THE LOWER DEVONIAN FLORA OF THE SENNI BEDS OF MONMOUTHSHIRE AND BRECONSHIRE

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[Plates 9–11]

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New fossil localities, of which the most important is Llanover Quarry, are recorded from the Senni Beds of the Lower Old Red Sandstone of Monmouthshire and Breconshire.

All the plants so far known from the Senni Beds occur at Llanover and a number are at present only known in Britain from this locality. The plants distinguished and described, in addition to some remains *incertae sedis*, are: *Drepanophycus spinaeformis*, cf. *Psilophyton princeps*, *Dawsonites arcuatus*, *Gosslingia breconensis*, *Zosterophyllum* cf. *australianum*, *Z. llanoveranum* n.sp., *Zosterophyllum* sp., *Cooksonia* sp., *Sporogonites exuberans*, *Sciadophyton steinmanni*, *Taeniocrada* sp., *Prototaxites* sp., *Nematothallus* sp., *Pachytheca* sp.

The remains of *Drepanophycus* include shoots bearing sporangia and have **H**-shaped branching in what was probably the lower region of the plant.

The remains of a spiny plant of *Psilophyton princeps* type have a hitherto undescribed fructification in organic connexion with the vegetative shoots. This fructification is quite unlike *Dawsonites*, of which typical examples also occur.

The numerous specimens of *Gosslingia* have shown that the sporangia were not borne on special fertile branches, as was originally supposed, but on the margins of the regular dorsiventral branch system.

A distinction of two subgenera within the genus *Zosterophyllum* is suggested. *Z.* cf. *australianum* belongs to *Eu-zosterophyllum* with radial spikes. A new species, *Z. llanoveranum*, has dorsiventral secund spikes of sporangia of the *Zosterophyllum* type and is placed in the subgenus *Platy-zosterophyllum*. A second smaller species belonging to this subgenus is also present.

Instructive remains of *Cooksonia* continue this type of plant from the Downtonian to the Senni Beds.

Sporogonites, *Sciadophyton* and *Taeniocrada* are recorded for the first time from British rocks.

Prototaxites and *Nematothallus* occur along with the vascular land plants, some of the pieces of the former being of large size.

Pachytheca is represented in several exposures.

The interesting composition of the flora, which is of non-marine and probably terrestrial habitat, is discussed.

The flora is of late Lower Devonian age, probably corresponding to the Siegenian of the continental succession. Comparisons are made with similar floras from Scotland and elsewhere.

Introduction

The purpose of this paper is to give a fuller account than has hitherto been possible of the flora of the Senni Beds. This can be done by the description of the plant remains found crowded together in a relatively small mass of rock in a disused quarry near Llanover, a short distance south of Abergavenny. Practically all the types of plants now known from the Senni Beds occur in this deposit, but what has been learnt from it will be supplemented by the mention of remains from a few other localities. As will be shown, this is now the most extensive and representative flora of late Lower Old Red Sandstone age in Britain.*

It is desirable before dealing with the fossil plants to make clear the position of the Senni Beds in the stratigraphical succession from the top of the Silurian upwards. The marine Ludlovian strata of the Silurian are followed by the Grey Downtonian and this is succeeded by what were earlier known as the Red Marls. The lower horizons of the latter are now classed as the Red Downtonian. In Mr Wickham King's subdivisions the Grey Downtonian is I.1 and succeeding horizons are denoted by I.2 to I.10. An account of the flora of the Downtonian in this extended sense was given in a recent paper (Lang 1937). The upper horizons of the former Red Marls group differ palaeontologically and constitute the Dittonian (II.1–II.4) of Mr Wickham King (1925, 1934). There is as yet no account of the flora of these beds; we can state, however, that it has much in common with that of the Downtonian portion of the Red Marls, but includes elements leading towards the flora of the still higher beds. To these higher beds the name Brownstones was broadly applied by earlier workers (e.g. Symonds 1872), and they were alternatively termed the Red Sandstones by the Geological Survey (Strahan *et al.* 1900). Later, mainly on lithological grounds, a lower horizon in these rocks was distinguished as the Senni Beds (Strahan *et al.* 1904). Their position is shown in the diagram on p. 11 of the second edition of the Abergavenny Memoir (Robertson *et al.* 1927). Thus in the region of England and Wales with which we are concerned these Senni Beds come above the Dittonian Red Marls and are succeeded by the Brownstones. The important point for the purpose of this work is that in the Senni Beds we are dealing with a flora of an upper horizon in the Lower Old Red Sandstone. This horizon appears to correspond to the Siegenian in the Continental succession, while the underlying horizons (the Dittonian and Downtonian) would correspond to the Gedinnian (cf. Evans 1929; Stockmans 1940; White 1938).

Previous records. Until recently practically nothing was known of the fossil plants of the Senni Beds. The earliest reference appears to be in the first edition of the Abergavenny Memoir (Strahan *et al.* 1900, p. 17) at a date before the Senni Beds had been distinguished; records of fragments of plants crowding the bedding planes of rocks on the Deri, and of plant remains from Kemeys, are from this horizon. Indefinite traces of plants are mentioned in other Memoirs.

Knowledge that is of botanical importance has been mainly due to the work of Dr Heard (1925, 1927, 1939) on material from the Brecon Beacons Quarry. In 1927 Heard described in considerable detail a new type of plant, *Gosslingia breconensis*, and also a tuberculate spherical body. In 1939 he recorded and figured *Arthrostigma* (*Drepanophycus*), and a slender specimen of *Prototaxites*; also a black incrustation with oval or circular areas under the name *Taitia*, and a single specimen of a pyritized 'fructification'. In the interval between these two papers by Heard and in dealing with the Downtonian flora (Lang 1937, p. 281) it was stated that there was evidence of the association of *Pachytheca*, *Prototaxites* and *Nematothallus* with vascular plants in

* The large collection of hand specimens of the plant remains on which this account is based was made by one of us (W. N. C.) in the course of geological mapping in the counties of Monmouthshire and Breconshire under the direction of Professor O. T. Jones, F.R.S. The geology will be dealt with elsewhere.

these higher beds. Leaving aside remains of uncertain nature, there are thus records, though in most cases little more, from the Senni Beds of *Drepanophycus*, *Gosslingia*, *Prototaxites*, *Nematothallus* and *Pachytheca*, which are all recognizable types of plants or plant remains.

Plant localities. The present investigation is mainly based on collections made from Llanover Quarry, a new locality. We are greatly indebted to Mr Wickham King for directing one of us to this exposure. The quarry, which is 3·8 miles due south of Abergavenny and 300 yards north-north-east of Rhyd-y-llwyfan farm, lies in a small beechwood on the edge of the prominent feature formed by the Senni Beds at the north-east corner of the South Wales coalfield. It has not been worked for a number of years. Plant remains are conspicuous on the surfaces of the rock in the tip-heaps. The best and most abundant material was obtained from the east end of the quarry where a part of its floor was less cut away. The beds in the lower part of this raised mass of the rock consisted of coarse flagstone; this gradually became finer grained upwards and passed with a sharp undulating junction into laminated mudstone, which in turn was overlain by a band of coarse massive sandstone. The flagstone contained abundant but usually very fragmentary and poorly preserved plant remains, and all the better preserved and more complete specimens came from the mudstone layer, itself crowded with plant debris. This layer was only about 10 in. thick at the thickest part and is now worked out.

Other localities, some previously known and others new, from which plant remains have been examined to supplement the almost complete representation of the flora at Llanover, may now be mentioned. There is first the Brecon Beacons Quarry referred to above as having provided the material studied by Heard. Except in the consideration of *Nematothallus*, remains from this locality are not described here. The old quarries on the Deri, 1½ miles north-north-west of Abergavenny, have been examined, the early record of plant remains confirmed, and some identifiable specimens found. Kemeys, from which plant remains were recorded in 1900, presented some difficulties. There are pieces of rock with plant remains from a locality of this name, collected by J. E. Lee, that are probably the grounds for the record in the Abergavenny Memoir; the specimens are in the British Museum Geological Department (V. 1785). Thanks to a suggestion from Mr E. Dixon, to whom we are much indebted for help in this problem, the reference was found to be to Kemeys Inferior, near Newport, and not to Kemeys Commander in the area of the Abergavenny Memoir; this was confirmed by the discovery of fragmentary plant remains on the top of the ridge known as Kemeys Graig. A locality, which will be referred to as Talybont, yielded plant remains in rock thrown out from the trench for the dam of the newly completed reservoir near the village of that name, which lies 7 miles south-east of Brecon. Lastly, a locality referred to as Llanthony must be mentioned, since it lies within 60 ft. of the base of the Senni Beds. The poorly preserved plants in coarse sandstone were discovered in the lower part of a daren or rock cliff immediately behind a cottage, nearly half a mile north-east of Llanthony Abbey in the Black Mountains. Without stressing this, since the flora throughout seems uniform, the indications are that of the localities mentioned Llanthony is undoubtedly the lowest, Talybont and Kemeys are at an intermediate level, and Brecon Beacons, the Deri and Llanover are fairly high in the Senni Beds.

Preservation. The Senni Beds consist of lenticular bands of hard sandstone and conglomeratic cornstone with subordinate mudstone and shale. They are dominantly reddish brown in colour, but the colour may change both laterally and vertically into a greenish grey, and it is in these grey beds that the plants occur. An exception is at Llanthony, where the plants are found as impressions in the reddish rock. The rock at Llanover, the Deri and Kemeys, unlike that from Talybont and Brecon Beacons Quarry, has suffered considerably from weathering, with the result that it is now porous and stained and the original grey colour has been replaced by brownish or yellowish tints.

The abundant remains at Llanover afford considerable information as to the external morphology of the plants, but the preservation is generally poor, no doubt due in part to the weathering. The majority of the specimens are represented by thin incrustations of cracked or powdery carbon, or, if this has fallen away, merely by impressions. Some portions are preserved in the solid, a few in pyrites, but the greater number as a granular, brownish mineral substance, probably a decomposition product of pyrites. Comparatively little has therefore been learnt as to the structure of the plants. Examination by reflected light has been helpful, especially in the study of epidermal features and vascular strands. Well-preserved spores have been found in some of the sporangia, but isolated examples in the rock were rare. Little additional information has been obtained by making film pulls and transfers. Since this applies also to the black carbonized incrustations in the relatively fresh rock at Talybont, the failure to obtain satisfactory preparations of cuticular structure, etc. from Llanover is not to be accounted for wholly by the weathering.

There has been considerable difficulty in figuring many of the specimens in the weathered rock from Llanover. In some cases it has been found useful to submerge them in xylol. We are greatly indebted to Mr E. Ashby for valuable assistance, especially with regard to the photographic illustrations. A few of the latter still do not demonstrate all that can be observed on the specimen. Almost all the hand specimens and preparations are preserved in the British Museum Geological Department; the registered numbers are given not only for all the figured specimens but also for some others which provide additional pieces of evidence.

List of plants described. A list may be given of the plants or types of plant remains in the order in which they will be described. All are represented at Llanover Quarry. When they are also known from any of the other localities mentioned above this is noted.

1. *Drepanophycus spinaeformis*	Brecon Beacons Quarry; Deri; Talybont.
2. Cf. *Psilophyton princeps*	Llanthony.
3. *Dawsonites arcuatus*	Brecon Beacons Quarry.
4. *Gosslingia breconensis*	Brecon Beacons Quarry; Deri; Talybont.
5. *Zosterophyllum* cf. *australianum*	Talybont.
6. *Zosterophyllum llanoveranum* n.sp.	Brecon Beacons Quarry.
7. *Zosterophyllum* sp.	
8. *Cooksonia* sp.	

9. *Sporogonites exuberans*	
10. *Sciadophyton steinmanni*	
11. *Taeniocrada* sp.	
12. Remains *incertae sedis* (axes; H-shaped branchings; sporangia; spores)	
13. *Prototaxites* sp.	Brecon Beacons Quarry; Talybont; Kemeys.
14. *Nematothallus* sp.	Brecon Beacons Quarry; Talybont; Kemeys.
15. *Pachytheca* sp.	Brecon Beacons Quarry; Talybont; Kemeys; Deri.
16. Spherical or circular bodies *incertae sedis*	Brecon Beacons Quarry.

1. *Drepanophycus spinaeformis* Goepp.

(Plate 9, figures 1–7)

This plant has been recorded from Brecon Beacons Quarry (Heard 1939). Abundant remains have been collected at Llanover, and it has also been found at Talybont and on the Deri. Considerable knowledge has accumulated as to the morphology and structure of *Drepanophycus spinaeformis* Goepp. (*Arthrostigma gracile* Daws.) by the study of specimens from Gaspé, Scotland, Norway, Germany, Belgium and China. Here we need only record the kind of remains found in the Senni Beds and deal with some features that are new, at least for Britain.

The specimens consist of completely flattened shoots forming thin incrustations or, when the organic material has disappeared, brownish impressions on the rock. The stems range in width from 2·5 cm. to under 0·5 cm. The large stems may show the position of widely spaced leaves, either indicated as scars or pits on the surface of the impressions, or clearly demonstrated as falcate leaves projecting from the margins. An example of a fairly complete leaf is shown in figure 3; it is over 1 cm. long and its vertically extended base measures 5 mm. A few comparatively narrow stems bear crowded leaves which are more slender and up to 6 mm. long (figure 4). Nothing has been seen of the epidermis or cuticle. The only structure sometimes preserved is the narrow central strand which shows the annular thickening of the tracheides.

Fertile shoots of *Drepanophycus* have been described from Germany (Kräusel & Weyland 1930, 1935) but have not been recorded from elsewhere. It is therefore of interest that three of the more slender shoots from Llanover were of this type. One of them is shown of $\frac{9}{10}$ natural size in figure 5. In relation to some of the leaves, or lying beside the shoot, are a number of rounded bodies of considerable size which can reasonably be regarded as the sporangia. They occur from the base to the summit of the shoot. One of the attached sporangia from near the base of figure 5 is enlarged 2·7 diameters in figure 6. A portion of the impression on the rock of a different specimen is seen at the same magnification in figure 7; two fertile leaves arise from the left-hand side of the axis and each bears a sporangium. Other leaves of this shoot were similar. The bodies regarded as sporangia measure 4–7 mm. in maximum diameter, and are thus only slightly smaller than the German specimens which they resemble in general appearance. As in some of these, they give the impression of being terminal on the leaf. In the light, however, of the best specimens described later by Kräusel & Weyland (1935), which show the reniform and tangentially extended sporangium situated on the fertile leaf at some distance from its base but not at the tip, the terminal appearance may be attributed to unsatisfactory preservation.

Branching. Branching of two types was exhibited by some of the specimens. In a few examples from Talybont occasional lateral branches, which may be from less than half to almost the same width as the parent axis, are given off at a more or less acute angle (V. 26532). A number of specimens from Llanover, on the other hand, show a distinct and characteristic H-shaped type of branching which has not hitherto been described for this plant.* Part of a fine specimen is shown in figure 1. The main axis, which is 1·8 cm. wide and bears a few short spine-like leaves, gives off lateral branches, one to the right- and one to the left-hand side. These are only 6–8 mm. wide and stand out at right angles to the main axis for about 1 cm. They then divide at an angle of nearly 180° so that one division, presumably the main branch, turns up parallel to the main axis, while the other (which can be regarded as arising from the branch as it turns up) bends downwards. It is not always easy to decide which way up such specimens should be placed. In figure 1 the upper limb of the right-hand branch system increases rapidly in width. Both limbs, however, bear a few clear marks of leaf insertions. The lower limb of the branching on the left evidently divided again shortly. Other examples show essentially similar relations of the parts. The interesting specimen, reduced to 0·45 natural size in figure 2, has at least four such branchings, and its proper position could be determined with certainty. The downwardly directed limbs of the branch systems are more slender than the upturned branches. Further, in one case on the right-hand side there are two downwardly directed branches, which appear lateral to the upwardly curved branch.

Though this type of branching has not been previously recognized for *Drepanophycus*, there are indications of it in earlier descriptions. The clearest of these is in a specimen from Scotland figured by Kidston (1893, figure 2), who speaks of the narrow downwardly directed branch as 'perhaps a root'.

The Llanover specimens clearly demonstrate that this H-shaped type of branching, first found in *Zosterophyllum myretonianum*, was a feature of the presumably basal or rhizomatous region of *Drepanophycus*. It must be taken into account in picturing the probable growth of the plant, and the reconstruction suggested by Kräusel & Weyland (1935) requires amendment in the light of it. It is as regards this branching and the recognition of the fertile shoots in Britain that the Llanover material has added to our knowledge. But further, the fact that this widely distributed plant is established as a member of the Senni Beds flora is of stratigraphical significance.

2. Cf. *Psilophyton princeps* Daws.

(Plate 9, figures 8–15)

Pieces of stem and branch systems bearing projecting spines, or marked by the places of insertion of spines, were fairly abundant at Llanover. The natural inference on inspecting them is that they demonstrate the presence in the flora of a plant of the

* Since this was written, branching of this type has been recorded in specimens of *Drepanophycus* from Belgium (Stockmans 1940).

general type of *Psilophyton princeps*. This name is used in the comprehensive sense employed and discussed in dealing with specimens from the Strathmore Beds (Lang 1932, pp. 512 ff.). In the case of the specimens to be considered here there is, on the one hand, no evidence of connected spineless branch systems that might justify reference to the *goldschmidtii* form, nor does the preservation allow of structural details of spines or epidermis being brought into the comparison. Partly because of the absence of such characters, but also on account of the stoutness of the main stems and the shortness of the spines, the specimens from the Senni Beds are recorded here as cf. *Psilophyton princeps*. This may, perhaps, be excessive caution but seems the more advisable since a hitherto undescribed type of fructification occurs in connexion with some of these vegetative remains.

