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On the Spines, Sporangia, and Spores of Psilophyton princeps, Dawson, Shown in Specimens from Gaspe

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VIII. *On the Spines, Sporangia, and Spores of* Psilophyton princeps, *Dawson, shown in Specimens from Gaspé.*

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[PLATES 27, 28.]

Introduction.

Psilophyton princeps, though still incompletely known, is one of the most important Early Devonian plants, both on account of its morphology and of the place it occupies in the history of investigation of Pre-carboniferous vegetation. It was originally distinguished and described by DAWSON from specimens collected in the Gaspé peninsula, Canada. As shown in the restoration, published in the 'Geological History of Plants' (DAWSON, 1882), he regarded the plant as consisting of horizontally growing rhizomes, from which sprang erect branch-systems; the branching was dichotomous and the fine distal ramifications terminated in large ovoid sporangia.

From the description (DAWSON, 1871) it is clear that the lower portions of the subaerial branch-systems were markedly spiny, while the spines, though present, became less numerous and more distant in the distal, fertile regions. The distribution of the spines according to DAWSON is not shown in his restoration; it is well illustrated in a modification of DAWSON's restoration by PIA (1926, fig. 109).

Although the original description dates from 1859 the various parts shown in the reconstruction were most clearly described and illustrated by DAWSON in 1871, from abundant material collected in the preceding year. There are figures of rhizomes; of the spiny, branched, aerial stems; and of the more slender, relatively smooth axes, bearing the sporangia on their fine subdivisions. The figures do not, however, provide evidence of the connection of these various parts in one plant, and no specimens are known demonstrating this. The specimens described by DAWSON as the rhizomes of *Psilophyton princeps* are generally regarded as unsatisfactory and, as I have nothing to add concerning them, may be left out of consideration here. Critical discussion has centred on the justification of regarding as parts of the subaerial shoots of one plant the stems bearing numerous prominent spines and the relatively smooth axes which bore the sporangia. It is to be noted that from his earliest descriptions DAWSON described the stems of *Psilophyton princeps* as bearing spines, though he emphasises the marked development of the spines on the specimens collected in 1870, which he distinguished as var. *ornatum*. But he not only regarded these spiny stems as the barren or vegetative shoots of the plant which bore the fertile branch-systems, but he explicitly refers to the presence of spines on the axes which bore the sporangia. This point will be dealt with fully later.

The question as to whether the spiny shoots and the fertile axes form parts of one plant, has been discussed by SOLMS-LAUBACH (1895), WHITE (SMITH and WHITE, 1905), and HALLE (1916). They also consider the question as to the nature of the remains on which DAWSON'S original description of the species is based. It is unnecessary to enter into these discussions fully here, and reference may especially be made to HALLE'S treatment of the subject. In agreement with WHITE and SOLMS-LAUBACH, he decides that the only practicable course to follow is the rather informal one of basing our conception of *Psilophyton princeps* (though the species was first described by DAWSON in 1859) on the specimens figured and described in 1871. HALLE regards the spiny stems "figured by DAWSON in 1871 under the name of var. *ornatum* as typical representatives of *Psilophyton princeps*." Under this name he would retain the spiny stems only, and he separates the sporangia and the axes bearing them as *Dawsonites arcuatus*. He does this not only because continuity of the two types of remains is unproved, but partly because he regarded the fertile axes as devoid of spines. "None of our specimens of *Psilophyton princeps* show the characteristic striation seen in the main branches of *Dawsonites*, and not even the thickest of the latter have any spines or spine-scars."

In this separation of the two types of remains, which DAWSON associated together, HALLE differs from WHITE. The latter investigator (although he separated certain spineless axes as the Campbeltown type of plant) keeps the fertile axes and sporangia under *Psilophyton princeps*. "The fragments of fertile pinnæ from Gaspé lent me by Professor PENHALLOW, though obscure, seem to correspond to DAWSON'S fig. 102, and are distinctly punctate and thus referable to the typical species." HALLE'S comment on this, in limiting the name *Psilophyton princeps* to the markedly spiny stems, is that "not even this punctation can be considered as a proof of specific identity."

Though DAWSON'S figures of the longitudinally grooved or striate fertile axes do not show spines, it is quite clear from his descriptions that they were usually present. In the diagnosis of the species (DAWSON, 1871) he states "Leaves rudimentary, or short, rigid and pointed; in barren stems, numerous and spirally arranged; in fertile stems and branchlets scattered or absent; in decorticated specimens represented by minute punctate scars." And in the general description he speaks of the spines on the fertile stems as becoming "hard, spinose and prominent." It will be seen below that an examination of specimens confirms DAWSON'S description.

In whatever way the question may be determined, as to whether or not the markedly spiny stems and the longitudinally grooved, relatively spineless stems that bear the sporangia form parts of the one plant, it is desirable to ascertain as many details as possible regarding both types of remains. Fortunately they are definitely characterised and recognisable. In the case of *Psilophyton princeps*, DAWSON, there are no particular type specimens to which reference can be made. But specimens from the original locality, named and distributed by the author of the species and agreeing with his published figures and descriptions can for all practical purposes be treated as type specimens. Such specimens fortunately exist in various collections in this country, and this work is based on some of them.

I had the advantage a number of years ago of examining some specimens from Gaspé sent to the late Dr. Kidston by Dawson and now in the Kidston Collection at the Geological Survey Museum. A specimen of the fertile region in the Manchester University Museum yielded some definite information as to the sporangia and the axes bearing them. To confirm and extend this information the specimens of Gaspé rock, bearing fertile axes and sporangia and labelled by Dawson "*Psilophyton princeps* (fructification)" that are in the British Museum Collection were entrusted to me for examination. I have to express my indebtedness to the authorities of these three museums for permitting me to examine and describe the specimens.

The study of some of these specimens by modern methods has resulted in the addition of details to previous descriptions. It is of morphological interest to ascertain all that can be learnt about these well-defined types of early plant-remains. The facts ascertained also have their bearing on the question whether the two types of remains can be regarded as parts of the one plant. Further, by adding to the critical characteristics of the "type specimens" they will have value when apparently similar remains from other regions have to be specifically determined. It is an additional source of interest in these two types of remains that specimens agreeing in general features with them occur, also in association, in Lower Devonian rocks of regions widely distant from Gaspé. The present account will, however, be confined to observations made on specimens named and distributed by Dawson from the original locality in Canada.

The details to be described can be grouped naturally as concerning :—

(1) The spiny shoots and especially the spines.

(2) The relatively smooth, longitudinally grooved axes and especially the demonstration of Dawson's description of these as bearing spines.

(3) The sporangia, with regard to the structure of the wall and the demonstration of the contained spores.

Typical Spiny Stems ; Spines.

Observations were made on a small well-preserved specimen labelled by Dawson "*Psilophyton princeps*, var. *ornatum*." This is No. 107 in the Kidston Collection. A small piece of the rocky matrix from this was treated with hydrofluoric acid and yielded fragments of flattened axes similar to those on the specimen, and also isolated spines. The results obtained from this material are supplementary, not only to Dawson's description but to the recent work of Mr. W. N. Edwards (1924), who reinvestigated specimens of this type from Gaspé in the British Museum Collection.

