresponding more to a family or broader taxonomic grouping, with correspondingly wider climatic implications. However, within the limits of our very incomplete knowledge there is undoubtedly greater similarity of vegetational facies between the Lower Carboniferous plants of southern Ghana and Libya than between the present-day floras of these two regions. The palaeogeographic aspect of African Lower Carboniferous plant fossils and spores is obviously a challenging problem. A further enigmatic aspect of the Palaeozoic history of the Gondwanan area is that we still have no clearly Upper Carboniferous continental plant-bearing deposits in Africa south of the Atlas mountains. It is to be hoped that future work on both spores and plant macrofossils will help to fill this apparent gap between the Lower Carboniferous *Lepidodendropsis* flora and the first appearance of the (? Carbo-Permian) *Gangamopteris*/*Glossopteris* flora on the African continent.

Acknowledgements. We are very grateful for financial help from the Special Research and Conferences Fund of the University of Ghana and for help from the Ashanti Goldfields Corporation which made possible the visit of one of us (M. K. M.) to London in connection with this work.

This paper is dedicated to Professor Chester A. Arnold in the year of his official retirement as Professor of Botany at the University of Michigan, and in honour of his distinguished service to the fields of morphology and paleobotany.

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