A typical piece of spiny stem from Llanover is shown of $\frac{9}{10}$ natural size in figure 8. It is a little over 8 mm. wide and gives off at an acute angle a much narrower branch, under 3 mm. wide. Numerous spines 1–2 mm. in length project along the margins, and the marks of insertion of others can be seen on the surface of the impression. The sympodial branch system in figure 10, which will be considered further below on account of other features it presents, may be referred to here as another example. Spines and marks of their insertion were clearly shown by this and other stems in the same piece of rock (figure 11). It is unnecessary to figure larger portions but it may be stated that the longest specimen found at Llanover (V. 26565), incomplete at both ends, measured 16 cm., and that a piece of stem with three lateral branches at Llanthony (V. 26514) was 24 cm. long and over 1 cm. wide. These and other pieces evidently came from a plant of considerable size and rigidity.

The spines seen in profile along the margins of flattened stems may be directed slightly upwards, stand out at right angles or point backwards. They are seen in figure 8, and a number along the edge of another piece of stem are enlarged 3·6 diameters in figure 9. They taper gradually from a relatively wide base. The spines are rather short as compared with many, though not all, specimens from other localities. They are often about 1 mm. in length but range from 0·5 to 2·5 mm. When removed on film transfers they have always been black and opaque and usually incomplete, so that it has been impossible to ascertain anything of their structure, and in particular of the nature of the tip. For similar reasons nothing has been learnt of the epidermis or cuticle from transfers. Some of the impressions of the stems, however, show by reflected light a pattern of the epidermal cells which seems not unlike that described by Halle (1916) for Norwegian specimens. One stem about 5 mm. wide (V. 26511), which was preserved as brownish mineral in the solid, showed by reflected light the annular tracheides of the vascular strand. It also showed the bases of broken off spines, some of which were circular in cross-section, though the majority were oval and vertically extended. The depressions which mark the insertions of spines on the surface of impressions are also frequently more or less circular. In some cases, however, a considerable proportion are transversely extended and slit-like; this is possibly due to the flattening of the conical spines against the stem. The spine pits often retain portions of the thin carbonaceous incrustation which has disappeared from the rest of the impression; they then appear as black spots. They show a considerable range in size on different stems and on different regions of the same stem.

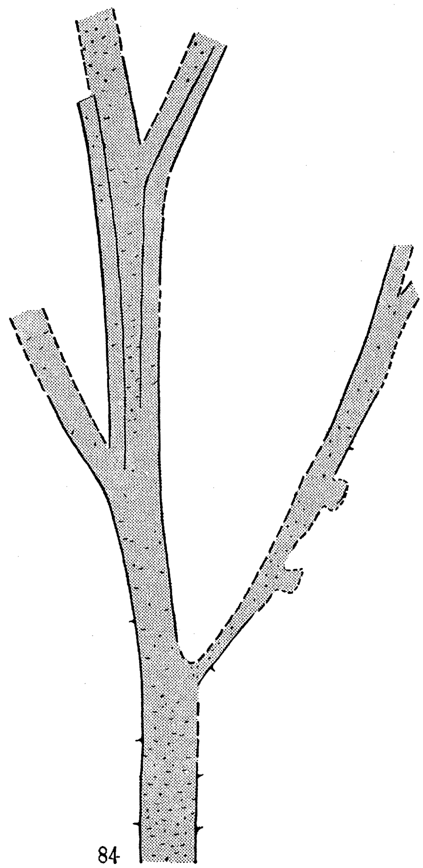
Fertile specimens. The outstanding interest of these remains of a spiny plant of the general type of *Psilophyton princeps* from Llanover is that some of the specimens provide evidence of the presence of what can only be regarded as the sporangia of the plant. The clearest example of this fructification is that photographed of $\frac{9}{10}$ natural size in figure 12. It is poorly preserved in rather coarse rock as a discontinuous carbonized film. The total length is 13·5 cm., and the stem at the lowest part is 8 mm. wide. Some 4 cm. above this there is a division which is almost dichotomous; the wider stem continues for some distance on the left, while a somewhat narrower branch runs parallel to it on the right. After about 3 cm. the latter gives off a slender and imperfectly preserved fertile branch to the right and continues as the more complete and better preserved fertile axis. These two last subdivisions, about 6·5 cm. long, which are also shown as photographed under xylol in figure 12*a*, bear rounded appendages which are presumably short-stalked sporangia. Six can be seen along the left side of the left-hand division, and the points of attachment of two others near the distal end. There are also indications of sporangia and their points of attachment along the right-hand side of this axis and along the other division. As the figure shows, they appear to be oval erect structures, supported on short thick stalks which stand out horizontally from the axis and are attached near the base of the sporangium. The fourth sporangium from below on the left is enlarged 3·6 diameters in figure 13. Its height, about 5·5 mm., is slightly less than that of the sporangia below, while those that succeed it appear to be smaller.

The specimen represented in figure 12 did not provide quite conclusive evidence that the fructification just described was part of the spiny plant, though it rendered this very probable. No spines were visible along the margins of the stems nor were there clear indications of spine insertions of the usual size. The lower part of the stem, however, has numerous small pits usually retaining a little carbon or brownish mineral on the surface of the impression. These pits are smaller and more numerous than in typical specimens of the spiny stems, but several of the latter have them of similar size and distribution.

Fortunately there is further clear evidence to connect these sporangia with the spiny plant of *Psilophyton princeps* type. A number of stems in another block of the rock may, from the direction and mutual relations, be treated as one specimen. The branch system displayed on one surface (figure 10) has been referred to above. The stems throughout the block bear small distinct spines projecting from the margin and also spine pits on the surface of the impressions (figure 11). Several of these spiny branches bear bodies like those which in the specimen in figure 12 have been regarded as sporangia. They are not, however, in terminal spikes but occur in small numbers on branches which show undoubted evidence of spines. Thus in the specimen shown in figure 10 (cf. figure 84) two or three were recognizable on the right-hand side of the lowest branch on the right.* Similarly, three sporangial bodies were found along one side of another piece of spiny stem from the same block. The lower half of this piece of stem is represented, enlarged 1·8 diameters, in figure 14. It shows in the lower part

* On the surface of the rock between the branches of this specimen there are also two groups of sporangium-like bodies which suggest portions of spikes.

the marks of spine insertions and also a number of spines projecting from the margin. Near the top of the portion of the stem figured there were two sporangia on the left-hand side, one being clearly seen in the photograph. Still farther up on the same side, but on the portion of the stem not included in the figure, there was another sporangium. This is represented, enlarged 4·95 diameters, in figure 15, the agreement of which with figure 13 will be evident.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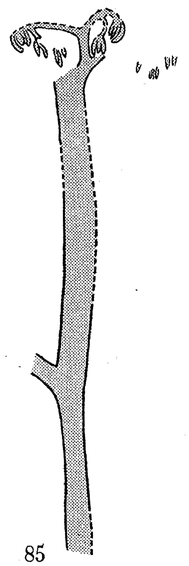
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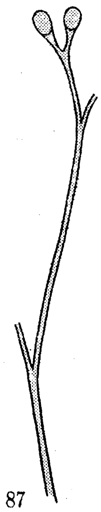
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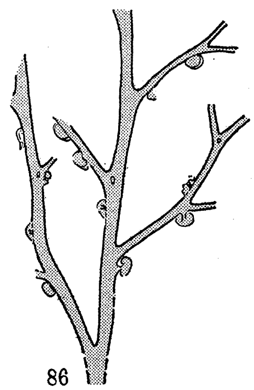
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FIGURE 84. Cf. *Psilophyton princeps*. Outline drawing of specimen in figure 10, plate 9, to show the position of the sporangia and spines on the branch system. Nat. size.

FIGURE 85. *Dawsonites arcuatus*. Outline drawing of specimen in figure 16, plate 10, to show the position of the branches and of the pendent sporangia. Nat. size.

FIGURE 86. *Gosslingia breconensis*. Outline drawing of specimen in figure 20, plate 10, to show the branching and the position of the sporangia. Nat. size.

FIGURE 87. *Cooksonia* sp. Outline figure of the largest and most complete specimen found, showing the dichotomous branching and the terminal sporangia. Nat. size. (V. 26463.)

The evidence from the specimens in this block is thus clear that the sporangium-like bodies were borne on stems with good spines, and there is therefore no reason to doubt that the specimen bearing them in terminal spikes (figure 12) belongs to the same spiny plant. The bodies themselves, though their outline is fairly clear (figures 13, 15), are otherwise obscure and must remain so until better preserved specimens are available for study. But their appearance seems to admit of no other interpretation than that they were sporangia.

There is no doubt as to the presence in the Senni Beds of a plant of the general type of *Psilophyton princeps*, using this name in a comprehensive sense. The resemblance is especially close to some of the larger specimens from Röragen. *Psilophyton* would naturally be expected to occur in a deposit of the age of the Senni Beds. Whether the Llanover specimens will prove to be the first examples of *P. princeps* with the fertile region in connexion or a distinct though similar spiny plant must be left for future investigation to decide. The group of remains described in this section certainly raises the much disputed question of the reproductive organs of *Psilophyton* in a new fashion, and may lead to its solution.

3. *Dawsonites arcuatus* Halle

(Plate 10, figures 16–19)

A number of fertile branch systems from Llanover are naturally placed in *Dawsonites* (Halle 1916), and there seems no reason to exclude them from the species *D. arcuatus*. The fertile region consists of a branch which subdivides repeatedly, the fine divisions bending in a way which suggests that the fusiform sporangia in which they end were pendent. These fertile branches arise laterally from broader axes and appear to have been radially arranged. Figure 16 (cf. figure 85) shows a piece of a relatively main axis with the base of a lateral branch fairly low down on the left. Near the top of the main axis, which though broken away evidently continued, there is another branch departing on the right and toward the far side. The rock is broken so as to show the subdivision of the branch and the spreading out and bending down of the ultimate divisions which bear the terminal sporangia. Figure 17 shows a portion of a main axis, a branch on the left, the dichotomous subdivision of this and a few pendent sporangia. The subdivision of a fertile branch and the fusiform terminal sporangia are enlarged 4·95 diameters in figure 18. These three specimens will suffice to show, though not to demonstrate fully, the general appearance of this type of plant as found at Llanover.

The axes are about 3–5 mm. in width and are preserved as brown flattened incrustations. They are sometimes smooth but may be longitudinally wrinkled, though not usually ribbed or grooved. No indications of spines have been seen, and the axes have shown no structure except the occasional preservation of a vascular strand. The branches are narrower than the main axes and rapidly diminish in width as they divide, until the ultimate ramifications may be only 0·25 mm. wide. The sporangia are fusiform, bluntly pointed and in some cases curved. Their usual length is about 3 mm. (1·5–4·0 mm.) and the width ranges from 0·5 mm. to over 1 mm. Those of any one branch system tend to be of similar size and shape.

A number of the sporangia have been removed as film preparations and have given further information as to the wall and the contents. The wall may show a layer of opaque, coherent or cracked carbon, and also a brown translucent layer sometimes with a pattern of elongated pointed cells. Several sporangia from one specimen have yielded spores which are visible on the transfer against the brown layer of the wall or lying free in the cavity. The spores are yellowish brown and smooth-walled; they sometimes show the tri-radiate marking or split. The not very numerous examples have shown a considerable range in size, from 50 to 85 μ. A few are represented in figure 19.

The specimens described above agree generally with those of *Dawsonites arcuatus* from other localities, especially Gaspé (Dawson 1871) and Norway (Halle 1916), in the main features of the fertile branches and the shape of the sporangia. Minor differences are that the sporangia are somewhat smaller and that the axes do not show marked ribbing. In the structure of the sporangial wall and the character of the spores there is detailed agreement with specimens from Gaspé (Lang 1931) and Scotland (Lang 1932). The Llanover specimens provide no evidence in favour of their being the fertile region of *Psilophyton princeps*. Even bearing in mind that occasional spines have been demonstrated on the axes from Gaspé (Lang 1931), Halle's separation of these remains under the name *Dawsonites* seems fully justified. It must also be remembered that, as recorded in the previous section, a fructification of a quite different kind was borne on the spiny stems of *Psilophyton princeps* type in this deposit.

4. *Gosslingia breconensis* Heard

(Plate 10, figures 20–28)

Gosslingia breconensis, which is so far known only from the Senni Beds, was described by Heard (1925, 1927) from Brecon Beacons Quarry. The description here, based on numerous specimens from Llanover, gives a more complete picture of the external morphology, necessitating an important modification of the diagnosis as regards the distribution of the sporangia; it adds little to our knowledge of the structure of the plant obtained by Heard's study of pyritized axes.

Branching. The branch systems were especially abundant throughout an inch of the mudstone layer over an area of about 2 sq. yd. and were observed to lie parallel and in one direction (V. 26473).* The mode of occurrence was suggestive of the plant having grown in situ, but proof of this is lacking. The numerous branch systems, up to some 8 cm. in length, though all incomplete, were strikingly similar in size and appearance. There was no evidence that they were parts of a larger branch system. On the other hand, no evidence was obtained of their having been borne on a rhizome. The morphology of the complete plant is still not demonstrated.

The branching is always in one plane and the appearance of the branch systems suggests that they were dorsiventral. They have a very regular, alternate, sympodial branching, but this is not completely displayed in any one specimen, since the distal regions are usually wanting. The width of the main axis may be 2 mm. or slightly more, and the lateral branches diminish from a width of $1\frac{1}{2}$ to $\frac{1}{2}$ or $\frac{1}{4}$ mm. In the

* The same occurrence of numerous parallel branch systems has been observed at Brecon Beacons Quarry (V. 26575). Heard refers to the plant as 'gregarious'.

specimen shown in figure 20 (cf. figure 86) a relatively main axis, about $1\frac{1}{2}$ mm. wide, gives off four alternating branches in a length of a little over 4 cm. and the base of a fifth branch is seen at the upper end. The two branches on the right show their first branching and the position of this, as in all cases noted, is on the side away from the main axis, i.e. katadromous. The lowest branch on the left is not subordinated to the main axis, but is behaving as the main axis of another sympodial branch system; the branching in this and other similar specimens amounts to dichotomy. The small sympodial branch system on the right-hand side of figure 21, which is enlarged 1·8 diameters, has three alternating lateral branches. Only the basal portions of the two lowest remain, but the uppermost branch on the left continues to its tip, which is circinately coiled. Here, as in other examples, the curving of the coiled or hooked tip is away from the relatively main axis. Isolated circinate tips, such as Heard figured, were also found at Llanover.

Sporangia. These two rather small branch systems are chosen for illustration not only on account of their comparative completeness but also because they show the distribution of the sporangia. Thus in figure 21 the complete branch bears two sporangia on the side away from the main axis, while another is borne on the side of the latter just below the point of departure of the branch. A similar distribution of more numerous sporangia was demonstrated by the branch system in figure 20. Not all the sporangia are visible in the photograph but their position is represented in figure 86, in the preparation of which the information from the counterpart has also been used. As in the previous specimen, the sporangia are borne on the abaxial side or edge of lateral branches, but may also occur on the side of the relatively main axis. They are more numerous on the finer branch systems, which no doubt belonged to the more distal regions, and many of the larger axes show none. As a rule not more than two sporangia are present on any one joint of the branch system. It is clear from the specimens in figures 20, 21 and many others that the sporangia of *Gosslingia* were borne laterally on the axes composing the dorsiventral branch systems and not on special fertile branches.

There is no doubt that the short-stalked reniform structures, the distribution of which has just been considered, are the sporangia, but, though numerous examples have been removed on film transfers, no spores have yet been found. Heard considered correctly that they were originally 'bladder-like sporangia with relatively thin walls'. This view is confirmed by some of the Llanover specimens preserved as internal moulds (figure 28), which can be isolated and demonstrate the reniform shape of the sporangial cavity. Such moulds may also show the line of dehiscence along the whole extent of the convex margin. The line of dehiscence is also readily observed in the flattened incrustations on the rock (figures 21, 22, 27), especially when the valves of the sporangium are mutually displaced. This is the more clearly shown because the rims of the valves are often more strongly carbonized as though they had been thicker than the rest of the wall, but no structural details were ascertained. The sporangium is seated on a stalk which does not exceed 1 mm. in length and is about $\frac{1}{2}$ mm. broad; it is well shown in the upper sporangium in figure 22. The sporangium itself lies with its longer axis parallel to the branch bearing it and in the plane of the branch system.

This longest measurement is about 2 mm. (3·2–1·5 mm.) and the height of the sporangium is a little over 1 mm.