The specimen in the Kidston Collection which is shown of natural size in fig. 1, is a piece of fine-grained grey rock on which are two axes, that appear to be diverging branches of a dichotomy. The axes are between 3 and 4 cm. long and 3 mm. in width. The black layer represents the outermost tissues only of the stem. The internal tissues have wholly disappeared, the thin peripheral layer being complete, but flattened into a double film. Numerous spines project almost at right angles from the edges and the places on the surface from which spines have been torn on splitting the rock are indicated by clear spots. On the lower side the spines doubtless extend from the surface into the matrix.

As regards the width of the axes, this specimen agrees with those of medium size figured by DAWSON (1871), and also corresponds to the Gaspé specimens re-figured by EDWARDS. The carbonised layer is exceptionally complete. DAWSON's figures of such stems show the general external appearance in branched specimens of considerable size. An important result of EDWARDS's reinvestigation was the demonstration of the shape of the epidermal cells and of the stomata present in the epidermis. As regards these two points I have, indeed, nothing to add to his description. Though a number of pieces of macerated cuticle were obtained, the outlines of the epidermal cells were often indistinct and sometimes wholly lost. But occasional areas were met with where the cell-walls appeared clear and well preserved. These favourable areas showed the cells as described and figured by EDWARDS, with the oval or linear mark in the outer wall of each, and also occasional clear stomata. One example of the latter is photographed in fig. 2 and may be compared with the stoma in text-fig. 2 of EDWARDS's paper, which shows the pore closed. The dark thickened ridges along the outer walls of the guard cells and on both sides of the pore are evident. I have not observed anything to lead me to doubt that these are the guard-cells or to entertain the possible alternative view mentioned by EDWARDS that they are subsidiary cells. While thus confirming EDWARDS's account of the epidermis and stomata I have been unable to find any support for his tentative suggestion that the epidermis bore scattered hairs in addition to the spines.

It is with regard to the spines that additional information has been obtained. Our previous knowledge is from DAWSON's description supplemented by EDWARDS. DAWSON's figures show the spines as they appear on the rock. They are represented as pointed structures narrowing from a vertically extended basal region. As seen attached at the margins of the flattened stems they curve upwards, project at right angles, or curve downwards. While the figures give a good idea of the distribution and general appearance of the spines, they afford no information as to structural details.*

The work of EDWARDS on macerated pieces of epidermis demonstrated the vertical extension and the vertically flattened condition of the basal region of attachment of the spine. It further showed the change to more elongated cells on passing from the

* One figure (DAWSON, 1871, fig. 129A) that is described as showing cellular structure and a stoma has rightly been dismissed on critical consideration by HALLE and EDWARDS.

general surface of the epidermis to the base of a spine (*loc. cit.*, text-fig. 3). The spines of which outline figures are given are both imperfect distally and show no structural details. Edwards mentions the appearance of longitudinal striation " while especially near the tip they were of a much darker colour than the epidermal cells, as if they were highly cuticularised."

A considerable number of spines, either isolated or attached to portions of the surface of the stem, were obtained for detailed study, and, having been set free by solution of the matrix, were in many cases uninjured and complete specimens. Like the dark surface layer of the stem, though sometimes not to such an extreme degree, they were opaque and showed little indication of structure until macerated. Such structure as persisted was best revealed by moderate maceration. On carrying the process further only the cuticle remains, but such extreme maceration did not usually render the epidermal cells more distinct.

The spines exhibited a considerable and possibly significant range in size. Many of the larger ones were about 2 mm. in length or a little longer ; the shortest were between $\frac{1}{3}$ and $\frac{1}{2}$ mm. Those shown in figs. 3–8 are all at the same magnification and give a fair idea of the range in size. A point of considerable interest is that spines of very different lengths may be found attached close together on the surface (*cf.* figs. 5–7). The flattened spines all taper from the vertically extended base. Some exhibit a distinct upward curvature, others are almost straight, while some are slightly bent backwards. The most important differences in shape concern the terminal region or tip and these will be described later.

Some of the spines showed a relatively coarse longitudinal striation that was clearly due to folds that had taken place during preservation ; in other cases the sides are free from such folds and exhibit the epidermal surface. In suitably macerated specimens (figs. 3, 4) a fine longitudinal striation is apparent, which depends on the shape of the epidermal cells. The pattern seems due mainly to the convexity of the outer walls of the cells. It is only exceptionally that the cell-walls can be seen in any completeness. Careful examination of a considerable number of spines has not led to the recognition of any stomata. In the light of the varying clearness with which stomata can be demonstrated in different fragments of the epidermis of the stem, it is, of course, possible that they may yet be found on the spines. But the negative results of my observations are in agreement with those of Edwards. Were stomata of regular occurrence on the spines they should be evident, at least occasionally ; considerable weight therefore attaches to these negative results. My observations further confirm those of Edwards in another point. No trace of a vascular strand has been found in any of the spines examined. Since, however, the vascular tissue was not apparently preserved in the stem of this specimen, the negative evidence on this point is of less weight than that regarding the absence of stomata. There is so far nothing known which suggests that the spines of *Psilophyton princeps* had a vascular supply.

The above observations not only confirm those of Edwards but support his inference that the spines were probably not specialised organs of assimilation and are, perhaps, best regarded as emergences. In this connection some positive information has been obtained regarding the tips of the spines, which is suggestive of their having been of glandular nature.

It has already been mentioned that differences in external form of the spines concern especially the distal end or tip. Sometimes the spine tapers to a fairly acute tip, though the sharpness of the point may partly depend on a contraction during preservation. Complete and intact spines often taper gradually to a rather blunt and more or less rounded tip (figs. 3, 4). In a considerable number of cases there is a dilation or widening at the tip, or just behind this, and sometimes this feature is very marked (fig. 9). Not only was this dilation evident when the spine, as mounted, is seen in side view or profile, but while the specimen was still movable in water it could be seen that this region was wider from side to side than the rest of the flattened spine. The dilation or thickening was thus in all directions.

All the features mentioned in the preceding paragraph can be seen in spines isolated by treatment with hydrofluoric acid but not macerated. Spines with imperfect tips, in which there is any reason to think accidental fracture has been concerned, have, of course, been excluded from consideration. Unmacerated spines are, however, met with which exhibit an open terminal region that is not due to accident and contrasts with the rest of the spine. The distal part of such a specimen is represented in fig. 10 ; while the main part of the spine was black and opaque the tip is a clear epidermal or cuticular tube open at the end. This, like the rest of the spine, was flattened and compressed in this specimen.

A similar appearance, the main part of the spine being dark and the terminal region an open and clear tube, is seen in both the examples in fig. 7 ; these, however, have been subjected to moderate maceration, so that the possible effects of this must be kept in mind. It is, however, probable that the spines in fig. 7 resembled the spine shown in fig. 10 before they were macerated. When spines which, to begin with, are throughout dark and opaque and have apparently intact tips are macerated, the dark material within the cuticle is oxidised and the specimen gradually clears. This clearing process can in many cases be carried to completion, the spine being then represented by a pale yellow cuticular layer showing more or less obscure indications of elongated epidermal cells. Not infrequently the terminal region remains of a dark colour longer than the rest of the spine (figs. 6, 8). This may be partly due to the epidermal cells of this region being different or altered, but in the most definite cases it is largely dependent on a mass of more resistant black material within the somewhat swollen tip. A good example is represented in fig. 8. This spine had been thoroughly macerated, so that the main portion is clear, but a very definite black mass has persisted within the tip. This was swollen in all directions ; when, after the photograph in fig. 8 was taken, slight pressure was applied with a clip, a system of cracks was produced in the black terminal mass. The enlarged photograph of the tip in fig. 11 was taken after this had happened.