Axillary bodies and other structural features. No satisfactory evidence has been obtained of the presence of a branch attached in a subaxillary position behind the departure of a lateral branch of the sympodial branch system, although this has been carefully looked for. It is, of course, quite possible that a slender branch may sometimes have developed, and structures presenting various appearances have been found in this position in a fair number of the branch systems, though absent from many others. These structures are by no means easy to interpret, and all that can be done at present is to record and illustrate a few characteristic examples. It seems clear that these 'axillary bodies' in *Gosslingia* projected on one side only of any branch system, a particular feature confirming the view that the latter was dorsiventral. The axis preserved as a flattened incrustation of some thickness in figure 23 shows an axillary structure projecting markedly from the surface behind the departure of the branch below and to the left. The summit is broken across, and it is impossible to say with certainty whether it was originally a convex bulge or the base of an actual branch. If such a branch system is viewed from the other side no axillary structures are evident, but the counterparts of similar specimens have an oval region in this position occupied by a plug of the material of the incrustation (figure 24). A number of attempts to trace the continuance of such structures into actual branches all gave negative results. A somewhat similar appearance of oval axillary bodies on the impression surface is given by the specimen in figure 25, but here, and in other examples, the area of the body is occupied by rocky matrix and is not a solid plug of the incrustation. It is clear that the structures in figures 23–25 are various expressions of the 'projection' which Heard recognised in this position. Their appearance, especially as shown in figures 24 and 25, is very similar to that presented at branchings of smooth axes described from the Middle Devonian of Europe, the Middle Old Red Sandstone of Scotland and the Upper Silurian of Australia. They were regarded as 'bourgeons' by Potonié & Bernard (1904), but no direct evidence of their nature has been obtained. In one or two Australian specimens (Lang & Cookson 1930; Cookson 1935) a branch seemed to occupy this position, and in describing them the possible comparison with *Gosslingia* was mentioned. It is useless at present to enter further into the general question of the nature of these axillary structures, which are now known to have been present in various early plants without being satisfactorily understood in any of them.

Little has been ascertained as to anatomical structure. In some cases the vascular strand was recognizable by reflected light, and it may be noted that the thickening of the tracheides appeared to be annular and not, as stated by Heard, 'spiral or reticulate'. His photographs of the much better preserved, pyritized specimens from Brecon Beacons Quarry appear to be quite consistent with the thickening, as in so many early plants, being annular. Many of the incrustations of axes showed numerous small and distinct tubercles that left corresponding small pits in the impression. These seem to be the emergences recognized by Heard in his structurally preserved material. As shown in figure 26, enlarged 3·6 diameters, these structures on the incrustations from Llanover were usually somewhat elongated and measured 0·1–0·2 mm. They were apparently absent from many impressions which show a fine longitudinal striation indicating the cellular structure.

Discussion. Gosslingia breconensis was recognized by Heard as a distinct and well-characterized type. What has been learnt from the numerous specimens at Llanover agrees in many points with what he had ascertained. This applies to the leafless branch systems, the presence of emergences, the circinate tips to the branches, and the shape and mode of attachment of the sporangia to pieces of axes; our knowledge of the anatomical structure remains based on Heard's pyritized specimens. The most important correction of his account and amendment of the diagnosis concerns the position of the sporangia. These have now been shown to be borne laterally on axes of the sympodial branch system and not on special fertile branches in the position of the axillary structures. Further, while the morphology of the branch system has been clearly seen in numerous examples, nothing has been learnt as to the lower regions of the plant. It remains an assumption, however likely this may seem, to hold that the branch systems were borne on a rhizome. *Gosslingia* agrees closely with *Zosterophyllum* in the features of its sporangia but differs in that the sporangia are not borne in spikes. Our knowledge of it as based on clear specimens is considerable and increasing, but it is still incomplete as regards a number of important points.

Zosterophyllum

The genus *Zosterophyllum*, with the type species *Z. myretonianum*, was founded by Penhallow (1892) on remains from the Carmyllie and Cairnconnan Beds. Penhallow, and Reid & Macnair (1898), recognized as belonging to the plant the tufts of leafless axes, the branchings of H-shaped type and terminal spikes of short-stalked sporangia. All these kinds of fragmentary remains had been previously known to Hugh Miller and figured by him. Nothing is said in Penhallow's diagnosis as to whether the spikes were radial or distichous, nor is the shape of the sporangia recognized as reniform. As now more fully known (Lang 1927; Lang & Cookson 1930), *Z. myretonianum* consists of branched leafless axes growing in tufts from a rhizomatous basal region where the branching is of the H-shaped type; the erect axes end in spikes of short-stalked sporangia which are extended tangentially and reniform; the line of dehiscence runs along the whole distal margin and is bounded by the thickened rims of the valves; there is evidence that the sporangia were radially arranged on the main axis of the spike. Two other species of the genus have been described since. In *Z. australianum* (Lang & Cookson 1930; Cookson 1935) from the Upper Ludlow of Victoria, Australia, only the compact radial spikes are known. *Z. rhenanum* (Kräusel & Weyland 1935), from the Lower Devonian of Germany, resembles *Z. myretonianum*; in it also the arrangement of the sporangia is radial.

The remains from the Senni Beds to be described in the next three sections include a small number of spikes which resemble those of *Z. australianum*. They also include abundant remains of a plant with terminal spikes of sporangia like those of *Zosterophyllum*; the sporangia are not, however, radially arranged as in the three species mentioned in the preceding paragraph but are borne in two lateral rows and tend to be bent towards one face of the main axis. For reasons that will be given after it has been described, this new plant is included in the genus *Zosterophyllum*, two sections of which are distinguished: *Eu-zosterophyllum* with radial spikes and *Platy-zosterophyllum* with dorsiventral spikes. *Z. llanoveranum* n.sp. becomes the type of the subgenus *Platy-zosterophyllum*, of which a second species, not for the present named, also occurs at Llanover.

5. *Zosterophyllum* (*Eu-zosterophyllum*) cf. *australianum*

(Plate 10, figures 29–31)

A few specimens from Llanover and one from Talybont as mentioned above closely resemble the spikes of *Z. australianum*. The spikes are terminal on short lengths of naked, unbranched axes; nothing is known of the rest of the plant. The largest and smallest, both from Llanover, give a good idea of the appearance of these fossils which, so far as it goes, is characteristic.

The largest specimen is represented of natural size in figure 29 and enlarged 3·6 diameters in figure 30. It consists of a short piece of axis, the upper part of which is invested with overlapping sporangia forming the compact spike. The carbonized axis, which is seen more clearly on the counterpart, is 3 mm. wide. The spike tapers somewhat but is incomplete above; it has a maximum width of 7 mm. and is about 12 mm. long. There were probably five vertical rows of sporangia, since three, one seen laterally, are exposed. The specimen, and this holds for all the others, is preserved in low relief and the individual sporangia are somewhat convex. They are regularly disposed and were evidently spirally arranged. The limit between sporangium and stalk cannot be distinguished, so that it would be an assumption to say that the sporangium itself was reniform. The lowest of the median row, which shows the shape most clearly, has a maximum width of about 5 mm. and the height, including the stalk, is about 4 mm. The sporangia in the upper part of the spike are somewhat smaller. The widening out tangentially of the sporangia and their curved distal margins are well shown in the figure. The line of dehiscence which ran along this margin was most clearly evident on the exposed edge of the middle sporangium of the right-hand row, where the two-lipped appearance, which was so marked in *Z. australianum*, could be made out under reflected light. The smallest specimen, enlarged 3·6 diameters in figure 31, has a maximum width of about 4 mm. The spike is some 8 mm. long and the naked unbranched axis below is over 2 cm. long and about 2 mm. wide. The individual sporangia, though of similar height to those of the large specimen, are much narrower, only measuring 2 mm. across, and the distal margin is more strongly arched. These differences, including the small size of the spike, may be accounted for to some extent though not entirely by immaturity.

Neither of these spikes shows any structure when examined by reflected light. A film transfer of another spike (V. 26475) showed the general outline of the cells composing the wall of a sporangium; they are elongate and radiate out from the base toward the curved distal margin. No spores have been demonstrated in this or in other sporangia.

Comparison of figures 29–31 with those of *Z. australianum* (Lang & Cookson 1930; Cookson 1935) will show the agreement in mode of preservation, in general appearance and in the shape of the stalked sporangia. The Australian specimens also exhibited a similar range in size, though none of the spikes from Llanover is as large as the largest of the Australian examples. On account of the striking general resemblances, the specimens described here are recorded as *Z.* cf. *australianum*. Our knowledge in the case of both plants is so incomplete that details to confirm a strict specific identification are lacking. The much greater similarity of the compact spikes from the Senni Beds to those of *Z. australianum* than to the spikes of either *Z. myretonianum* or *Z. rhenanum* is, however, indicated by the procedure adopted.

6. *Zosterophyllum* (*Platy-zosterophyllum*) *llanoveranum* n.sp.

(Plate 10, figures 32–40)

Diagnosis. Plant probably of tufted growth, consisting of leafless axes up to 20 cm. long and usually under 2 mm. wide, infrequently branched. Sporangia borne distally in two alternating rows, forming rather lax secund spikes; short-stalked, erect, reniform, of relatively small radial thickness, often folded by compression, opening by a slit along the tangentially extended summit, edges of the valves thickened, average width 4–5 mm. Spores smooth-walled, 55μ (45–65μ).

Holotype. V. 26515. Brit. Mus. Nat. Hist. (Geol. Dept.).

Horizon and locality. Senni Beds division of the Lower Old Red Sandstone. Llanover Quarry, near Abergavenny, Monmouthshire; also from Brecon Beacons Quarry.

Age. Late Lower Devonian; probably corresponding to the Siegenian of the Continental succession.

The following description is based on the material from Llanover, but the plant has also been found at Brecon Beacons Quarry (V. 26519). The arrangement of groups of the axes lying almost parallel and pointing in the same direction in a considerable thickness and area of the rock is suggestive of a plant of tufted growth. There is, however, no proof of connexion of the axes below and nothing is known of the lower regions. The most complete of these tufted specimens is taken as the holotype (V. 26515); it covered an area of 19 × 14 cm., but is now broken up into several pieces. The axes, more than twenty in number, were distributed through a thickness of not less than 1·5 cm. of the matrix. The largest piece, reduced to 0·45 natural size in figure 32 (cf. fig. 88), shows a number of the subparallel axes, most of them bearing sporangia distally. Some of the axes of the plant were at least 20 cm. long. They range in width from 2·5 to 1·0 mm., but are usually less than 2·0 mm. Occasional branching was seen, the branch departing at a wide angle. Little has been ascertained as to the structure, but there were indications of a central strand of annular tracheides and of elongated superficial elements.

The short-stalked sporangia are borne in spikes which are sometimes rather lax, though there are no irregular intervals. The longest spike seen, more than 9 cm. in length, is visible at the right of figure 32 and is photographed of $\frac{9}{10}$ natural size in figure 33; as in most cases, the sporangia are seen in profile along one side of the axis. Other spikes of the same specimen (figure 34) show the sporangia in two alternating rows.

They are often bent round so as to lie more or less over one face of the axis, the pedicels of the sporangia remaining straight. Proof that the sporangial stalks arose in two vertical rows, and not in a single row with the sporangia bent alternately to right and left, is given by the axis of a spike preserved in the solid which shows the stalks of sporangia arising alternately from the margins (figure 35). Confirmatory evidence is afforded by transfers of thin incrustations like the upper part of figure 34. Also, between the sporangia of some of the apparently one-rowed spikes the edges of other sporangia at a deeper level in the stone may be seen; these clearly belong to the second row which in such specimens is only incompletely exposed.

Sporangia and spores. The sporangia are terminal on short stalks which are branches of the main axis arising at a more or less acute angle. The stalks are about 1 mm. wide and usually 1–2 mm. long, but in the lower part of a spike they may attain a length of 4 mm. The shape of the sporangium is best seen when it is in face view. This is the less frequent position on the surface of the rock, but examples can be found seen either from the front (adaxial) or back (abaxial) side. The isolated specimen enlarged 3·6 diameters in figure 37 shows a short piece of the stalk and the marked tangential widening of the sporangium; this has a rounded distal edge continuing downwards and inwards to meet the stalk on both sides. It is reasonable to regard the sporangium as reniform but, since no limit between it and the stalk is visible, the shape of the sporangial cavity is not certainly established. Another isolated sporangium (figure 36) is even more suggestive of being reniform. In this specimen the line of dehiscence along the convex margin is clearly demonstrated and is brought out by the thickened margins of the valves where more abundant carbon persists. The first of these two sporangia, which are fairly representative as to size, measures 6 mm. across and the second 5 mm.; the vertical height as shown in the second (figure 36) is appreciably less than the width.

Usually the sporangia are seen from another aspect which may be described as a profile view of the more or less folded sporangium. This has then the shape of the capital letter P, the stalk coming up to the base of the half of the sporangium that is visible. A number of the sporangia in the spikes shown in figures 33, 34 present this appearance. This suggests a sporangium of relatively small thickness, which was also convex on the abaxial side and concave adaxially. There is some direct evidence of this. Such a structure would be readily folded if compressed and would then appear P-shaped. In sporangia thus preserved the line of dehiscence is seen for about half of its extent; it runs from the summit along the edge of the portion projecting toward the main axis until it nears the sporangial stalk. The rims bounding the valves of the wall can be seen as dark lines in some of the P-shaped sporangia in figure 34. In the specimen shown in figure 38 the two thick rims, each about 180μ wide, which meet at the line of dehiscence, are preserved in the solid in mineral material. They appear to consist of elements elongated at right angles to the line of dehiscence itself and evidently differed structurally from the rest of the sporangial wall.

Some spikes are preserved more or less in the solid, the sporangial cavities being filled with brown contents, which suggested masses of spores, while the walls are carbonized. When portions of the brown material were removed and treated with hydrofluoric acid, the numerous spores became separate from one another and, after suitable treatment, could be mounted in Canada balsam. A group of the spores is shown in figure 39 at a magnification of 180 diameters. The spores are spherical, pale yellow in colour and the wall appears to be smooth. The usual diameter is 55μ ($45–65\mu$). Some were still united in tetrads and some showed the tri-radiate marking or split (figure 40).

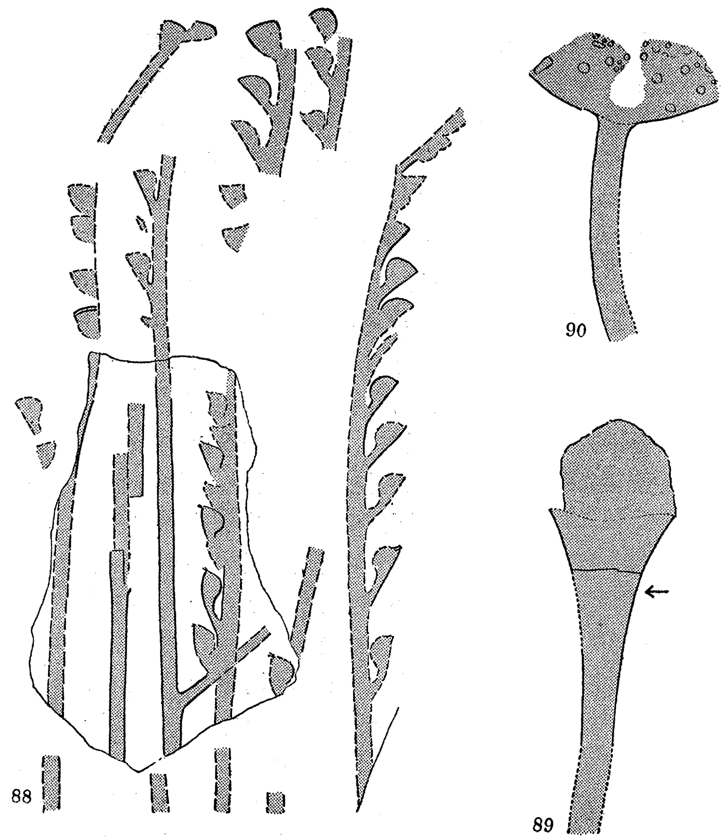

FIGURE 88. *Zosterophyllum* (*Platy-zosterophyllum*) *llanoveranum* n.sp. Outline drawing of part of holotype in figure 32, plate 10, to show parallel grouping of the secund spikes. Nat. size.

FIGURE 89. *Sporogonites exuberans*. Outline drawing of specimen in figure 55, plate 11, to show the widened base of the stalked capsule and the incomplete terminal region with spores. The arrow indicates the position of the stoma in figure 61, plate 11. × 5.

FIGURE 90. *Sciadopbyton steinmanni*. Outline drawing of specimen in figure 61, plate 11, to show lateral view of stalked disk, with positions of dark spots. × 3.

Discussion. The plant described above is not only a new species but presents a combination of characters not hitherto met with. The short-stalked, tangentially extended and apparently reniform sporangia, with the line of dehiscence extending along the whole convex margin and the edges of the valves thicker and differently constructed to the rest of the wall, agree closely with those of *Zosterophyllum*. Sporangia of similar type also occur in *Gosslingia*, but in that plant are borne along the edges of the sympodial branch system and on one side only of any one joint. In the plant under consideration, as in the species of *Zosterophyllum* hitherto described, they are borne in terminal spikes on the leafless branch system. All the plants so far placed in *Zostero-*

phyllum have had the sporangia radially arranged on the main axis. In this plant, however, they are borne in two lateral rows and also tend to be bent towards one face of the main axis, so as to give in lateral view the appearance of a secund spike. In these two respects the Llanover plant suggests comparison with *Bucheria*. But in that genus, described by Dorf (1933, 1934, 1934*a*) from the Lower Devonian of North America, the sporangia, which are only imperfectly known as thin incrustations, were sessile or almost sessile and ovate. While it would be possible to place the main weight on the distichous dorsiventral arrangement of the sporangia and to treat the Llanover plant as a species of *Bucheria*, this could not be done without unduly widening the definition of that genus. Such a course would have the further disadvantage of minimizing the significance of the close and detailed agreement of the tangentially extended sporangia with those of *Zosterophyllum*. It would attach undue significance to dorsiventral and radial symmetry, a difference which is not by itself treated as a generic character in other cases.* It has, therefore, seemed best, for the present at least, to place this plant in *Zosterophyllum*, distinguishing in this genus sections with radial and dorsiventral spikes as has been done above (p. 145). This plant is therefore described as *Zosterophyllum* (*Platy-zosterophyllum*) *llanoveranum*.

7. *Zosterophyllum* (*Platy-zosterophyllum*) sp.

(Plate 10, figures 41, 42)

One piece of rock from Llanover when split revealed crowded, branched, leafless axes and also short spikes of sporangia of what was evidently a distinct plant which could be placed in the same subgenus (*Platy-zosterophyllum*) as *Z. llanoveranum*. A portion of the rock surface bearing the thin, black, structureless incrustations is represented of $\frac{9}{10}$ natural size in figure 41, and some axes and spikes from this region are enlarged 2·7 diameters in figure 42.

The leafless axes are about 1 mm. wide; there are indications that some tips were circinately coiled. They branch dichotomously but in distal regions, where branches follow in quick succession, they may appear lateral and form a sympodium. Some of these ultimate branches, which show no diminution in breadth, bear the short-stalked sporangia; these arise alternately from the margins forming short dorsiventral spikes. The stalks are curved so that the sporangia are turned upwards and inwards; they are thus directed towards the main axis or even slightly across one face of this. They are reniform and there is evidence of a line of dehiscence along the extended convex margin. The sporangia measure about 2 mm. across and are about 1 mm. in height.

This smaller species is recorded and figured here without for the present giving it a specific name. The study of further material is desirable before doing this, but the plant is included in this account of the flora of the Senni Beds at Llanover, since it is of interest to find there a second species of *Zosterophyllum* with spikes that are clearly not radial but laterally symmetrical.

* For example, in the shoots of Ferns or of *Selaginella*.

8. *Cooksonia* sp.

(Plate 11, figures 43–51)

Among the remains from Llanover were fairly numerous specimens of the simple type of vascular plant distinguished from the Downtonian (Lang 1937) under the name *Cooksonia*. They were mostly preserved as thin structureless incrustations (figures 43, 44), but one specimen, which will require special consideration, was preserved in the solid and had structure (figures 45–51). The slender, leafless, dichotomously branched axes terminate in oval sporangia. The largest example (V. 26463), which was unsuitable for photographic illustration, was 6·5 cm. long and had three successive dichotomies, the ultimate divisions ending in sporangia (figure 87).

The sporangia are more or less oval, some being almost twice as long as wide while in others the length and breadth are almost equal. A frequent size is 2·5 or 3·0 mm. in length by 2·0 or 2·5 mm. in breadth, but both smaller and larger examples are met with. The largest specimens seen were some 4·0 mm. long by 3·5 mm. wide. The axes are usually about 1·0 mm. wide, but some are almost twice that width and they may diminish as they subdivide to a width of 0·25 mm. Beyond the appearance by reflected light of elongated epidermal cells and, in one specimen (V. 26464), of the annular tracheides, nothing has been learnt as to their structure.

The flattened incrustations of sporangia have been studied both on the rock (figure 43) and as removed on film transfers (figure 44). They are all very similar and, in spite of the number available, have shown nothing certain as to structure. The central region is occupied by a thin carbonized layer, sometimes detachable as a continuous film but usually more or less cracked and imperfect. This was opaque in transfers and neither spores nor the sporangial wall were revealed by maceration. Around this central region is a brownish zone of considerable width (about 250μ); this becomes less wide on nearing the stalk where it disappears. No definite structure is shown in this zone in transfers (figure 44), although it was evident that the brown colour was in some way due to organic material. This zone is a regular and characteristic feature of the sporangia as thus preserved. There is, however, no proof that it represents the thick sporangial wall; if that were the case, the black incrustation would be derived from the compressed mass of spores. An alternative and perhaps more probable view would be that the black area represents the whole sporangium and that the zone around has come in some way from its compression. The preservation of these sporangia presents a problem that has not been satisfactorily solved.

Semi-petrified sporangia. The one differently preserved specimen was found on splitting a piece of the rock from Llanover. Over an area of some 2×2 cm. were more or less connected branch systems, some of which ended in complete sporangia (figures 45, 46). There were also several damaged sporangia that were particularly instructive (figure 47). While the specimen under consideration suggested a plant of smaller size than many of the flat incrustations, it comes well within the range of measurements of these, and all the remains appear to belong to one species of *Cooksonia*, preserved in different ways.

One of the most complete of the sporangia is shown in figure 45, and another, which terminated the other branch of the same dichotomy, in figure 46. These can be compared with the thin incrustation in figure 44 which is at the same magnification. They both showed clearly that the superficial cells of the sporangial wall were elongated. At one region, on the right-hand side and near the base of the sporangium in figure 45, the wall has fortunately been broken through. The edge of the break showed part of the thickness of the wall, at a deeper level elongated cells of this were exposed, while in a central strip the contained spores were visible. The details of this specimen are not figured, but instead another very instructive crushed sporangium may be described. The appearance of this as broken across is seen on the right in figure 47. It is completely filled with a mass of brown spores enclosed within a wall of considerable thickness. Close beside it is another crushed and broken sporangium, which also showed the wall in vertical section. A film-pull made from the counterpart shows the remains of these sporangia in the same relative positions (figure 49). The sporangium below and on the right is filled with spores and shows portions of its wall in vertical section and at the upper end a small portion tangentially. The wall of the broken sporangium on the left is similarly shown. Figure 48 is a view by reflected light of a small portion of the wall of the first of these sporangia at a magnification of 90 diameters; it demonstrates the thick sporangial wall, with a dark outer line and a structureless yellow region within, and against this the closely packed mass of spores.

The thickness of the sporangial wall in these specimens is about 75μ. The structure is not fully demonstrated though better than in any example of *Cooksonia* yet known. For the most part the wall is converted into yellow amorphous material, but at places, especially where seen tangentially, was evidently composed of elongated elements. There are no indications of any region of dehiscence, and the appearance of the various sporangia supports the view that they were indehiscent. Spores were removed on the film-pull of the two sporangia shown in figure 49. A few from the left-hand sporangium are magnified 360 diameters in figure 51 and a few from the other sporangium in figure 50. The spores are smooth-walled, mostly oval, and about 35μ in the longer measurement by 30–20μ in the other.

Discussion. The material of *Cooksonia* from Llanover, and especially the semi-petrified specimen, afford information as to the wall and contents of the sporangium, which is of general significance in our knowledge of this type. It is noteworthy that the sporangia preserved in the solid show no indication of the outer zone or halo so prominent in all the flattened incrustations. The structurally preserved material demonstrates, what was previously indicated by examples of *C. hemisphaerica* from Targrove, that the sporangial wall was thick and that it readily broke down during fossilization. There are, however, great difficulties in establishing any correspondence between the thick wall and the much wider outer zone of the incrustations, and the interpretation of the latter must be left open for the present. Though connected dichotomous branch systems with terminal sporangia are known from various other localities and horizons as well as from Llanover, nothing has yet been seen of the lower region of *Cooksonia*, and a complete example of this small vascular plant has yet to be discovered.

In dealing with an increasing number of sets of remains of this simple plant, which was evidently plastic as regards size and as regards the size and shape of its sporangia, it seems inadvisable to multiply specific names. Owing to the simplicity of the plant there are few differential characters, and the distinction of species may well be deferred until material has accumulated for a critical comparative treatment of what is a readily recognizable generic type. We therefore for the present record the remains described in this section as *Cooksonia* sp., even though they are as instructive as any yet studied and in some respects more so. In the size of the plant and in the size and shape of the sporangia the larger examples from Llanover seem to resemble most closely *C. downtonensis* (Heard, 1939) founded on a single rather ill-preserved specimen from the Tilestones of Capel Horeb. Both this specimen and those described here differ from *C. hemisphaerica* from the upper beds of the Downtonian at Targrove (Lang 1937) in that their sporangia are larger and definitely longer than wide. There is, however, a specimen of *C. hemisphaerica* now known in which the sporangium appears oval and measures slightly over 2 mm. in length by 2 mm. in width, thus approaching in shape some of the examples from Llanover and coming well within the range of size of these. Nothing is yet known of the spores of *C. downtonensis* and *C. hemisphaerica*, so that comparisons cannot be extended to this character. An undescribed specimen from the Dittonian presents general resemblances both to the Llanover plant and to *C. hemisphaerica* and has spores of the same size and shape as the former. On the other hand, in the size and shape of the sporangia and of the spores the Senni Beds specimens are clearly distinct from *C. pertoni* (Lang 1937) which also appears to have been a smaller plant. The specimens from Llanover not only add some points to our knowledge of *Cooksonia* but establish the continuance of this type of plant, known throughout the Downtonian and in the Dittonian of England and Wales, into the Senni Beds.

9. *Sporogonites exuberans* Halle

(Plate 11, figures 52–60)

A few specimens from Llanover consist of short straight lengths of slender axis passing into a terminal body which contained large numbers of small spores. Features which attracted attention were the parallel sides of the terminal body and the ridging of the sterile basal region of this. These and other characters distinguished the specimens from *Cooksonia* and led to comparison with *Sporogonites exuberans* (Halle 1916, 1936). The description will be based on two specimens which in various respects are most instructive and certain. The others, one of which is represented in figure 56, are naturally placed with these but are in themselves less distinctive.

The best specimen as regards form and also the largest of the set is shown of $\frac{9}{10}$ natural size in figure 52 and enlarged in figures 53 and 54. A piece of axis, 3 mm. long and over 1 mm. broad, widens to form the basal region of the terminal body, which is about 7 mm. in total length and 3·5 mm. wide. This length is made up of about 2 mm. for the sterile basal region and 5 mm. for the fertile region. The line of junction between the two regions is horizontal. The summit is bluntly rounded. The brown material, which represents the remains of the stalk and the fertile region, has mostly fallen away from the basal region leaving this as a clear impression on the stone. Three ridges are distinctly visible on this impression; if the specimen were viewed from the outside they would be grooves separating wider ridges. There are some indications of the fertile region having been bounded by a fairly thick wall.

The second specimen (figure 55, cf. fig. 89) has the fertile region incomplete but is in other respects very instructive. The straight axis is about 7 mm. long and 1 mm. broad and is preserved as brown mineral in the solid, though somewhat flattened. This applies also to the basal region which broadens out to a width of about 3·5 mm. The impression left where a portion of the solid material of the basal region has fallen away, on the left in figure 55, is ridged as in the first specimen though the ridges are not so fully shown. The fertile region maintains the same width but its outline is lost where the specimen is imperfect above; nothing can therefore be said as to the shape of the upper end. The surface in the portion of the fertile region that is preserved is covered with brown material which at places had the appearance under reflected light of a mass of spores. When small portions were removed and treated with hydrofluoric acid numerous spores were obtained, which were mounted with some difficulty in Canada balsam. Those that endured the treatment showed the structural features clearly. A small mass of ill-preserved spores is shown at a magnification of 360 diameters in figure 58, and a well-preserved spore in a small group is magnified 900 diameters in figures 59 and 60. The wall of the spore showed at one level of focus what appeared to be a reticulate pattern (figure 59), but where it was in optical section was seen to be of uniform thickness and slightly papillate. On raising the focus slightly a dotted appearance was obtained (figure 60), the dark spots which represent the summits of the papillae corresponding to the clear areas in the previous view. The spores range in size from 17·5 to 25μ; many measure about 20μ.

The upper part of the stalk and its passage into the basal region in this specimen gave a clear picture of the epidermis when examined under a low power by reflected light. The epidermal cells are markedly convex; they are elongate and fit together with pointed ends. At one place a little below the basal region a stoma is clearly seen (figure 57). The curved guard-cells, which are at the level of the epidermal surface, enclose a small depression representing the pore. In the same region of the stalk there were indications of two more stomata, but the general preservation of the epidermis is sufficiently good to make it certain that they were only sparingly distributed.

Discussion. The features exhibited by the specimens described above are all characters of *Sporogonites*, originally described from the Lower Devonian of Norway by Halle (1916, 1936) and since met with in Belgium (Lang 1937*a*; Stockmans 1940) and in Australia (Lang & Cookson 1930). The agreement with *S. exuberans* seems to be so close in size, shape of the whole terminal structure and its rounded rather than bluntly pointed summit as to justify specific identification. This is confirmed by the size and structure of the spores. The Llanover specimens add the presence of stomata to our knowledge of the plant. They do not provide any evidence as to whether or not the axis had a vascular strand, nor on the question, which Halle (1936) now leaves open, as to whether a sterile columella was present in the fertile region. They do not assist in deciding whether *Sporogonites* should be regarded as the terminal sporangium of a simple Vascular Cryptogam or as a sporogonium. The discovery in the Senni Beds, however, of specimens preserved in the solid and showing details of structure increases the hope that further evidence may be forthcoming on these and other questions.

10. *Sciadophyton steinmanni* Kr. & Weyl.

(Plate 11, figures 61–64)

Sciadophyton steinmanni, as founded on abundant but still imperfectly understood remains from Germany (Kräusel & Weyland 1930), consists of stellately arranged vascular axes, sometimes branched and ending in peltate expansions. The latter were often found as isolated disks with a more or less irregular margin; the disks include numerous 'spherical bodies'. No specimens showing the characteristic stellate form of the whole plant have been found at Llanover, but about 20 disk-like structures, which agree with those described from Germany, have been collected. Three of them are still attached to their stalks.

One of the stalked specimens is represented of $\frac{9}{10}$ natural size in figure 61 (cf. fig. 90) and another enlarged 2·25 diameters in figure 62. The stalk is slightly over 1 mm. wide, and the subtriangular outline of the laterally compressed disk seen from the side suggests that the peltate disk must have been originally more or less funnel-shaped. Two examples of isolated disks spread out on the rock are shown in figures 63 and 64. Like many of the others, they were about 1 cm. in diameter, but specimens ranging from 0·4 to 2·5 cm. have been seen. They show the irregular margin, which appears to be a real and not an accidental character, and also an indication of the place of attachment of the stalk in a central position. In all the figures the presence of small black spots, which evidently correspond to the 'spherical bodies' in the German specimens, is a characteristic feature. They are more widely spaced and larger in the central region and smaller and more closely placed near the edge, where their distribution appears to follow the irregularities of the margin of the disk. These round or oval black spots, which range in diameter from 0·15 to 0·6 mm., are more clearly seen when the specimens are examined in xylol, for, unlike the rest of the disk, they are heavily carbonized. They were also probably thicker than the intervening regions, for in some specimens there are shallow, slightly convex impressions in the rock where the carbon of the spots has fallen away. The disks have been studied both on the rock and as removed in film transfers. The preservation is very poor. They may show a striation or wrinkling radiating out from the position of attachment of the stalk, but nothing definite has been ascertained as to their structure nor as to the nature of the black spots.

The Llanover specimens are somewhat larger than the German specimens,* and the spots are rather smaller than the 'spherical bodies' in the latter. The detailed agreement in the shape of the stalked and isolated disks and in the distribution of the spots, however, justifies the identification of the remains as *Sciadophyton steinmanni* and the record of this from Britain, even though the lower regions of the plant have not been found.

11. *Taeniocrada* sp.

(Plate 11, figures 65, 66)

At the end of Llanover Quarry, opposite to that where the other plant remains described in this paper occurred, rock from another lenticular band was found in the

* In this comparison we have had the advantage of studying specimens from Wahnbachtal in the British Museum Collection.

tip. This sandy mudstone, which splits with a blocky fracture, was traversed by very numerous, thin, flattened incrustations of one kind of plant. These were ribbon-shaped and often about 5 mm. wide; examples were found up to 8 mm. and others down to 2 mm. in width. Branching specimens were fairly numerous; in a number of cases the branch appeared lateral and bent so as to lie parallel to the main axis. Sometimes more than one branch arose at or about the same level. The specimen in figure 65, which has lost most of the cracked layer of carbon, shows the appearance in impression of a piece of the plant with branching at two places. No reproductive organs were seen. Nothing has been ascertained as to structure beyond the presence in some of the axes of a slender vascular strand, that may be more or less displaced from its median position. It is shown in the piece of axis in figure 66.

These specimens and their mode of occurrence in the rock are very characteristic and distinct from the other plant remains in the quarry. They agree generally with the description and figures of *Taeniocrada decheniana* (*Haliserites*), long known from the Lower Devonian of Germany and recently more fully described and renamed by Kräusel & Weyland (1930). They are very similar to specimens of *Taeniocrada* which have been described from Belgium (Stockmans 1940); we have had the opportunity of comparing the Llanover material with these. The resemblance of the vegetative axes is indeed so close that we feel justified in recording them as *Taeniocrada* sp. They are the first specimens indicating the occurrence of this plant in Britain.

12. *Axes with* H-*shaped branching; spore masses; and other remains* incertae sedis

(Plate 11, figures 67–70)

The plants described in the preceding sections have been clearly distinguished in the deposit at Llanover; all are known to be vascular plants, or, in the case of *Sporogonites*, to be possibly of that nature. Before passing to consider other distinguishable types that are not vascular plants, brief mention may be made of some specimens that are indeterminable but of some interest.