When thoroughly macerated spines with black tips are transferred to alcohol, before clearing and mounting, the altered dark material in the tip may sometimes be further affected, and diffuse out into the liquid. This was the case for the spine the tip of which is shown in fig. 12. To begin with, this tip had looked something like fig. 9; it had remained during maceration dark like fig. 11. When carried into alcohol, however, the dark material escaped, leaving a well-defined cavity in the enlarged region just behind the actual tip. Traces of the outlines of the epidermal cells are visible in the layer bounding this cavity and forming the tip.

Such tips in which the disappearance of dark material follows on maceration must be considered along with unmacerated examples showing an empty open terminal region. As already pointed out, it is uncertain to what extent the evident open clear tips to the spines in fig. 7 are dependent on their having been macerated. What seems quite certain is that open tips of this kind are distinct from any appearances due to accidental fracture of spines. Comparison of complete tips with pointed or more or less rounded ends with those which have apparently opened has not revealed anything as to the mode of formation of the opening. The more pointed specimens suggest a simple separation of the elongated epidermal cells. The larger of the two spines in fig. 5, on the other hand, gave a suggestion of the separation of a discoid terminal cap; corresponding specimens, though looked for, have not, however, been found.

Several microtome series of transverse sections of spines, both macerated and unmacerated, were successfully cut for me by Mr. ASHBY.* The fully macerated specimens proved to be represented by the cuticle only which could be traced as a continuous film. Following the series, section by section, there was no apparent break in this. To the limited extent of the observations made, therefore, the sections confirmed the absence of stomata from the epidermis of the spine. In complete series of an unmacerated and of a partially macerated spine the cuticle could be traced following the ridges of the inner dark material, which were due to the convex epidermal cells in cross-section. The cellular structure was only very indistinctly defined. In the lower part of the spine the whole thickness could be thus accounted for. But in the terminal dilated region the sections showed that the spine was wider and almost isodiametric in transverse section. In this region, wherever the material within the cuticle showed any detail in the black mass, there were indications of a layer of epidermal cells and also of cellular structure in the small area within. The appearance was inconclusive, but was at least as suggestive of the tip having been sclerenchymatous as of its having been secretory.

The various appearances presented by the spines, and especially by their tips, which have been mentioned above are mostly represented in the photographs on Plate 27. The sections of spines have merely been described, as figures of them were not sufficiently instructive. There are, of course, limits, which are soon reached, in the detailed investigation of material preserved in this way and the interpretation of the results has to be

* I have to express my thanks to Mr. ASHBY for his assistance in this and other ways, and in the photographic illustration of this paper.

cautious and tentative. It seems clear that the tip of the spine differed from the main part in some way that affected its preservation. So far as the darker appearance of the tips of intact spines is concerned and the appearance of sections across this region, a possible explanation would be that the cell-walls here were thickened, the spine ending in a harder point. But the occurrence of spines with apparently naturally open tips and the appearance in other cases of a dark mass within a dilation of the tip appear more consistent with an alternative suggestion, viz., that the tip was glandular and normally liberated a secretion, perhaps produced by breaking down of cells. No certainty of interpretation is possible on the present evidence. But the specimens figured will afford those familiar with glandular emergences and with the leaves of microphyllous plants some grounds for considering these alternative explanations. The figures in any case demonstrate the peculiar appearances presented by the tips of these spines. These detailed characters can be used for comparative purposes, even if their functional interpretation remains doubtful.

Relatively Smooth, Longitudinally Grooved Axes.

The second type of axis included by DAWSON under *Psilophyton princeps* appears longitudinally grooved or striated. As already mentioned it is kept distinct from the spiny axes by HALLE, under the name *Dawsonites arcuatus* and regarded as destitute of spines. Though little new can be added regarding it there are points in DAWSON'S description, and in particular his statement that spines occur on such axes, which require to be re-established and demonstrated by photographic illustrations. DAWSON regarded this type of axis as coming from the upper fertile part of the plant, the lower vegetative region of which had the markedly spiny character described in the preceding section. He usually labelled specimens of this type, whether associated with sporangia or not, *Psilophyton princeps* without any varietal qualification.

Thus, for example, there is a specimen of this kind, without sporangia, in the Kidston Collection (No. 103), labelled "*Psilophyton princeps*, Erian, Dalhousie." A closely similar specimen (No. 112) from Gaspé, is simply labelled "Fragments of *Psilophyton*." This may be figured here (fig. 13), since it demonstrates the occurrence of a few spines standing out at right angles from the stem. A portion of this specimen is enlarged $5\frac{1}{2}$ diameters in fig. 14; this shows the shallow longitudinal ridging or grooving and a stout spine projecting from the right-hand side of the axis. The thin superficial carbonaceous layer has almost completely disappeared from the axis and spine. The tip of the latter is, however, black and is peculiarly blunt.

Similar specimens, labelled by DAWSON *Psilophyton princeps* and showing occasional spines, have been seen in other museum collections but need not be dealt with further here. It is more instructive to consider the same type of axis as found in association with the sporangia which it undoubtedly bore. Such fertile specimens were also regularly named by DAWSON *Psilophyton princeps*. They are consistently of the one type and there is no question as to their being the Gaspé specimens which HALLE separated under the name *Dawsonites arcuatus*. Specimens from DAWSON in the Kidston Collection, in the Manchester University Museum and in the British Museum Collection have been examined.

In the Kidston Collection there are two small but good specimens (Nos. 105, 106), which show sporangia clearly and have associated with them small pieces of the axis. Short as the portions of the axis are, they not only exhibit the characteristic grooving but in both specimens bear one or two spines.

The specimen in the Manchester Museum Collection (No. LL180) shows only a few pieces of axis along with sporangia. One small piece is of interest, since it is not, as usual, flattened, but is represented by an uncompressed cast with traces of the carbonised superficial tissues ; it is enlarged $5\frac{1}{2}$ times in fig. 15. This shows the ridging or grooving, both on the cast and on the impression on the surface of the rock. The appearance of this and other specimens suggests that the grooving might be an expression of their delicacy and due to contraction of the soft tissues before fossilisation. This particular portion of axis further has a single spine projecting from the right-hand side. The tip of the spine has the same blunt appearance as that in the adjacent fig. 14.

The set of specimens of the fructification of *Psilophyton princeps*, as they are labelled by DAWSON, that are in the British Museum Collection afford a full demonstration of this type of axis and the presence of more or less numerous spines upon it. The thin layer of carbonised superficial tissues has for the most part disappeared from the axes, which exist in the form of flattened casts or impressions (figs. 16–19). As is shown by the two specimens represented of natural size in figs. 15, 16, the axes range in diameter from 5 mm. to 0·25 mm., the finest divisions bearing the terminal sporangia. The pieces of rock are crowded with these axes and sporangia, without any mixture of other remains. Spines occur on axes of medium size but are more numerous on the wider axes. The axes have the characteristic striated appearance due to the ridges and intervening grooves. There are some four or five grooves visible on the exposed surface of the wider axes ; they are less numerous on the narrower axes and apparently absent from the very slender ones.

Two pieces of axis, represented slightly magnified in figs. 18, 19, may be described, as demonstrating the features just referred to.

The surface of rock, enlarged two diameters in fig. 18, bears the impressions of some moderately small axes and of one broad piece of considerable length. These show the longitudinal striation clearly and should be considered in the light of the solid cast in fig. 15. The grooves in the impressions correspond to the ridges on the cast. They are more numerous on the broader axis ; five or six can be made out on the latter, while only two or three are indicated on the narrower impressions to the right. The broad piece of axis was selected for illustration because it shows the spines clearly. Some are seen in profile projecting from the edge of the axis into the rock ; one good example is near the upper end and on the right-hand side, while another is lower down on the left.