A number of pieces of axes exhibited H-shaped branching. They differ in width and, being isolated fragments, cannot be referred to any of the plants described though they may well have been derived from some of them. Two examples are shown of $\frac{9}{10}$ natural size in figures 67 and 68; in the one case the width is 2 mm. and in the other fully 3 mm. This type of branching was first recognized in the Carmyllie Beds of Scotland, and the specimens there were found to belong to the rhizomatous region of *Zosterophyllum myretonianum*. It was for a time natural to regard H-shaped branching in axes about 2 mm. wide as an indication of the presence of this plant elsewhere. When such branchings occurred in the Australian deposits along with *Z. australianum* they were tentatively attributed to that plant. Evidence is, however, steadily accumulating that this type of branching was widespread among early plants. Unless, therefore, evidence is forthcoming to relate such specimens as those in figures 67 and 68 to particular plants, they can only be recorded, as is done here, as *incertae sedis*.

The specimen, represented enlarged 3·6 diameters in figure 69, shows two flattened black incrustations, about 3·5 mm. long by 2·5 mm. wide, lying beside one another on the stone. That on the right is clearly terminal on an axis 0·5 mm. wide; it is uncertain whether the two are borne on a dichotomous branch system or not, though the appearance is suggestive of this. One of the thin incrustations was readily detached as a coherent black film. On maceration it proved to be a flattened mass of spores. Some of these from the edge of the mass are magnified 180 diameters in figure 70; they have smooth walls and measure about 50μ. No further examples have been found and nothing is known of the plant. The specimen can only be described as *incertae sedis*, but is interesting on account of its preservation. This contrasts with the structureless condition of the thin black incrustations of *Cooksonia* sp. described in a previous section, and the size of the spores clearly separates it. These spore masses may, of course, have belonged to a similar, though distinct, plant.

Other indeterminable remains include slender branched axes, sometimes with indications of terminal bodies that may have been sporangia. A number of specimens of another type are pointed and apparently bifid bodies (V. 26768) that may have been sporangial. One very obscure branch system (V. 20713) suggested tentative comparison with *Hedeia*. There are numerous indeterminable pieces of axes of various widths in the debris. Most of these may have been derived from one or other of the types of plants recognized in more complete specimens. There were, however, doubtless other plants that have yet to be distinguished when better specimens are discovered. It would serve no scientific purpose and even be misleading to select some of the branched axes for record as '*Hostimella* sp.'; remains such as have been described from other deposits under this name were not characteristically present at Llanover.

A number of the plants described in previous sections have borne sporangia, some of which contained the spores. Isolated spores in the rock have, however, been rare in the preparations so far made, and they have not presented distinctive features. They have therefore not been figured and described although a further study of the isolated spores in the Senni Beds may later be worth while for comparison with other deposits. It must be borne in mind that isolated spores may be derived not only from Vascular Cryptogams but from more anomalous types of plants.

13. *Prototaxites* sp.

(Plate 11, figures 71, 72)

The occurrence of the characteristic and peculiar type of plant *Prototaxites* (*Nematophyton*) in the Senni Beds is known from a small fragment at Kemeys (Lang 1937, p. 281) and by the description and figures of a single very slender specimen from Brecon Beacons Quarry (Heard 1939). It is now possible to extend these records by an account of remains of *Prototaxites* at Llanover and Talybont. At Talybont there are fragments of considerable size in the coarse rock along with *Pachytheca* (figure 71), the mode of occurrence being very similar to what has long been known, especially in the Downtonian. The remains from Llanover are even more interesting for, in addition to similar fragments and some elongated slender examples, large specimens were found. Some examples on weathered slabs in the tip were over 10 cm. wide, and one specimen found in situ (V. 26551) was 29 cm. long by 9·5 cm. wide and is incomplete both as regards length and breadth.

It is not necessary to illustrate the various specimens or to give the evidence upon which each has been identified. Their recognition by the appearance presented by the wide tubes under reflected light and by the study and measurement of these tubes removed from the incrustations has been confirmed by cutting microtome sections of suitable fragments. A small region of such a transverse section of a specimen from Llanover is represented in figure 72. It shows the wide tubes, in this case about 20μ in diameter, and between them the system of narrow tubes. These were about 3μ in diameter, but others, which are more conspicuous in the figure, were wider. The structure is characteristic of *Prototaxites* but, owing to the small size of the fragments that could be studied in this way, nothing certain has been ascertained as to the distribution of the narrow tubes, though there are indications that at places they were associated to form 'medullary spots'. The large tubes from other specimens were found to be of greater width, 30–40μ or more. It is not, however, desirable to attempt specific distinctions on this or other grounds.

Special mention may be made of some specimens (e.g. V. 26553) found at Llanover, which are unbranched, some 5 cm. long and 2·5–6·0 mm. wide. They were preserved in pyrites or brownish mineral and were evidently similar to the specimen described by Heard, though considerably larger. When ground and polished the wide tubes were clearly seen by reflected light, but there was no evidence to show that these slender specimens were intact axes of the plant. The indefinite and structureless peripheral zone was clearly due to alteration during preservation.

Another interesting specimen (V. 26549) was a very friable black incrustation, 6·5 cm. wide and 13 cm. long, found in situ at Llanover. Besides wide tubes of ordinary size this showed longitudinally running rods up to 160μ in diameter. Though these at first sight appeared to be very wide tubes, they proved on detailed examination to be made up of the usual wide and narrow tubes. This peculiar type of preservation recalls that of certain specimens from Germany described by Kräusel & Weyland (1934, Taf. xxi, fig. 6) which in transverse section showed more or less circular areas separated by broken-down material.

The occurrence in abundance of *Prototaxites* in the Senni Beds along with a flora composed mainly of vascular plants is thus fully established. It is of interest that many of the specimens were of large size.

14. *Nematothallus* sp.

(Plate 11, figures 73–77)

The presence of *Nematothallus* in the Senni Beds has been known for a number of years, but, although recorded (Lang 1937, p. 281), no evidence from figured specimens has been provided. This evidence will be given here without, however, entering into any full study of the remains. A number of poorly preserved thin incrustations in the rock at Llanover were apparently this type of plant. Most of them were structureless and indeterminable, but some showed fragments of recognizable cuticle and pieces of tubes. One specimen, measuring 6 × 4 mm., when removed as a film transfer proved to be well-preserved cuticle showing the 'cellular' pattern very clearly; a small portion of this is represented in figure 74. Remains of this type of plant from Kemeys and from Talybont give little information but suffice to indicate its occurrence.

The demonstration of the characteristic structure of *Nematothallus* may be given by one example from Brecon Beacons Quarry. A block of the grey rock from this locality, collected a number of years ago by Professor O. T. Jones and given to one of us, showed numerous thin black incrustations in close association with the vascular plants. One of these black patches is represented of $\frac{9}{10}$ natural size in figure 73. When it was examined by reflected light the associated-tube structure could be seen. This was more clearly demonstrated by film-pulls, which also showed fragments of cuticle. The wide tubes are mostly about 10μ wide; the fine tubes among them were largely broken down, but at places were found to be about 2μ wide. Wide tubes and some remains of the narrow tubes are shown in figure 75 and from another region of the preparation in figure 76. The latter figure also shows a spore embedded among the tubes in what was evidently its natural position. Lastly, figure 77, from the same specimen but at a higher magnification, shows pieces of two black structureless wide tubes and a short length of a wide tube that clearly exhibits annular thickening.

The specimens figured here evidently agree in general features with those from the Downtonian (Lang 1937), but in the size of the wide tubes and the type of annular thickening they exhibit differences of detail which will require further consideration. They suffice, however, to demonstrate the presence of this peculiar structural type of plant in the Senni Beds and to justify its inclusion in the flora.

15. *Pachytheca* sp.

(Plate 11, figures 71, 78)

Pachytheca has been found at Llanover, the Deri, Kemeys and Talybont. It is thus clear that it is distributed in the deposits containing the vascular plants of the Senni Beds flora. The more numerous and better preserved examples occurred along with fragments of *Prototaxites* at Talybont (figure 71). Figure 78 is a photograph of another specimen from that locality, enlarged 4·95 diameters. It is split across and shows the medulla and cortex, the latter with the usual radial striation. The specimens range in diameter from 2 to 4·5 mm. In some of them the cortex was rather thin (0·5 mm.) and the medulla proportionally large. They are mostly too poorly preserved to yield much information as to structural details. With the exception of one partially pyritized specimen from Talybont, they were carbonized and largely converted into coal, some of them breaking with a shining fracture. From a few preparations which it was possible to make it was ascertained that the filaments of the medulla and the radiating tubes of the cortex were about 7μ in diameter and did not exceed 12μ. While there are points of agreement with the Downtonian specimens that have the narrowest cortical tubes, here also there is nothing to justify specific distinctions. The Senni Beds specimens are therefore recorded as *Pachytheca* sp.

16. *Spherical or circular bodies* incertae sedis

(Plate 11, figures 79–83)

A number of specimens of spherical or flattened circular bodies of various types but all quite distinct from *Pachytheca* were met with at Llanover. In the absence of knowledge of their construction their nature is quite obscure. Since, however, more or less comparable objects have been described from other regions in beds of correspondingly early age, they may possess some stratigraphical significance. Some have the surface covered with short conical projections while others are smooth. Specimens of the former kind are shown in figures 79–81, enlarged 3·6 diameters, while two specimens without tubercles are enlarged 1·8 diameters in figures 82, 83.

That represented in figure 79 has the surface covered with small tubercles except at one region where there is a single larger tubercle. This type is thus directly comparable with the pyritized specimen described from Brecon Beacons Quarry (Heard 1927) and it is of similar size. In the specimen in figure 80, which is smaller (3·5 mm.), the surface also shows small tubercles but, if present, no larger tubercle is exposed. The third specimen of this tuberculate type (figure 81) is preserved as a flattened film of brownish material. It shows a number of short projections round the margin and the impressions of others on the surface. These tuberculate bodies may be tentatively compared with obscure specimens described from the Lower Devonian of Röragen (Halle 1916, plate 3, figures 34, 35) and from the Upper Silurian of Australia (Cookson 1935, figures 3–5).

The smooth body in figure 82 measures 6 mm. across and has an undulating or dimpled surface. It resembles bodies long known from the Carmyllie Beds of Scotland and also met with in the Dittonian and Downtonian of England and Wales. The second, slightly larger, specimen (figure 83) is on the whole similar but has a dark zone around it. Specimens of equally obscure nature showing this feature occur in the Downtonian.

General discussion

The Senni Beds are a relatively high horizon of the Lower Old Red Sandstone of England and Wales. Though recognizable plants have only been found in them in the last fifteen years, it will be evident from the preceding account that a fairly rich flora is now known. This is more extensive than the flora of generally corresponding age that has long been known from the Strathmore Beds, high in the Caledonian Lower Old Red Sandstone, which includes *Drepanophycus* (*Arthrostigma*), *Psilophyton princeps* and the form *goldschmidtii*, *Dawsonites*, *Nematothallus* and *Pachytheca* (Lang 1932; Henderson 1932). It need not be considered in detail here, since all the main types are represented in the Senni Beds flora. It may be useful to note, however, that remains of *Psilophyton princeps* in the Strathmore Beds are typical and exhibit detailed agreement with specimens from Gaspé; this is a point of some interest since such agreement has not been demonstrated for the remains of *Psilophyton princeps* type from the Senni Beds. Other plant-containing beds in Britain that are probably of corresponding age, such as the Cosheston Beds and the Foreland Grits, have not, as yet, yielded determinable plants, though the general type of the fragmentary plant remains in them is similar. The following brief discussion can therefore be based on the Senni Beds flora.

Without undue repetition of the information afforded by the list of plants in the Senni Beds (p. 134) and the descriptive accounts of these, the interesting composition of the flora may be pointed out. It mostly consists of vascular plants which there is every reason to regard as terrestrial. The largest plant is *Drepanophycus*, remains of which were fertile and also provided new facts regarding the branching of the presumably basal region. *Psilophyton*, recorded as cf. *P. princeps*, is represented by remains of large size with short spines and has shown a new type of fructification. *Dawsonites* is fairly well represented but has added nothing to our knowledge. These three forms of relatively advanced vascular plants are of some stratigraphical importance. A second interesting element in the Senni Beds flora comprises those leafless plants that bear in various ways stalked sporangia which appear more or less clearly reniform, dehiscing along the convex margin, and resemble the type of sporangium first known from *Zosterophyllum myretonianum*. Such plants may be collectively spoken of as Zosterophyllaceae (Kräusel 1938). The group includes *Gosslingia*, as yet peculiar to the Senni Beds, with sporangia borne on the edge of finer divisions of the sympodial branch system. It further includes terminal spikes of tangentially extended sporangia which are referred to *Zosterophyllum*. Some of the spikes are radially symmetrical and closely resemble those of *Z. australianum*. Others of special interest are remains of two species of plants with the sporangia borne in two alternating rows and not radially. These have been included in *Zosterophyllum*, as *Z. llanoveranum* n.sp. and *Zosterophyllum* sp., by recognizing a subgenus, *Platy-zosterophyllum*, characterized by the dorsiventral arrangement of such sporangia contrasting with *Eu-zosterophyllum* which comprises the forms with radially arranged sporangia. The still simpler type of vascular plant, *Cooksonia*, is a member of the Rhyniaceae; the thick-walled, indehiscent, terminal sporangia were well shown in some of the specimens. *Taeniocrada*, *Sciadophyton* and *Sporogonites* are plants of still undetermined affinity; they are of stratigraphical interest and their occurrence in the Senni Beds provides the first records of them from Britain. Lastly, the flora includes a good representation of the Nematophytales (*Prototaxites*, *Nematothallus*) and the Alga, *Pachytheca*.

The Senni Beds flora is thus sufficiently abundant and sufficiently well known for some comparisons to be made. Floras of similar composition are known from Scotland, Germany, Belgium, Norway (Röragen), the United States (Wyoming), Canada (Gaspé), and Australia (Victoria). All of these have been regarded in whole or in part as Lower Devonian. In Europe this age is accepted geologically for the Scottish, German and Belgian floras; the age of the corresponding Norwegian flora is inferred from the plants. In North America the age of the Wyoming flora is established as Lower Devonian on palaeontological evidence. The Gaspé Sandstones, however, from which this type of flora was originally described, have more recently been regarded on palaeontological grounds as Middle Devonian (Hamilton) though with a small persistent element of Lower Devonian (Oriskany) types (Clarke 1908; Kindle 1938). The flora of Lower Devonian type from Australia is regarded from the associated Graptolites as Ludlovian (Lang & Cookson 1935), but it has been suggested that the highest beds containing it, from which Graptolites are absent, may be a continuation of the sedimentation into the Lower Devonian (Skeats 1928; Lang & Cookson 1930). It is unnecessary to give lists of these floras, since in an important recent work Stockmans (1940) has provided such comparative lists; all that is necessary in using them is to expand the list for the Senni Beds for which he was only able to give the one plant, *Gosslingia*. Without therefore entering into detailed comparisons of these floras, it may be pointed out that there are significant resemblances between them and the flora described here. The similarity of general grade of organization attained by the plants in all the floras is supported by the occurrence of the same identifiable plants in a number of cases. Thus *Drepanophycus*, *Psilophyton* and *Dawsonites* are widespread. *Zosterophyllum* is known in close association with *Drepanophycus* in Germany and from the Australian flora. *Sporogonites* occurs in Norway, Belgium and Australia. *Sciadophyton*, first recognized in Germany, is known from Belgium and Gaspé, and *Taeniocrada* from Germany, Belgium and perhaps elsewhere. *Prototaxites* and *Pachytheca*, though from their extended range they have not the stratigraphical value of some of the other plants, are known in the corresponding floras from Gaspé, Belgium and Germany; *Pachytheca* is also recorded from Australia. These points will be sufficient to show the close correspondence between this late Lower Devonian flora of Britain and what have been regarded as Lower Devonian floras elsewhere. These floras on the continent are classed as Siegenian-Emsian (Coblentzian), and it is here that the Senni Beds are rightly placed in Stockmans's lists.

Apparently hardly anything is known of the plants of the underlying Gedinnian strata on the continent. It is therefore of interest that, in the region of England and Wales with which we are concerned, a sequence of floras can be followed up through strata that correspond to the Lower and Upper Gedinnian of the continental succession into the Senni Beds. The relation of the Senni Beds flora to the plants in these lower beds, the Downtonian and Dittonian, thus calls for brief comment. *Pachytheca*, *Prototaxites* and *Nematothallus* are all traceable from the Silurian to the Senni Beds. *Cooksonia* is known throughout the Downtonian, in the Dittonian and on into the Senni Beds. *Zosterophyllum* appears in the upper part of the Downtonian, is found in the Dittonian and, as has been seen, is well represented along with similarly organized plants (*Gosslingia*) in the Senni Beds. The sudden appearance, on passing to the Senni Beds, of such larger vascular plants as *Drepanophycus*, *Psilophyton* and *Dawsonites*, is the striking floristic change in this sequence of rocks.*

This change in the type of a flora, which is, on the other hand, linked continuously with those below, leads to a consideration of the conditions of accumulation of the strata in the area and its bearing on the probable habitats of the plants. The Old Red Sandstone rocks of the Anglo-Welsh cuvette are very generally considered by geologists to represent the stratified deposits of deltas which spread southward into the Devonian sea from rising land areas to the north. Though initially marine, they became increasingly terrestrial. There is a disappearance of marine invertebrates within the

* For the sake of simplicity and brevity the consideration of the sequence of strata and floras from the Silurian to the top of the Lower Old Red Sandstone has been confined to the Anglo-Welsh region. A corresponding sequence of floras, though with less continuity of the plants, has long been known in Scotland. A few plants, including *Pachytheca* and Nematophytales, are known from the Downtonian. The flora of the Carmyllie and Cairnconnan Beds corresponds generally with the Dittonian and includes *Pachytheca*, *Prototaxites*, *Nematothallus*, *Parka* and *Zosterophyllum myretonianum*. The flora of the Strathmore Beds (which correspond generally to the Senni Beds), separated by a considerable thickness of rock from the Carmyllie Beds, includes *Drepanophycus*, *Psilophyton* and *Dawsonites*. The whole of the Caledonian Lower Old Red Sandstone has long been regarded as continental.