In addition to spines seen thus, the surface of the axis shows a number of small circular or somewhat elongated marks that often retain remains of the carbonaceous material. These are evidently the bases of spines extending down into the matrix. Their situation in the grooves of the impression indicates that they were attached on the ridges of the axis. The closeness of such marks of spines on the broad impression in fig. 18 shows that they were fairly numerous at places. They were not, however, nearly so crowded as on the typical spiny axes and their occurrence was correctly described by DAWSON as "sparsely scattered or absent." The appearance presented in surface view is evidently the punctate condition referred to by DAWSON and WHITE.

The specimen enlarged 5½ diameters in fig. 19 is a moderately narrow axis. It shows the grooving rather obscurely, but was selected on account of bearing two spines that are seen projecting from the left-hand edge. The vertical distance between these was less than 1 cm. The lower spine has a blunt end while the upper one appears pointed.

A number of spines have been examined in side view as they project from the margins of axes into the rock. Examples are represented in figs. 14, 15, 18 and 19. In the majority of cases they appear as if blunt or truncated at the end. In only a few instances, such as the upper spine in fig. 19, did they appear pointed. Even in this case it is difficult to be certain that the appearance provides conclusive evidence; it might result from the position in which a truncate spine is viewed. The truncate appearance is so frequent as to suggest that it is not to be accounted for by damage to pointed spines; it might be due to some such change of the tip as has been discussed in connection with the spines borne on the other type of stem.

The preservation of these axes is different from that of the spiny stem and no corresponding material that might yield isolated carbonised spines is available for study. Until such material is forthcoming it is impossible to make the detailed comparision of the spines on the two types of axes that is desirable. The carbonised layer on the surface of these casts or impressions was also insufficient for any detailed study, nor did it appear promising. Mr. EDWARDS records that he failed to obtain any satisfactory epidermal preparations from the axes bearing sporangia. The chief result of the re-examination of axes of this type has, therefore, been the confirmation of DAWSON's statement that they bore more or less numerous spines.

The Sporangia and Spores.

The large sporangia are borne on the ultimate ramifications of axes of the type described in the preceding section. No specimens showing such favourably isolated fertile branch-systems as those in DAWSON's figures (DAWSON, 1871, figs. 102, 103) have been seen. But not only are the grooved axes and the sporangia crowded together in the various hand-specimens available (*cf.* figs. 16, 17) but all gradations in size of axis are met with, down to the fine divisions which can be seen to branch and to end in sporangia. A slender branch bearing sporangia, from the specimen represented of natural size in fig. 17, is represented enlarged in fig. 20 (Plate 28). The sporangia are terminal on the fine divisions which are repeatedly dichotomous. The common appearance of the sporangia being in pairs result from this.

It has naturally been assumed from DAWSON'S description onwards that these structures were sporangia. He remarks that under the microscope they "show indications of cellular structure and appear to have been membranous in character" and further states that "no spores could be observed in any of the specimens, though in some the surface was marked by slight rounded prominences, possibly the impressions of the spores within." So far as I know there has been no further investigation. HALLE, however, in considering the similar specimens from Röragen along with the Gaspé fossil, makes the remark that "these structures have not been shown to contain spores, and it cannot be regarded as proved that they are sporangia. It is, however, probable that this is the case." Since the required proof is provided here the term sporangium will be used in the description without any reserve.

The sporangia exhibit a considerable range in size. The longest noted was 6·5 mm. and the widest 2 mm. But these are rather extreme measurements and most of the sporangia are 4–5 mm. long and 1–1·5 mm. wide. On the whole they tend to be obovoid, widening out from the slender stalk and having a rounded distal end, but in others the tip may be more pointed. DAWSON refers to indications of a longitudinal dehiscence but I have been unable to obtain critical evidence of this. As pointed out by several investigators, many of the sporangia are preserved in the round, the cavity being filled with a cast of fine mineral material, generally similar to that of the matrix.

Examination of the sporangia by reflected light confirmed DAWSON'S statements but did not provide clear evidence of their nature. Indications of cellular structure were sometimes evident, a striation that appeared to depend on the presence of elongated cells being suggestive of a sporangial wall. Nothing definite could be ascertained with regard to the presence of spores by this method.

In the light of the success which had attended attempts to demonstrate the presence of spores in the sporangia of *Zosterophyllum australianum* and *Z. myretonianum* (LANG and COOKSON, 1930) it seemed possible that evidence might be obtained, without injury to the specimens, by properly employing the method of cellulose film-pulls. The film-transfer method, though it might have given better results, was, of course, inapplicable since it involved destruction of the hand-specimen. Film-pulls were, therefore, made from an area on the back of the Manchester Museum specimen (LL180), at first without treatment with hydrofluoric acid and subsequently with this preliminary treatment of the surface. The results were satisfactory, the preparations affording information as to the wall of the sporangium and providing decisive evidence of their nature by the demonstration of spores remaining in the cavity. While, however, the great majority of the spores were of one type and evidently belonged to the sporangia, there were a few others on the film so much smaller as to be clearly distinct. To check these results a suitable group of sporangia on one small specimen in the British Museum Collection (v 21107) was similarly investigated, several film-pulls being made without any treatment with hydrofluoric acid. These revealed the same features in the construction of the wall and also the presence in numbers of the same type of spore as had been found in the sporangia of the Manchester Museum specimen. The confirmation was the more satisfactory in that no spores of other types were met with on the pulls from the second specimen. The results from the study of the two specimens can be dealt with together.

Since the sporangia on the back of the Manchester Museum specimen were isolated in the matrix and presented no definite external features there was no advantage in figuring them as they appeared on the surface of the rock. The group of sporangia thus studied on v 21107 is, however, shown in fig. 21, enlarged $5\frac{1}{2}$ diameters. The photograph was taken after pulls had been made but, since the surface had not been treated in any way, the appearance of the specimen was almost unaltered. The removal of thin surface layers on the films had defined the outline of the sporangial walls somewhat more sharply and made the sporangia look as if viewed in section. We had evidently to do with a group of sporangia terminating a fine dichotomous branch-system, though the slender axis is not preserved. There is a pair of closely associated sporangia on the right and another on the left. A third sporangium, which may perhaps belong to the group, lies to the right of the left-hand pair, while an isolated sporangium lies horizontally below the pair on the right-hand side of the figure.

The two sporangia on the right in fig. 21, and a portion of the adjacent isolated sporangium are seen, as they appear in a film-pull, in fig. 22. It must be borne in mind that they are reversed as compared with their position on the rock. A pair of sporangia from the Manchester Museum specimen are represented as they appear on a film-pull in fig. 23 at the same low magnification of 10 diameters.

The sporangia in fig 22 appear almost as if in longitudinal section. The outline is given by a broken black line, made up of fragments of the carbonised outer layer of the wall. Only at one or two places, as at the narrow upper end of the large sporangium, does this black layer extend more or less across the surface. The dark mass within the lower end of the lower sporangium is remains of the mineral contents or cast. But in the middle part of this sporangium, and extending over a considerable area in the upper sporangium, there are remains of a thin, translucent, brown layer, derived apparently from a persistent inner layer of the wall. The four or five darker spots on this in the upper sporangium are spores. The sporangia in fig. 23 show the same two layers of the wall, but the fragmented carbonised layer is not merely seen in section but extends partly or completely across the sporangium. Where it is absent or between its fragments there is a considerable representation of the inner, brown, translucent layer.

The portion of a pull of another sporangium more highly magnified in fig. 24 shows mainly the fragmented black outer layer, but where it is absent the brown layer is apparent. Fig. 25 shows some of the black outer layer but mostly traces of the brown layer; in relation to this is a single spore. A well-preserved and fairly extensive portion of the inner brown layer is shown in fig. 26.

As these figures show, the condition of the sporangial wall does not allow of much more being ascertained as to its structure than the distinction of the thick, black, outer layer and the thin, translucent layer. The black carbonised layer is usually cleft into irregularly shaped pieces and shows no structure. There is sometimes a suggestion of the division of cells, but this is never certain. When a pull shows linear cellular outlines, such as have been noted as sometimes visible in surface view by reflected light, it seems more probable that these are derived from the inner layer rather than from a special preservation of the carbonised layer. The inner, brown layer is a feature of all the preparations made. When first seen, the possibility that it might not belong to the wall, but be derived from a flattened mass of spores, was considered. But it was clear from the best examples that it was a thin coherent layer that could sometimes be traced around the concavity of a sporangium. Further, it seemed to have been evidently derived from elongated cells the longitudinal walls of which were sometimes distinct (fig. 26).

The film-pull method has thus yielded considerable insight into the construction of the sporangial wall. But it must be remembered that we are studying a wall that is altered and imperfectly preserved and also that the method (which involves the dragging of a thin film of the less rigid material from an irregular surface) has its limitations. It is perhaps remarkable that so much has been learnt.

In the two small areas of rock that have been investigated no case has been met with of a sporangium filled with the mass of spores it had originally contained. But within most of the sporangia on the film-pulls more or less numerous spores of a constant and uniform type remained. The mode of occurrence of these residual spores, and their agreement in the two distinct hand-specimens studied, left no doubt as to their being the spores belonging to these sporangia. This having been established, I did not feel justified in extending the investigation to other museum specimens, in the hope of obtaining a more striking or more easily illustrated preparation of a flattened sporangium full of spores.

The demonstration of spores in the sporangia is dependent on favourable spots in the film-pulls, where spores that lay against the wall at the periphery of the sporangial cavity have been detached from the mineral matter filling the latter. An example has been noted in the sporangium represented in fig. 25. Here the film-pull extending across the whole width of a sporangium has removed fragments of the black outer layer of the wall, portions of the thin translucent brown layer and a single spore. Another somewhat similar area is represented at a higher magnification in fig. 27. Portions of the outer carbonised layer of the wall are seen to either side. Within this the indistinct remains of the inner brown layer of the wall were represented mainly by the longitudinal walls of the cells. Against this, and in a central position in the figure, were some five spores, with flattened yellow cuticularised walls. The position and general outline of these can be seen in the photograph (fig. 27), though even in this favourable example photography renders imperfectly what can be readily observed under the microscope.

The difficulty of figuring is increased by the spores lying in slightly different planes. One spore of this group is shown at a higher magnification in fig. 28, the others being, of course, out of focus.

In some other cases photographic illustration of areas of the film, which to observation provided definite evidence of the presence of numerous spores in a sporangium, was impossible, owing to the spores being distributed through a fragment of the mineral matter forming the internal cast of the sporangium. For example, the lower of the pair of sporangia on the right in fig. 21 has an enormous number of spores distributed throughout the contained mass of mineral matter. In the pull of this sporangium that is figured—it is the upper sporangium in fig. 22—none of the mineral matter was removed from the specimen, but a few spores are present pressed against the brown inner layer of the wall on the left-hand side of the sporangium. The next pull that was made removed a small flake of the mineral contents in this position; and this was only partially dissolved by subsequent treatment of the film with hydrofluoric acid. Microscopic examination of the preparation (British Museum Collection, No. 21107 B) shows that in this area of matrix, measuring about 1 sq. mm., some 25 to 30 yellow spores can be distinguished. They were all of the type to be described below and it is evident that an enormous number must be present in this sporangium.

The spores in the specimens so far referred to were in the flattened condition which seems to be the usual state of preservation. Occasionally spores are met with that appear oval or rounded. Examples are shown in figs. 33–35. Fig. 33 shows a portion of the dark layer of the sporangial wall and within this, in contact with remains of the brown layer, a single uncompressed spore. In fig. 34 the solitary uncompressed spore, which is of rather small size, lies, along with a fragment of the brown layer, against portions of the black outer layer. In fig. 35 there is a group of some five rounded spores just within a portion of sporangial wall; three of the spores of various sizes are in focus.

All the examples of the spores in figs. 28–35 are photographed at the same magnification of 200 diameters. They show that there is a considerable range in size of the spores. In the flattened state many of the numerous spores that have been measured were 100 μ across. Others, even adjacent spores in the same sporangium, were considerably smaller being 75 μ or even 60 μ across. The few found in the unflattened condition mostly gave the lower measurements; their apparent size would have been somewhat increased by flattening.

The spore-membrane was evidently quite smooth, bearing no spines or other appendages. As usually preserved the greater part of the compressed double layer of wall has a clear yellow tint and may exhibit some irregular wrinkles. A constant feature is a triangular mark of relativly small size and of a deeper brown colour (*cf.* figs. 28–32). In favourable examples it can be seen that three small triangular surfaces were based on the three sides of the brown triangle. This area was apparently the rather small surface by which the spores had been in contact in the tetrad.

That this interpretation of the triangular area is correct seems to be demonstrated by one of the spores in the sporangium on the preparation v 21107 B, referred to above. This spore was, as usual, flattened but, since it lay at one edge of the small fragment of mineral contents, it was viewed obliquely. The three small brown surfaces were not only seen from the side but their projection was exaggerated by compression, so that they formed a beak-like elevation from the yellow disc representing the collapsed and flattened spore-wall. The beak-like region just referred to is photographed at a magnification of 400 diameters in fig. 36. The general outline of the spore, lying at a lower level, is not in focus.

It will be evident from the above account and the figures on Plate 28 that there is a type of spore that can be related with certainty to the sporangia originally described by DAWSON. It has been found within practically all the sporangia studied, both from the Manchester University Museum and from the British Museum specimen. In some sporangia these spores were present in such large numbers as to suggest that few or none had escaped. The spores have mostly been met with in a flattened condition, though occasional examples were rounded or oval. In size they ranged from 100 μ to 60 μ; the wall was smooth and there was a relatively small pyramidal apical region.

Concluding Remarks.

The main purpose of this paper is to make some additions to our knowledge of the remains from Gaspé which DAWSON included under the name *Psilophyton princeps*. The facts ascertained from the specimens available for study suggest the need of more detailed examination of other small-leaved Early Devonian plants. Any full discussion of the questions on which the new data bear would be premature until the corresponding features of these other remains have been ascertained. All that can be done at present is to comment briefly on the directions in which some of the observations recorded here seem to point.

The details as to the appendages borne on the markedly spiny stems from Gaspé are of interest for themselves and also provide characters that may be of use in comparative morphology. The observations made on the well-preserved spines have not only confirmed previous statements as to their being flattened in the vertical plane, but have added some structural details. No evidence is forthcoming that the appendages had a vascular supply, though the nature of the preservation does not justify a definite negative conclusion on this point. The fact that no stomata have been found, although the pattern of elongated epidermal cells was more or less evident, supports the view that stomata were absent from the spines. These negative observations are confirmatory of views that have been expressed by previous investigators (HALLE, 1916; EDWARDS, 1924) that these structures were not specialised organs of assimilation and should be regarded as "emergences" rather than "leaves."