Downtonian and its upper beds were quite probably fresh water. That the Dittonian, in which no marine animals have been found, were probably fresh-water deposits is a view that has been expressed by geologists. The Senni Beds would represent a stage some time after the establishment of continental conditions; this is in accord with their lithological characters, for the impersistent conglomeratic bands, false-bedding and ripple-marking all point to fluviatile deposition in shallow water. The evidence of the few animal remains (*Pteraspis dunensis*, *Cephalaspis* sp. and a Eurypterid) found in the Senni Beds points in the same direction, and that provided by the plants, or at least the majority of them, shows that the flora as a whole had lived under terrestrial conditions. It is not, of course, excluded that some of the forms from the Downtonian to the Senni Beds may have been aquatic or marsh plants. But, even in the case of the earlier floras, the presence of vascular plants with firm-walled and presumably air-borne spores and the fact that some of the spores were shed from sporangia that had special arrangements for dehiscence are indications of subaerial life. The evidence for a definitely terrestrial habitat becomes still stronger in the case of the larger plants of the Senni Beds. In South Wales the change indicated by the appearance of these plants occurs at the base of the Senni Beds and within a few hundred feet of rock with no stratigraphical break. It seems clear that the change in the flora here is not evolutionary but ecological. It can be correlated with the alterations in the physical conditions indicated by the increase of sandy over muddy sediments and by the decline in the fish fauna.

Very special interest attaches to the continued presence in the Senni Beds, along with the large and definite terrestrial vascular plants, of the peculiarly organized Nematophytales (*Prototaxites*, *Nematothallus*). *Nematothallus* is abundant and readily demonstrated at Brecon Beacons Quarry and occurs at Llanover, Talybont and Kemeys. *Prototaxites* also has been found in all these exposures. The most striking fact, however, concerns the occurrence at Llanover not merely of fragments of *Prototaxites* but of large specimens. It is not necessary to return here to the general question of the possible terrestrial habitat of these plants, which was fully considered in relation to the Downtonian flora (Lang 1937). It need only be pointed out that the presence of *Prototaxites* in the Senni Beds affords strong additional support for regarding the Nematophytales as land plants.

The desirability of further collecting and detailed work on all stages in the remarkable and continuous succession of plant remains from the Silurian to the Senni Beds will be evident. There is no advantage at present in entering upon the general questions involved further than the remarks in the preceding paragraphs. What is needed is the building up of our knowledge not only of the morphology and structure of the plants but also of their modes of occurrence and probable habitats. The present paper is such a contribution of fact regarding the plants of the Senni Beds.

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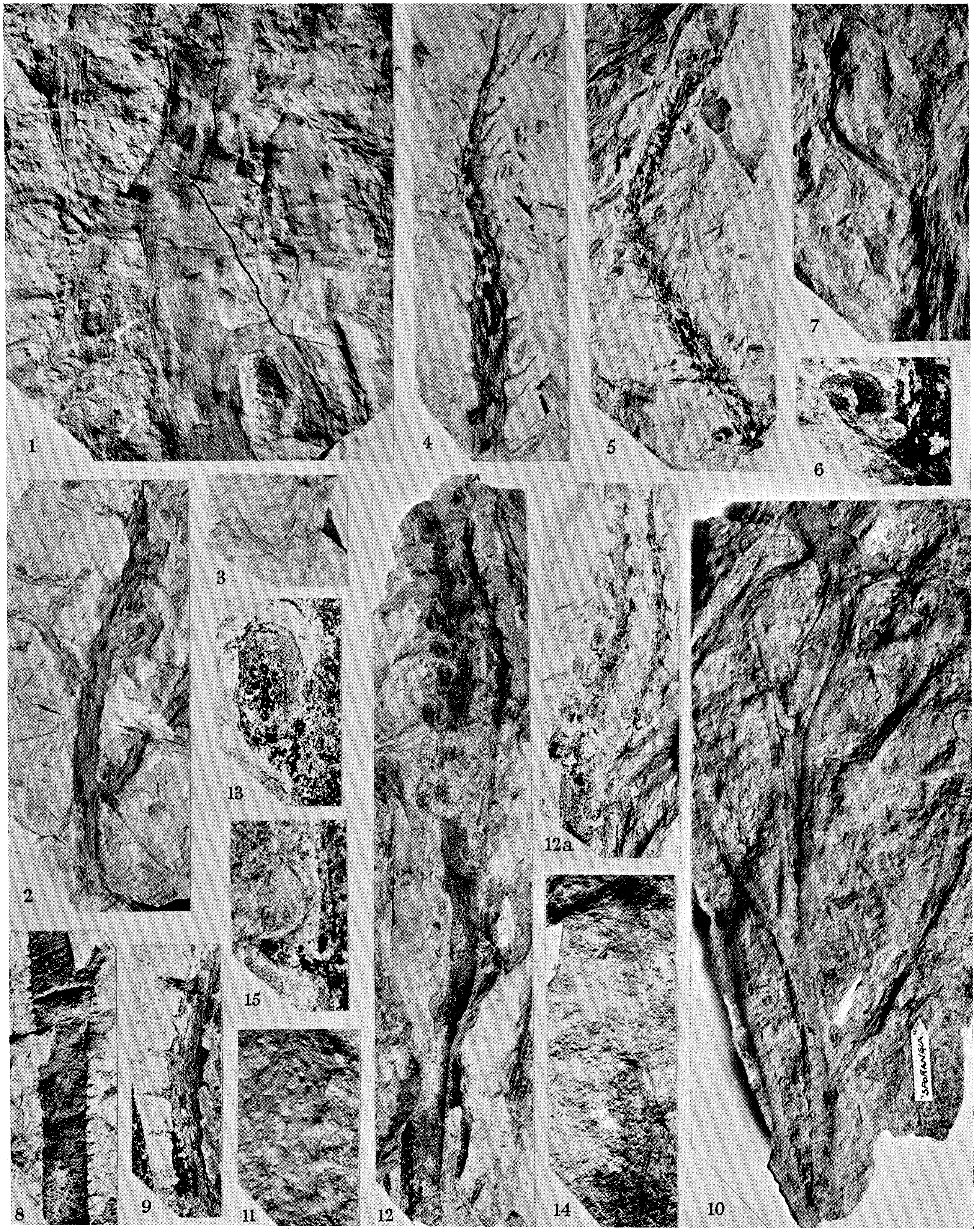
PLATES 9–11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'SPORANGIA'

Explanation of plates 9–11

(All the figures are from untouched photographs. Unless otherwise stated, the specimens were collected at Llanover Quarry and are in the Geological Department of the British Museum (N.H.), to which the registered numbers refer. The specimens in figures 5, 6, 9, 12*a*, 13, 15, 17, 18, 20–22, 29–31, 34, 36, 43, 52, 53, 61–64, 81, 83 were photographed under xylol and figures 32, 33 under water. The unusual magnifications are due to a reduction of the plates by $\frac{1}{10}$ which was not foreseen when the photographs were taken in the preparation of the paper.)

Plate 9

Drepanophycus spinaeformis, figures 1–7

Figure 1. Impression of wide stem bearing two branches, each of which gives off a downwardly directed limb. $\frac{9}{10}$ Nat. size. (V. 26520.)
Figure 2. Similar stem bearing a number of upturned branches from all of which one or two downwardly directed branches arise at the bend. $\times 0{\cdot}45$. (V. 26523.)
Figure 3. Spine-like leaf from a wide stem seen in profile. $\frac{9}{10}$ Nat. size. (V. 26530.)
Figure 4. Narrow stem with numerous slender but broad-based leaves. $\frac{9}{10}$ Nat. size. (V. 26521.)
Figure 5. Slender fertile shoot with closely placed leaves and a number of sporangia. $\frac{9}{10}$ Nat. size. (V. 26522.)
Figure 6. Attached fertile leaf with a sporangium from near the bottom of the preceding specimen. $\times 2{\cdot}7$. (V. 26522.)
Figure 7. Two attached leaves from another fertile shoot showing the impressions on the stone that indicate the two sporangia. $\times 2{\cdot}7$. (V. 26524.)

Cf. *Psilophyton princeps*, figures 8–15

Figure 8. Typical piece of stem, showing spines along the margins, spine insertions on the surface and a lateral branch. $\frac{9}{10}$ Nat. size. (V. 26505.)
Figure 9. Spines seen in profile on the edge of another stem. $\times 3{\cdot}6$. (V. 26506.)
Figure 10. Sympodial branch system bearing spines and on one branch a few sporangia. $\frac{9}{10}$ Nat. size. (V. 26508.) Cf. figure 84.
Figure 11. Impression of another stem of this fertile branch system showing spines projecting from the margin and spine insertions. $\times 3{\cdot}6$. (V. 26508*a*.)
Figure 12. Branch system, the two ultimate divisions of which bear sporangia. Further description in text, p. 138. $\frac{9}{10}$ Nat. size. (V. 26507.)
Figure 12*a*. The two ultimate divisions photographed under xylol. $\frac{9}{10}$ Nat. size.
Figure 13. One of the sporangia in the preceding specimen. $\times 3{\cdot}6$. (V. 26507.)
Figure 14. Piece of stem from the same block as figure 10 which shows spines and on the left-hand side a sporangium. $\times 1{\cdot}8$. (V. 26508*b*.)
Figure 15. A sporangium borne on the continuation of the piece of stem shown in figure 14. $\times 4{\cdot}95$. (V. 26508*b*.)

Plate 10

Dawsonites arcuatus, figures 16–19

Figure 16. Piece of main axis with the base of a lateral branch on the left and, just below the top end, another lateral branch which subdivides and bears pendent sporangia. $\frac{9}{10}$ Nat. size. (V. 26495.) Cf. figure 85.

Figure 17. Portion of main axis from which a lateral branch arises, subdivides and bears a few sporangia on the ultimate divisions. $\frac{9}{10}$ Nat. size. (V. 26492.)

Figure 18. Branch system, probably a lateral branch, subdividing and bearing a number of terminal, pendent, fusiform sporangia. × 4·95. (V. 26493.)

Figure 19. Group of spores from within a sporangium removed on a film-transfer. × 180. (V. 26494*a*.)

Gosslingia breconensis, figures 20–28

Figure 20. An isolated and fairly extensive portion of a branch system bearing a number of sporangia. $\frac{9}{10}$ Nat. size. (V. 26483.) Cf. figure 86.

Figure 21. The branch system on the right shows the sympodial branching, a circinate tip and the position of the sporangia. × 1·8. (V. 26477.)

Figure 22. Portion of branch system showing the form and insertion of two sporangia and the marginal line of dehiscence between the thickened rims of the valves. × 4·5. (V. 26479.)

Figure 23. Incrustation of solid flattened axis showing the fractured end of a projecting axillary structure at the lower branching on the left and the base of another at the branching above. × 2·7. (V. 26478.)

Figure 24. The counterpart of a similar specimen showing the axillary structure as an oval plug of organic material. × 2·7. (V. 26485.)

Figure 25. Impression of another axis showing axillary bodies in relation to two branchings. × 2·7. (V. 26480.)

Figure 26. Incrustation of axis showing small tubercles on the surface. × 3·6. (V. 26485.)

Figure 27. Thin incrustation of an attached sporangium showing the reniform shape and the line of dehiscence. × 9. (V. 26704.)

Figure 28. Internal mould of a sporangium in fine mudstone showing the reniform shape. × 9. (V. 26481.)

Zosterophyllum cf. *australianum*, figures 29–31

Figure 29. Compact spike of radially arranged sporangia preserved in low relief. $\frac{9}{10}$ Nat. size. (V. 26471.)

Figure 30. The same spike enlarged to show the three vertical rows of sporangia and the curved distal margins of these. × 3·6. (V. 26471.)

Figure 31. Small spike showing similar characters. × 3·6. (V. 26472.)

Zosterophyllum llanoveranum n.sp., figures 32–40

Figure 32. Portion of tuft-like group of leafless axes, most of which bear sporangia in their distal regions. × 0·45. (V. 26515*a*; part of holotype.) Cf. figure 88.

Figure 33. A long spike from the preceding specimen showing the short-stalked sporangia along one side of the axis. $\frac{9}{10}$ Nat. size. (V. 26515*a*; part of holotype.)

Figure 34. Spike showing the sporangia in two alternating rows; most are viewed laterally and appear P-shaped and some show the line of dehiscence. × 1·8. (V. 26515*d*; part of holotype.)

Figure 35. Axis of a spike preserved in the solid and showing the bases of the stalks of the sporangia, arising alternately. × 3·6. (V. 26516*a*.)

Figure 36. Isolated sporangium showing the reniform shape, the curved distal margin and the thickened rims of the valves with the open line of dehiscence between them. × 3·6. (V. 26517*b*.)

Figure 37. Isolated sporangium in full face view from the abaxial side showing the rounded outline and part of the stalk. × 3·6. (V. 26517*b*.)

Figure 38. Sporangium, preserved in the solid, seen from the side and showing the two thickened rims of the valves still joined at the line of dehiscence. × 3·6. (V. 26516*c*.)

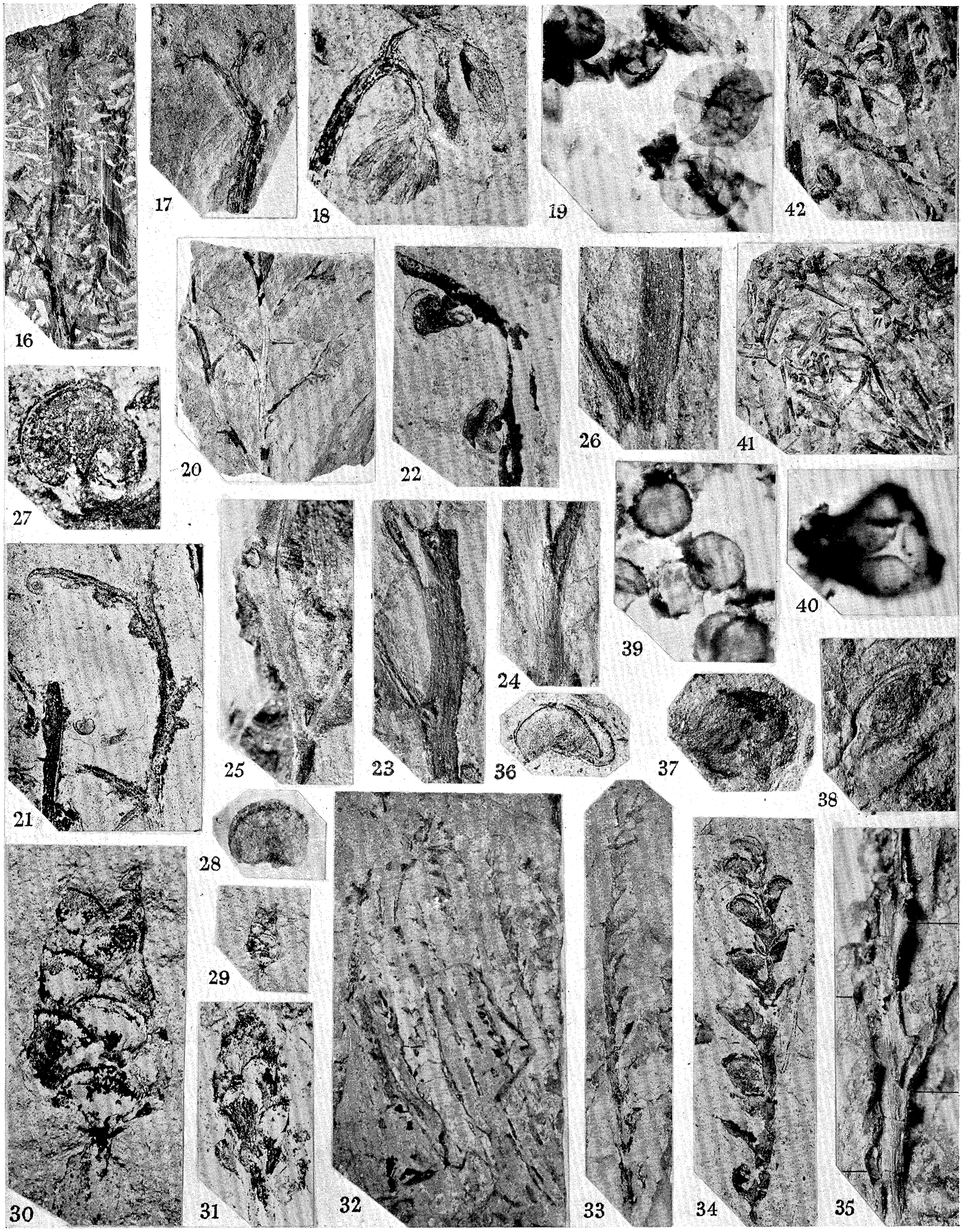
Figure 39. Group of spores removed from a sporangium. × 180. (V. 26515*f*.)

Figure 40. Single spore from the same preparation showing the triradiate split. × 360. (V. 26515*f*.)