Some other facts give further support to this view. One is the apparent irregularity of position of the spines, and especially the way in which examples of the most diverse sizes may be found attached close together on the surface of the stem. Another set of facts concerns the terminal region. It has been pointed out that there are features which render it possible, or even probable, that the tip of the spine was in some way of a glandular nature. If this were so, we should be dealing with an axis clothed with secretory emergences. The facts given in the body of the paper do not amount to a demonstration of this presumption, but they all appear consistent with it, and it is difficult otherwise to account for the occurrence of spines with open tubular tips, not due to accidental fracture. Whatever the ultimate decision as to the physiological nature of these structures may be, the objective features shown by the tips of the spines, such as dilation at or just behind the actual tip, presence of dark resistant material within the tip, opening of the tip, and the presence of a clear, empty, cuticular or epidermal tube in this region, are highly peculiar and characteristic. They afford definite points for comparison with other remains, where these are sufficiently known.

The question as to whether the two types of remains from Gaspé which HALLE separates as *Psilophyton princeps* and *Dawsonites arcuatus* were parts of one plant, as DAWSON believed, has been referred to in the introduction and need not be fully discussed. It should be pointed out, however, that the demonstration of the correctness of DAWSON's statement that the axes of the *Dawsonites* type bore more or less numerous spines lessens the contrast between the two types of axes. While HALLE's separation of the two types under different names is strictly justified, since the two have not been found in continuity, it may well be that the sparingly spiny, fertile axes formed the distal region of a branch-system that was of the markedly spiny type in its lower part.* This, as well as the further questions as to the relation of the aerial stems of the Gaspé plant to a rhizome and as to the general habit of the plant, must be left open until further evidence is available.

In utilising the additional features of the emergences of the spiny type of *Psilophyton princeps* for comparative purposes the first question of interest concerns the spines which have been shown to occur regularly, though more sparingly, on the type of axis that bore the sporangia. Unfortunately no material is available to allow of these latter spines being similarly and fully studied, and we are limited to observing their appearance in the hand-specimens by reflected light. It has been pointed out that, as thus seen, they usually show a peculiar blunt or truncated distal end. In the light of what is known of the spines on the other type of stem the question may be raised whether this may not indicate a natural incompleteness or opening of the tip. No solution of this problem is, however, possible at present.

The next extension of comparisons is naturally to those remains from other regions that, from their general characters in hand-specimens, have been referred with more or less confidence to *Psilophyton princeps* or to some closely related species. Here again in the case of such specimens from Norway and France the corresponding facts have not yet been ascertained and detailed comparison is therefore at present impossible. But

* This condition is realised in the remains named *Psilophyton Goldschmidti* (HALLE, 1916.)

so far as the appendages borne on some Scottish specimens of this kind are concerned I can state generally, from investigations that are in progress, that they agree in all main features with the Gaspé specimens described here. This particularly applies to the peculiarities of the terminal region of the spines. On the question of specific identity it will, of course, be necessary to take other characters into consideration. Some of the specimens may prove to be *Psilophyton princeps* and others not. The agreement as regards detailed features of the spines or emergences is, however, morphologically significant and an indication of close relationship. The frequent occurrence of spines with open tips also gives support to the suggestion that these peculiar emergences were of glandular nature.

Some of the spiny *Psilophyton*-like stems occur in close association with remains of the type of *Arthrostigma gracile* and specimens of intermediate character are met with. Various investigators have been led to raise the question whether *Psilophyton*-like shoots and typical *Arthrostigma* may not be the distal and main axes respectively of the same plant. It would evidently be of interest and of value for comparison to know to what extent the spines of *Arthrostigma* exhibit points of agreement in structural details with those of *Psilophyton princeps*. Here again the requisite details for *Arthrostigma* are not yet known. If, as seems not improbable, the spines of both should prove to be more of the nature of " emergences " than of " leaves " it would be readily conceivable that in the complete plant they should have been stouter and more distantly placed on the main axis and more crowded and slender on the finer branches. However this may be, it is a reasonable view on our present knowledge that in the remains classed as *Psilophyton* and *Arthrostigma* we are dealing with a natural morphological type of construction. This from its great antiquity is of special interest.

When the comparison is extended to other Early Devonian small-leaved plants points of difference become as marked as those of agreement. On the whole the small appendages clothing the stems of *Thursophyton* and *Asteroxylon* appear to be more like leaves than are the spines of *Psilophyton*. In so far, however, as they also show features comparable with the emergences of the latter plant, they suggest that, with further investigation, evidence may be forthcoming of a natural gradation between emergences and small simple leaves. Should this prove to be the case it would define by examples and perhaps help to solve historically one of the most fundamental problems in the morphology of the shoot ; that concerning the contrast of typically megaphyllous plants, such as the Ferns, and typically microphyllous plants, such as the Lycopods.

This question has been discussed by various morphologists both on general comparative grounds and in special connection with Early Devonian plants. It will not be entered into fully here. The present state of our knowledge regarding the small leaves of existing Vascular Cryptogams and of *Thursophyton* and *Asteroxylon* may, however, be referred to in order to indicate how the facts for *Psilophyton*, by adding to the rather limited sources of evidence, bear on the general problem.

The small, simple appendages of *Lycopodium*, to take this plant as an illustration of the

Lycopodiales for the present purpose, show the morphological and biological characters of leaves both in their construction and in their relation to the stem. The small leaf is here flattened and dorsiventral, provided with stomata and traversed by a single vascular strand, that is in continuity with the stele of the stem. The equally simple appendages of the *Psilotales* present their special problems, which need not be discussed here. But they also, in their relations to the stem, seem to correspond to leaves. It is true that the primary distal region of the leaf in *Tmesipteris* and the whole appendage in *Psilotum* are cylindrical, and that the mode of appearance of the appendages in the transition region from the leafless rhizome to the aerial shoot suggests comparison with what is known for *Asteroxylon*. These are points consistent with a comparison of the appendages with emergences, but do not render this necessary. For our present purpose it is enough to recognise how these existing types of small-leaved Pteridophyta, in contrast with the megaphyllous groups, indicate the problem on which historical evidence from the fossil record is desirable.

The interest of *Thursophyton* and *Asteroxylon* is, as was pointed out above, that their appendages are comparable on the one hand to definite small leaves and on the other to emergences such as those of *Psilophyton*. In all cases our knowledge of the facts is incomplete and needs to be critically extended. No structural details are available regarding the appendages borne by *Asteroxylon elberfeldense* from the Middle Devonian of Germany (Kräusel and Weyland, 1923, 1926, 1929). It is of interest that the lower part of the erect shoot of this plant has been compared with *Thursophyton* and a higher region of the branch-system with *Psilophyton*. Detailed comparative knowledge of the appendages in the various regions of this plant would evidently be most instructive.

In *Asteroxylon Mackiei* (Kidston and Lang, 1920) there is the advantage of our knowledge of the appendages being based on petrified material. They show a gradual increase in size in the transition region from the leafless rhizome to the small-leaved shoot. Each of the fully developed leaves on the latter has a vascular strand, coming from the stele of the stem, but the leaf-trace stops at the base of the leaf and is not continued into the free portion. This is extended tangentially, and, while not markedly flattened, was evidently an organ of assimilation. Stomata can be found in the epidermis and the parenchyma within appears to have been abundantly provided with plastids, presumably chloroplasts. There does not appear to have been anything peculiar about the tip that could be compared with, or throw light on, this region of the spines of *Psilophyton*. On the whole the appendages of *Asteroxylon Mackiei* appear to have attained the grade of simple leaves, though they have features which suggest that they are relatively rudimentary ; this might well be explained by their phylogenetic derivation from emergences.

Thursophyton is only known in the form of incrustations and our acquaintance with it is still imperfect. Here again the appendages have a base of insertion that is extended transversely. Nothing is as yet known of their structure, but the character of the margin, and possibly of the tip, seems more comparable with the type of leaf found in *Lycopodium* than with the emergences of *Psilophyton*. There is one point concerning their arrangement, however, in which the appendages of *Thursophyton* seem strikingly comparable to the spines of *Psilophyton*. It has been found that large and small appendages may be inserted close together on the shoot of *Thursophyton* (LANG, 1925, figs. 28–39). As in the case of *Psilophyton princeps* this feature became evident in isolated macerated portions of the incrustation, though it was not noticeable in the specimen on the rock.

These brief references to early microphyllous plants will suffice to show that there are indications of a series in complexity and specialisation from the type of *Psilophyton*, through that of *Thursophyton* and *Asteroxylon*, to that found in the Lycopodiales. Our detailed knowledge of the pertinent facts for these and other early microphyllous forms is still very inadequate. Sufficient has been said to indicate the interest, for comparative purposes, of additional information regarding the appendages of any of these plants as contributing to the solution of the morphological problem of the origin of the small Lycopod-type of leaf.

The details regarding the sporangia that are described in this paper do not call for much discussion. They afford the proof that the structures in question are sporangia, containing spores of one kind. The wall of the large sporangium is shown to be composed of two layers, an outer black carbonised layer and an inner, thin, brown, translucent layer. The black layer may reasonably be supposed to be derived from a strongly thickened epidermis. The inner layer may, perhaps, best be compared with the persistent inner layer of the sporangial wall of *Rhynia* and *Hornea*, which was termed a "tapetum" in the description of those plants. In partially decayed sporangia of *Rhynia* all that remained of the sporangial wall was the thickened epidermal layer and within this the persistent tapetum (KIDSTON and LANG, 1917, figs. 63, 63*a*). On our present imperfect knowledge the sporangia of DAWSON's *Psilophyton princeps* (*Dawsonites arcuatus*, HALLE) appear to have resembled the sporangia of *Rhynia* in the construction of the wall as well as in having been borne terminally on subdivisions of the axis. Other points of similarity are the large size and the absence of any recognisable method of dehiscence. As regards the spores, which are here described for the first time, the only points that call for comment are the considerable range in size they exhibit and the fact that they are smooth-walled.

It is perhaps worth while emphasising in conclusion that, though the attempt to estimate the bearings of the work has necessarily led to speculation, it is not the latter, but the addition of data that is of value. The few facts regarding the sporangia, spores and emergences of *Psilophyton princeps*, DAWSON, that are described in this paper are not completely understood and their comparative bearings and significance is a matter of opinion. But, since they are clearly demonstrated by specimens and preparations, they constitute another of the small steps by which our knowledge of the earliest vascular plants is slowly progressing.

Summary.

(1) Specimens collected from Gaspé, named *Psilophyton princeps* by DAWSON and distributed by him, have been investigated. They include examples of the markedly spiny stems, and of the relatively smooth branch-systems bearing sporangia.

(2) The features of the epidermal cells and stomata of the spiny stems, as described by EDWARDS are confirmed. Further details are ascertained regarding the spines. These range in size from $\frac{1}{3}$ mm. to over 2 mm. Their epidermis consisted of elongated cells, and stomata were absent. The terminal region or tip was peculiar; it was sometimes dilated, sometimes apparently naturally opened and clear. The appearance is suggestive of its having been of glandular nature. It is concluded that, on our present knowledge, the appendages are best regarded as emergences.

(3) DAWSON'S statement that the relatively smooth, longitudinally grooved axes, that terminated in the sporangia, regularly bore spines, is confirmed and demonstrated; the spines were much less numerous than on the typical spiny shoots. Their presence, however, lessens the contrast between the two types of axes.

(4) The large sporangia have been investigated by the film-pull method in two museum specimens. The existence in the sporangial wall of a black, carbonised, outer layer (probably representing a thick-walled epidermis) and of a thin, brown, translucent layer (representing a persistent tapetum) is demonstrated. These layers appear comparable to those shown in the sporangia of *Rhynia*.

(5) Spores have been demonstrated within a number of sporangia. They range in size from 100 μ to 60 μ, have smooth yellow or brown walls, and a small apical region.

(6) The bearings of these facts are indicated and briefly discussed.

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EXPLANATION OF PLATES.

(All the figures are from untouched photographs.)

PLATE 27.

FIG. 1.—Well-preserved, flattened incrustation labelled by DAWSON "*Psilophyton princeps*, var. *ornatum*" from Gaspé, nat. size. (Kidston Collection, No. 107, Geol. Survey Museum.)

Figs 2–12 are from fragments derived from the matrix of this specimen.

FIG. 2.—Stoma and surrounding epidermal cells. × 400. (No. 814.)*

FIG. 3.—Spine (emergence) of fairly large size, partially macerated, showing complete tip and indications of cellular structure. × 50. (No. 691.)

FIG. 4.—Moderately small spine, partially macerated. × 50. (No. 814.)

FIG. 5.—Two spines of different sizes, attached close together on a fragment of stem; partially macerated. The longer spine has a swollen tip, that appears to be detaching a small, terminal cap. × 50. (No. 690.)

FIG. 6.—Portion of surface of stem on which are borne the base of a large spine and a complete, small spine, which, in spite of the fairly thorough maceration, retains a dark terminal region. × 50. (No. 829.)

FIG. 7.—Two spines of different size attached to a portion of stem-surface; partially macerated. The terminal regions of both are open, clear, cuticular tubes. × 50. (No. 827.)

FIG. 8.—Well-macerated spine of moderate size; the main lower portion is thoroughly cleared, but a persistent black mass remains in the dilated tip. × 50. (No. 812.)

FIG. 9.—Tip of unmacerated spine, showing the marked dilation. × 100. (No. 813.)

FIG. 10.—Tip of unmacerated spine, represented by an open, clear, cuticular tube, terminating the opaque, black, lower region. × 100. (No. 828.)

FIG. 11.—Tip of the spine shown in fig. 8; the dilated black tip has cracked on slight compression. × 100. (No. 812.)

FIG. 12.—Tip of spine, which, after maceration, contained a black mass, but this disappeared on treatment with alcohol, leaving a cavity within the clear epidermis of the dilation just behind the actual tip. × 100. (No. 833.)

FIG. 13.—Specimen of the longitudinally striated, relatively smooth type of axis from Gaspé, labelled *Psilophyton* by DAWSON. Nat. size. (Kidston Collection, No. 112; Geol. Survey Museum.)

FIG. 14.—Portion of the axis in the preceding figure, enlarged to show the longitudinal grooving or ridging and a distinct spine with a blunt tip. × $5\frac{1}{2}$.

FIG. 15.—Piece of grooved axis preserved as a solid cast, bearing a blunt-tipped spine. × $5\frac{1}{2}$. (Manchester Univ. Museum, No. LL180.)