Zosterophyllum sp., figures 41, 42

Figure 41. Thin black incrustations of branched axes and short terminal spikes of sporangia exposed on surface of a piece of rock. $\frac{9}{10}$ Nat. size. (V. 26705.)

Figure 42. Portion of specimen in figure 41 showing the attachment of shortly stalked reniform sporangia on the two sides of the dorsiventral spike. × 2·7. (V. 26705.)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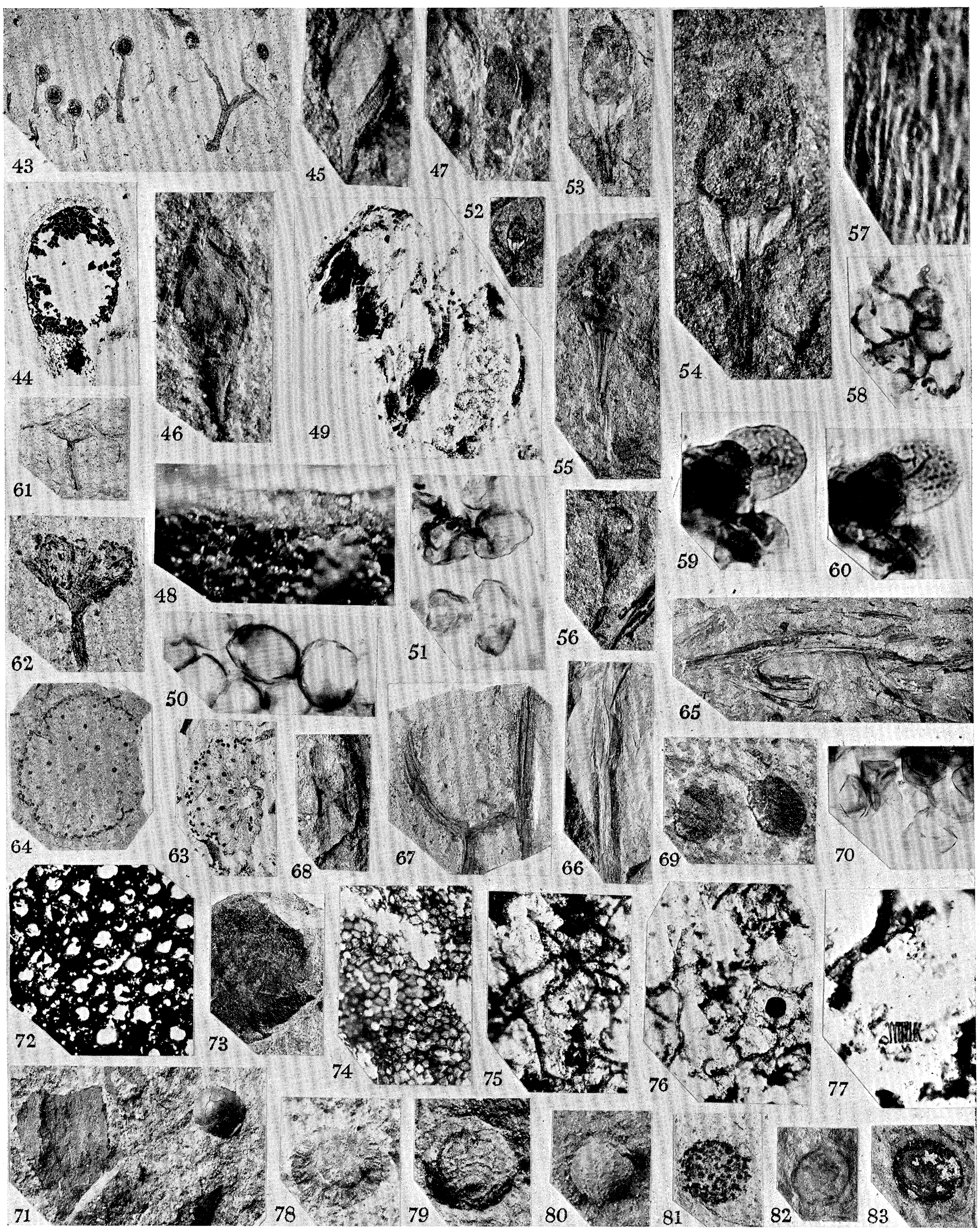
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Plate 11

Cooksonia sp., figures 43–51

Figure 43. Group of sporangia, borne terminally on short lengths of axis, one of which is dichotomously branched. $\frac{9}{10}$ Nat. size. (V. 26461.)
Figure 44. Sporangium, preserved like those in figure 43 as a thin flattened incrustation, removed on a film-transfer; it shows the stalk, remains of the thin black layer of the central region, and the surrounding zone. ×9. (V. 26462.)
Figure 45. Sporangium from a specimen in which the structure was partially preserved in the solid; spores were visible through the break in the sporangial wall to the right, below. ×9. (V. 26706.)
Figure 46. Another sporangium from the same specimen; it showed the cellular structure of the sporangial wall and stalk. ×9. (V. 26706.)
Figure 47. Sporangium broken across and showing the dark mass of spores within the thick sporangial wall; the crushed sporangium to the left of this one is slightly out of focus but also showed the thick wall in section. ×9. (V. 26706.)
Figure 48. Portion of the sporangium on the right of the preceding figure showing, by reflected light, the thick sporangial wall and the dark mass of spores within. ×90. (V. 26706.)
Figure 49. Film-pull of the counterpart of the specimen in figure 47 showing (on the right) the sporangium full of coherent spores and (on the left) portions of the wall of the broken sporangium that also contained spores. ×31·5. (V. 26706*a*.)
Figure 50. Spores from the right-hand sporangium in figure 49. ×360. (V. 26706*a*.)
Figure 51. Spores from within the left-hand sporangium in figure 49. ×360. (V. 26706*a*.)

Sporogonites exuberans, figures 52–60

Figure 52. Oval body terminal on a short length of stalk. $\frac{9}{10}$ Nat. size. (V. 26535.)
Figure 53. Same specimen. ×2·7. (V. 26535.)
Figure 54. Same specimen. This and the preceding figures show the distinction of the basal and fertile regions of the terminal structure, the ridges on the basal region and the rounded summit. ×4·95. (V. 26535.)
Figure 55. Another specimen showing a fairly long stalk, the basal region and an incomplete fertile region that contained spores. ×2·7. (V. 26537.) Cf. figure 89.
Figure 56. A third specimen showing less distinctive detail and smaller than the two preceding specimens. ×2·7. (V. 26536.)
Figure 57. Portion of the epidermis near the junction of stalk and basal region of the specimen in figure 55 showing, by reflected light, the outlines of the elongated epidermal cells and a stoma. ×90. (V. 26537.)
Figure 58. Group of spores from the fertile terminal region of the specimen in figure 55. ×360. (V. 26537*b*.)
Figure 59. Well-preserved spore in a small group from the same region at a fairly low focus showing the wall in optical section and an appearance of a reticulate surface pattern. ×900. (V. 26537*b*.)
Figure 60. Same spore as in the preceding figure at a relatively higher focus showing the dotted appearance due to the summits of the papillae outlined by the 'reticulum' in figure 59. ×900. (V. 26537*b*.)

Sciadophyton steinmanni, figures 61–64

Figure 61. Stalked specimen on the rock. $\frac{9}{10}$ Nat. size. (V. 26546.) Cf. figure 90.
Figure 62. Stalked disk showing the subtriangular form when laterally compressed, the radiating striation, the irregular margin and the dark spots. ×2·25. (V. 26543.)
Figure 63. Incomplete isolated disk giving a clear view of the spots and indented margin and an indication of radial striation. ×2·25. (V. 26544.)
Figure 64. Isolated disk showing the circular outline, the distribution of the spots and an indication of the central point of attachment of the stalk. ×2·25. (V. 26545.)

Taeniocrada sp., figures 65, 66

FIGURE 65. Linear flattened axis showing branching. $\frac{9}{10}$ Nat. size. (V. 26707.)
FIGURE 66. Linear flattened axis showing the narrow central strand. $\frac{9}{10}$ Nat. size. (V. 26708.)

Incertae sedis, figures 67–70

FIGURE 67. Axis showing H-shaped branching. $\frac{9}{10}$ Nat. size. (V. 26501.)
FIGURE 68. Another example of H-shaped branching in a narrower axis from the Deri. $\frac{9}{10}$ Nat. size. (V. 26712.)
FIGURE 69. Two flattened incrustations of spore-masses, possibly connected by their obscurely preserved slender stalks. ×3·6. (V. 26709.)
FIGURE 70. Edge of one of these spore-masses after maceration, showing the spores. ×180. (V. 26709*a*.)

Prototaxites sp., figures 71, 72

FIGURE 71. Piece of rock from Talybont showing a fairly large fragment of *Prototaxites* and a specimen of *Pachytheca*. ×2·25. (V. 26555.)
FIGURE 72. Portion of a microtome section of a fragment similar to that in the preceding figure but from Llanover, showing the wide and narrow tubes in transverse section. ×225. (V. 26550*b*.)

Nematothallus sp., figures 73–77

FIGURE 73. Black patch of *Nematothallus* on rock from Brecon Beacons Quarry. $\frac{9}{10}$ Nat. size. (Lang Coll., No. 257A.)
FIGURE 74. Portion of a piece of cuticle with 'cellular' pattern removed from the rock at Llanover as a film-transfer. ×90. (V. 26710.)
FIGURE 75. Portion of a transfer of the black patch in figure 73 showing the associated-tube construction. ×90. (Lang Coll., No. 1156.)
FIGURE 76. Another portion, showing associated-tube structure and a spore. ×90. (Lang Coll., No. 1157.)
FIGURE 77. Another region, showing portions of two tubes and a short length of a third that has annular thickening. ×360. (Lang Coll., No. 1156.)

Pachytheca sp., figure 78 (cf. figure 71)

FIGURE 78. Split specimen of *Pachytheca* from Talybont, showing the medulla surrounded by the cortex with its radiating tubes. ×4·95. (V. 26557.)

Spherical or circular bodies; *incertae sedis*, figures 79–83

FIGURE 79. External cast of a spherical tuberculated body with a single much larger tubercle. (The lighting is reversed so that the specimen appears convex.) ×3·6. (V. 26566.)
FIGURE 80. Spherical body with small tubercles. ×3·6. (V. 26567.)
FIGURE 81. Circular body with projecting tubercles. ×3·6. (V. 26569.)
FIGURE 82. Smooth circular dimpled body. ×1·8. (V. 26711.)
FIGURE 83. Smooth circular body with a surrounding dark zone. ×1·8. (V. 26563.)

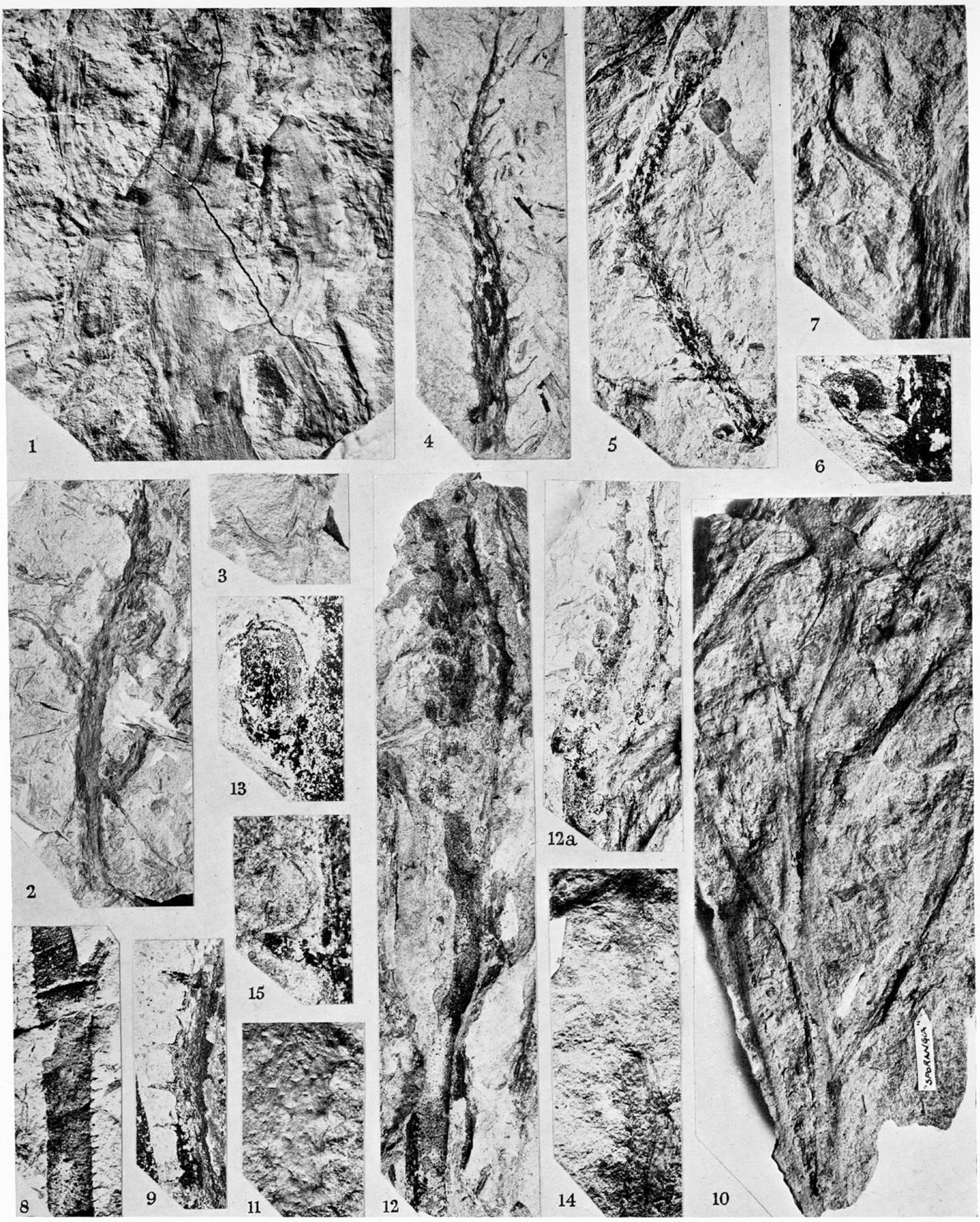

PLATE 9

Drepanophycus spinaeformis, figures 1–7

FIGURE 1. Impression of wide stem bearing two branches, each of which gives off a downwardly directed limb. $\frac{9}{10}$ Nat. size. (V. 26520.)

FIGURE 2. Similar stem bearing a number of upturned branches from all of which one or two downwardly directed branches arise at the bend. × 0·45. (V. 26523.)

FIGURE 3. Spine-like leaf from a wide stem seen in profile. $\frac{9}{10}$ Nat. size. (V. 26530.)

FIGURE 4. Narrow stem with numerous slender but broad-based leaves. $\frac{9}{10}$ Nat. size. (V. 26521.)

FIGURE 5. Slender fertile shoot with closely placed leaves and a number of sporangia. $\frac{9}{10}$ Nat. size. (V. 26522.)

FIGURE 6. Attached fertile leaf with a sporangium from near the bottom of the preceding specimen. × 2·7. (V. 26522.)

FIGURE 7. Two attached leaves from another fertile shoot showing the impressions on the stone that indicate the two sporangia. × 2·7. (V. 26524.)

Cf. *Psilophyton princeps*, figures 8–15

FIGURE 8. Typical piece of stem, showing spines along the margins, spine insertions on the surface and a lateral branch. $\frac{9}{10}$ Nat. size. (V. 26505.)

FIGURE 9. Spines seen in profile on the edge of another stem. × 3·6. (V. 26506.)

FIGURE 10. Sympodial branch system bearing spines and on one branch a few sporangia. $\frac{9}{10}$ Nat. size. (V. 26508.) Cf. figure 84.

FIGURE 11. Impression of another stem of this fertile branch system showing spines projecting from the margin and spine insertions. × 3·6. (V. 26508*a*.)

FIGURE 12. Branch system, the two ultimate divisions of which bear sporangia. Further description in text, p. 138. $\frac{9}{10}$ Nat. size. (V. 26507.)

FIGURE 12*a*. The two ultimate divisions photographed under xylol. $\frac{9}{10}$ Nat. size.

FIGURE 13. One of the sporangia in the preceding specimen. × 3·6. (V. 26507.)

FIGURE 14. Piece of stem from the same block as figure 10 which shows spines and on the left-hand side a sporangium. × 1·8. (V. 26508*b*.)

FIGURE 15. A sporangium borne on the continuation of the piece of stem shown in figure 14. × 4·95. (V. 26508*b*.)

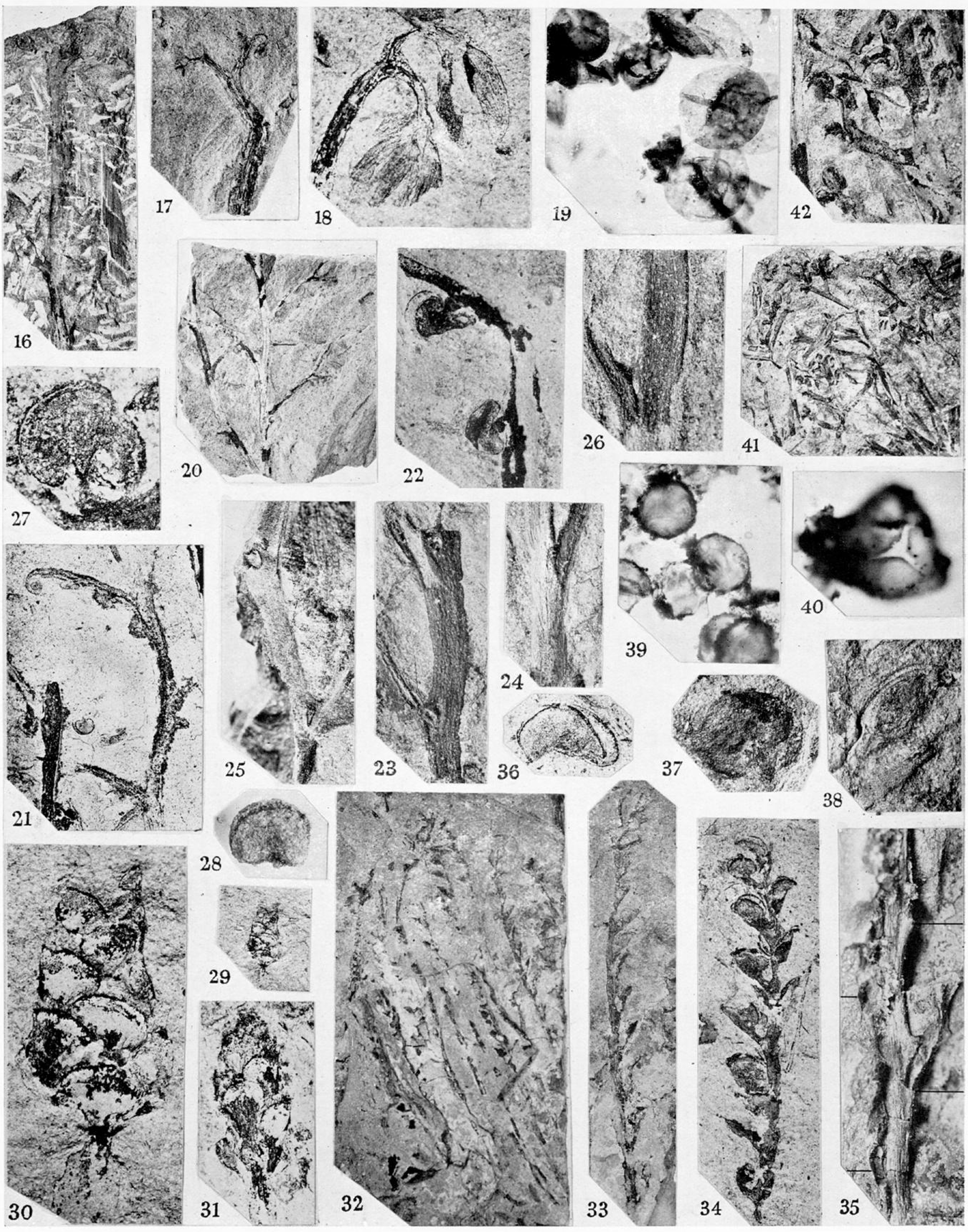

PLATE 10

Dawsonites arcuatus, figures 16–19

FIGURE 16. Piece of main axis with the base of a lateral branch on the left and, just below the top end, another lateral branch which subdivides and bears pendent sporangia. $\frac{9}{10}$ Nat. size. (V. 26495.) Cf. figure 85.

FIGURE 17. Portion of main axis from which a lateral branch arises, subdivides and bears a few sporangia on the ultimate divisions. $\frac{9}{10}$ Nat. size. (V. 26492.)

FIGURE 18. Branch system, probably a lateral branch, subdividing and bearing a number of terminal, pendent, fusiform sporangia. ×4·95. (V. 26493.)

FIGURE 19. Group of spores from within a sporangium removed on a film-transfer. ×180. (V. 26494*a*.)

Gosslingia breconensis, figures 20–28

FIGURE 20. An isolated and fairly extensive portion of a branch system bearing a number of sporangia. $\frac{9}{10}$ Nat. size. (V. 26483.) Cf. figure 86.

FIGURE 21. The branch system on the right shows the sympodial branching, a circinate tip and the position of the sporangia. ×1·8. (V. 26477.)

FIGURE 22. Portion of branch system showing the form and insertion of two sporangia and the marginal line of dehiscence between the thickened rims of the valves. ×4·5. (V. 26479.)

FIGURE 23. Incrustation of solid flattened axis showing the fractured end of a projecting axillary structure at the lower branching on the left and the base of another at the branching above. ×2·7. (V. 26478.)

FIGURE 24. The counterpart of a similar specimen showing the axillary structure as an oval plug of organic material. ×2·7. (V. 26485.)

FIGURE 25. Impression of another axis showing axillary bodies in relation to two branchings. ×2·7. (V. 26480.)

FIGURE 26. Incrustation of axis showing small tubercles on the surface. ×3·6. (V. 26485.)

FIGURE 27. Thin incrustation of an attached sporangium showing the reniform shape and the line of dehiscence. ×9. (V. 26704.)

FIGURE 28. Internal mould of a sporangium in fine mudstone showing the reniform shape. ×9. (V. 26481.)

Zosterophyllum cf. *australianum*, figures 29–31

FIGURE 29. Compact spike of radially arranged sporangia preserved in low relief. $\frac{9}{10}$ Nat. size. (V. 26471.)

FIGURE 30. The same spike enlarged to show the three vertical rows of sporangia and the curved distal margins of these. ×3·6. (V. 26471.)

FIGURE 31. Small spike showing similar characters. ×3·6. (V. 26472.)

Zosterophyllum llanoveranum n.sp., figures 32–40

FIGURE 32. Portion of tuft-like group of leafless axes, most of which bear sporangia in their distal regions. ×0·45. (V. 26515*a*; part of holotype.) Cf. figure 88.

FIGURE 33. A long spike from the preceding specimen showing the short-stalked sporangia along one side of the axis. $\frac{9}{10}$ Nat. size. (V. 26515*a*; part of holotype.)

FIGURE 34. Spike showing the sporangia in two alternating rows; most are viewed laterally and appear P-shaped and some show the line of dehiscence. ×1·8. (V. 26515*d*; part of holotype.)

FIGURE 35. Axis of a spike preserved in the solid and showing the bases of the stalks of the sporangia, arising alternately. ×3·6. (V. 26516*a*.)

FIGURE 36. Isolated sporangium showing the reniform shape, the curved distal margin and the thickened rims of the valves with the open line of dehiscence between them. ×3·6. (V. 26517*b*.)

FIGURE 37. Isolated sporangium in full face view from the abaxial side showing the rounded outline and part of the stalk. ×3·6. (V. 26517*b*.)

FIGURE 38. Sporangium, preserved in the solid, seen from the side and showing the two thickened rims of the valves still joined at the line of dehiscence. ×3·6. (V. 26516*c*.)

FIGURE 39. Group of spores removed from a sporangium. ×180. (V. 26515*f*.)

FIGURE 40. Single spore from the same preparation showing the triradiate split. ×360. (V. 26515*f*.)

Zosterophyllum sp., figures 41, 42

FIGURE 41. Thin black incrustations of branched axes and short terminal spikes of sporangia exposed on surface of a piece of rock. $\frac{9}{10}$ Nat. size. (V. 26705.)

FIGURE 42. Portion of specimen in figure 41 showing the attachment of shortly stalked reniform sporangia on the two sides of the dorsiventral spike. ×2·7. (V. 26705.)

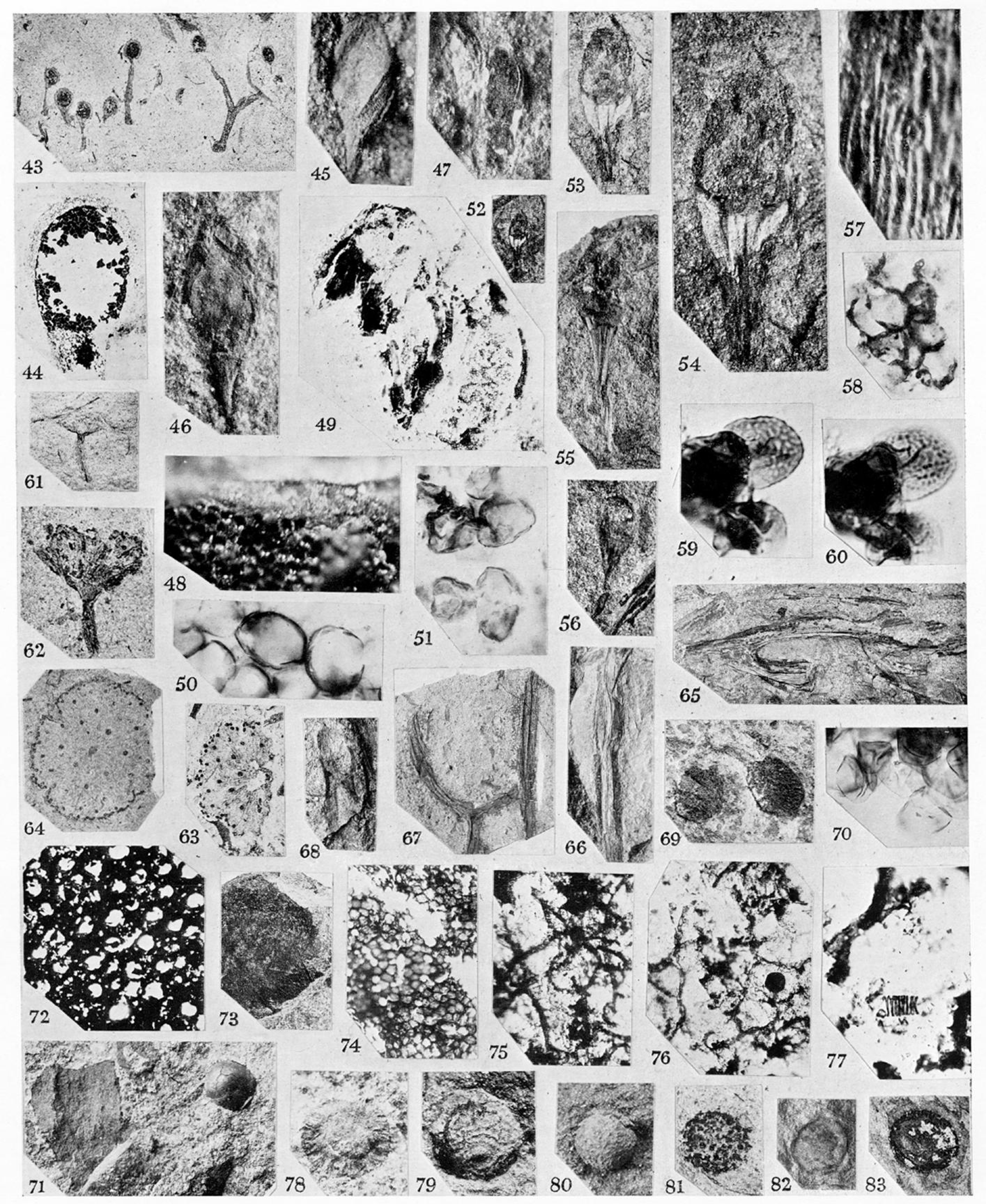

PLATE 11

Cooksonia sp., figures 43–51

FIGURE 43. Group of sporangia, borne terminally on short lengths of axis, one of which is dichotomously branched. $\frac{9}{10}$ Nat. size. (V. 26461.)
FIGURE 44. Sporangium, preserved like those in figure 43 as a thin flattened incrustation, removed on a film-transfer; it shows the stalk, remains of the thin black layer of the central region, and the surrounding zone. ×9. (V. 26462.)
FIGURE 45. Sporangium from a specimen in which the structure was partially preserved in the solid; spores were visible through the break in the sporangial wall to the right, below. ×9. (V. 26706.)
FIGURE 46. Another sporangium from the same specimen; it showed the cellular structure of the sporangial wall and stalk. ×9. (V. 26706.)
FIGURE 47. Sporangium broken across and showing the dark mass of spores within the thick sporangial wall; the crushed sporangium to the left of this one is slightly out of focus but also showed the thick wall in section. ×9. (V. 26706.)
FIGURE 48. Portion of the sporangium on the right of the preceding figure showing, by reflected light, the thick sporangial wall and the dark mass of spores within. ×90. (V. 26706.)
FIGURE 49. Film-pull of the counterpart of the specimen in figure 47 showing (on the right) the sporangium full of coherent spores and (on the left) portions of the wall of the broken sporangium that also contained spores. ×31·5. (V. 26706*a*.)
FIGURE 50. Spores from the right-hand sporangium in figure 49. ×360. (V. 26706*a*.)
FIGURE 51. Spores from within the left-hand sporangium in figure 49. ×360. (V. 26706*a*.)

Sporogonites exuberans, figures 52–60

FIGURE 52. Oval body terminal on a short length of stalk. $\frac{9}{10}$ Nat. size. (V. 26535.)
FIGURE 53. Same specimen. ×2·7. (V. 26535.)
FIGURE 54. Same specimen. This and the preceding figures show the distinction of the basal and fertile regions of the terminal structure, the ridges on the basal region and the rounded summit. ×4·95. (V. 26535.)
FIGURE 55. Another specimen showing a fairly long stalk, the basal region and an incomplete fertile region that contained spores. ×2·7. (V. 26537.) Cf. figure 89.
FIGURE 56. A third specimen showing less distinctive detail and smaller than the two preceding specimens. ×2·7. (V. 26536.)
FIGURE 57. Portion of the epidermis near the junction of stalk and basal region of the specimen in figure 55 showing, by reflected light, the outlines of the elongated epidermal cells and a stoma. ×90. (V. 26537.)
FIGURE 58. Group of spores from the fertile terminal region of the specimen in figure 55. ×360. (V. 26537*b*.)
FIGURE 59. Well-preserved spore in a small group from the same region at a fairly low focus showing the wall in optical section and an appearance of a reticulate surface pattern. ×900. (V. 26537*b*.)
FIGURE 60. Same spore as in the preceding figure at a relatively higher focus showing the dotted appearance due to the summits of the papillae outlined by the 'reticulum' in figure 59. ×900. (V. 26537*b*.)

Sciadophyton steinmanni, figures 61–64

FIGURE 61. Stalked specimen on the rock. $\frac{9}{10}$ Nat. size. (V. 26546.) Cf. figure 90.
FIGURE 62. Stalked disk showing the subtriangular form when laterally compressed, the radiating striation, the irregular margin and the dark spots. ×2·25. (V. 26543.)
FIGURE 63. Incomplete isolated disk giving a clear view of the spots and indented margin and an indication of radial striation. ×2·25. (V. 26544.)
FIGURE 64. Isolated disk showing the circular outline, the distribution of the spots and an indication of the central point of attachment of the stalk. ×2·25. (V. 26545.)

Taeniocrada sp., figures 65, 66

FIGURE 65. Linear flattened axis showing branching. $\frac{9}{10}$ Nat. size. (V. 26707.)
FIGURE 66. Linear flattened axis showing the narrow central strand. $\frac{9}{10}$ Nat. size. (V. 26708.)

Incertae sedis, figures 67–70

FIGURE 67. Axis showing H-shaped branching. $\frac{9}{10}$ Nat. size. (V. 26501.)
FIGURE 68. Another example of H-shaped branching in a narrower axis from the Deri. $\frac{9}{10}$ Nat. size. (V. 26712.)
FIGURE 69. Two flattened incrustations of spore-masses, possibly connected by their obscurely preserved slender stalks. ×3·6. (V. 26709.)
FIGURE 70. Edge of one of these spore-masses after maceration, showing the spores. ×180. (V. 26709*a*.)

Prototaxites sp., figures 71, 72

FIGURE 71. Piece of rock from Talybont showing a fairly large fragment of *Prototaxites* and a specimen of *Pachytheca*. ×2·25. (V. 26555.)
FIGURE 72. Portion of a microtome section of a fragment similar to that in the preceding figure but from Llanover, showing the wide and narrow tubes in transverse section. ×225. (V. 26550*b*.)

Nematothallus sp., figures 73–77

FIGURE 73. Black patch of *Nematothallus* on rock from Brecon Beacons Quarry. $\frac{9}{10}$ Nat. size. (Lang Coll., No. 257A.)
FIGURE 74. Portion of a piece of cuticle with 'cellular' pattern removed from the rock at Llanover as a film-transfer. ×90. (V. 26710.)
FIGURE 75. Portion of a transfer of the black patch in figure 73 showing the associated-tube construction. ×90. (Lang Coll., No. 1156.)
FIGURE 76. Another portion, showing associated-tube structure and a spore. ×90. (Lang Coll., No. 1157.)
FIGURE 77. Another region, showing portions of two tubes and a short length of a third that has annular thickening. ×360. (Lang Coll., No. 1156.)

Pachytheca sp., figure 78 (cf. figure 71)

FIGURE 78. Split specimen of *Pachytheca* from Talybont, showing the medulla surrounded by the cortex with its radiating tubes. ×4·95. (V. 26557.)

Spherical or circular bodies; *incertae sedis*, figures 79–83

FIGURE 79. External cast of a spherical tuberculated body with a single much larger tubercle. (The lighting is reversed so that the specimen appears convex.) ×3·6. (V. 26566.)
FIGURE 80. Spherical body with small tubercles. ×3·6. (V. 26567.)
FIGURE 81. Circular body with projecting tubercles. ×3·6. (V. 26569.)
FIGURE 82. Smooth circular dimpled body. ×1·8. (V. 26711.)
FIGURE 83. Smooth circular body with a surrounding dark zone. ×1·8. (V. 26563.)