FIG. 16.—Specimen from DAWSON, labelled "*Psilophyton princeps*, DAWSON, Gaspé (Fructification)." It shows longitudinally grooved axes of various widths, bearing occasional spines or punctate with their places of insertion; also a number of sporangia. Nat. size. (British Museum Coll., No. v 9464.)

FIG. 17.—Similarly labelled specimen showing axes and numerous sporangia. Nat. size. (British Museum Coll., No. v 3209.)

* The numbered preparations, except where otherwise stated, are in my own collection.

Fig. 18.—Portion of rather stout, longitudinally grooved axis, enlarged to show spines and the punctate appearance due to their places of insertion. × 2. (British Museum Coll., No. v 6301.)

Fig. 19.—Portion of more slender grooved axis, enlarged to show two spines projecting from the left-hand side into the matrix. × 5½. (British Museum Coll., No. v 6339.)

Plate 28.

Fig. 20.—Group of sporangia borne on the slender terminal region of an axis; from the specimen shown in fig. 17. × 5½. (British Museum Coll., No. v 3209.)

Fig. 21.—Group of sporangia which show the walls in outline, the cavities being filled with mineral material. × 5½. (British Museum Coll., No. v 21107.)

Fig. 22.—Cellulose film-pull from the specimen in fig. 21, showing two complete sporangia and portion of another. Description in text. × 10. (British Museum Coll., No. v 21107 a.)

Fig. 23.—Similar film-pull from specimen in Manchester University Museum (No. LL180) showing two sporangia. Description in text. × 10. (No. 809.)

Fig. 24.—Portion of a sporangium from a film-pull, showing the fragmented outer black layer of the wall and, in the intervals of the fragments, remains of the brown layer. × 50. (No. 834.)

Fig. 25.—Portion of a similar film-pull, showing remains of the outer black layer and of the inner brown layer of the wall and a single spore. × 50. (No. 833.)

Fig. 26.—Portion of another film-pull, showing fairly extensive and well-preserved remains of the inner brown layer ("tapetum"). × 75. (British Museum Coll., No. v 21107 c.)

Fig. 27.—Portion of film-pull of sporangium, showing fragments of the black outer layer of the wall, indistinct traces of the inner brown layer and several flattened spores. × 75. (No. 809.)

Fig. 28.—One of the spores from the preceding figure, associated with others not in focus. × 200. (No. 809.)

Fig. 29.—Isolated spore from film-pull. × 200. (No. 809.)

Fig. 30.—Isolated spore, not completely flattened. × 200. (No. 810.)

Fig. 31.—Two spores associated with remains of the inner brown layer of the sporangial wall. × 200. (British Museum Coll., No. v 21107 a.)

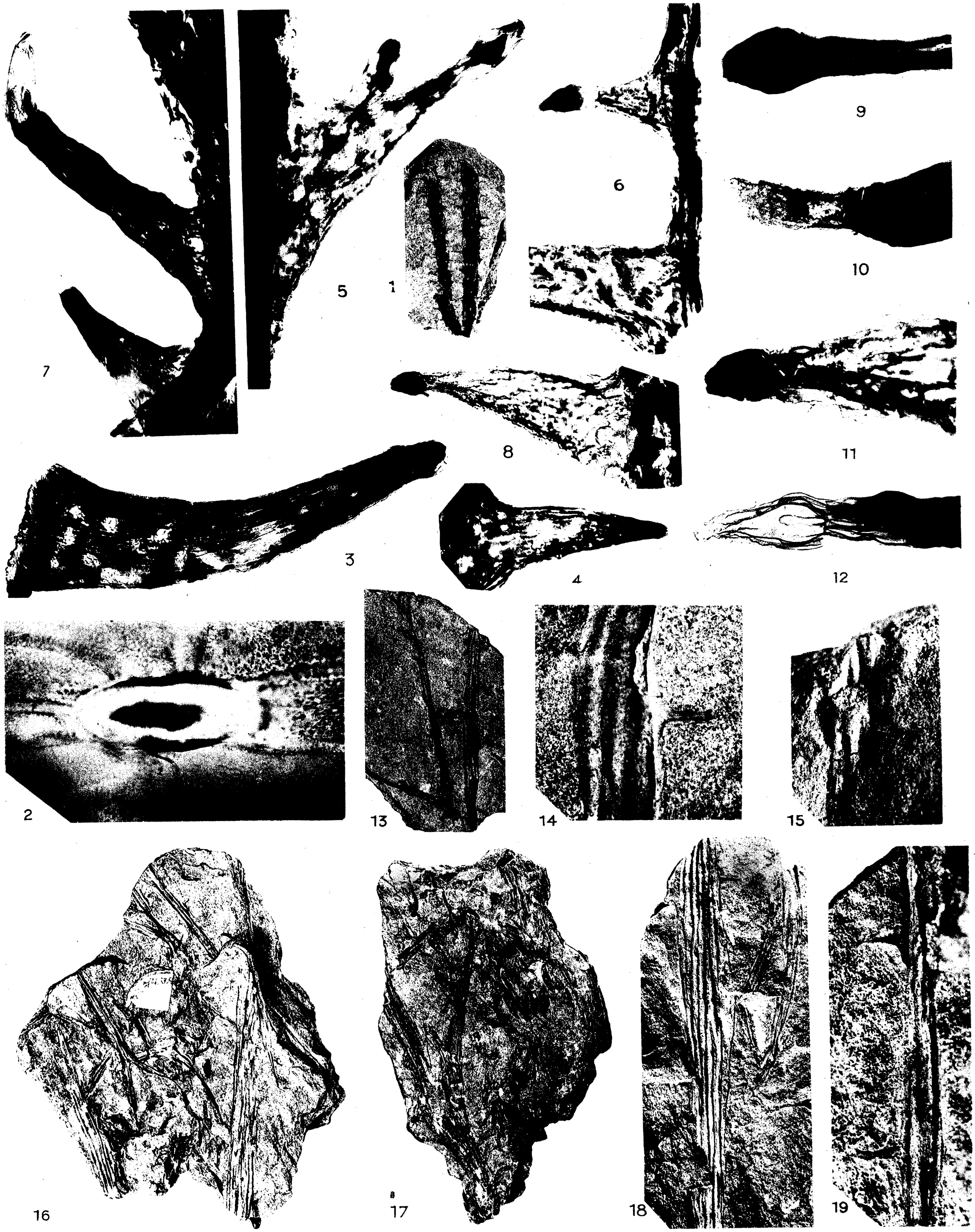
Fig. 32.—Single clearly isolated spore from a film-pull of a sporangium. × 200. (British Museum Coll., No. v 21107 d.)

Fig. 33.—Portion of black outer layer of wall on the left; within this remains of inner brown layer and against this a single spore the brown wall of which is not compressed. × 200. (No. 818.)

Fig. 34.—Small uncompressed spore from a sporangium shown in fig. 23. On the right is a black fragment of the outer layer of the wall; adjoining this is the single spore associated with fragments of the inner brown layer. × 200. (No. 809.)

Fig. 35.—Portion of black outer layer of the sporangial wall, on the right. Within this traces of the brown inner layer of the wall and a group of some five uncompressed spores of different sizes, three of which are in focus. × 200. (British Museum Coll., No. v 21107 a.)

Fig. 36.—Well-preserved apical area of a spore, seen laterally as forced up into a beak-like prominence. The main area of the spore being at a lower level, is not in focus. × 400. (British Museum Coll., No. v 21107 b.)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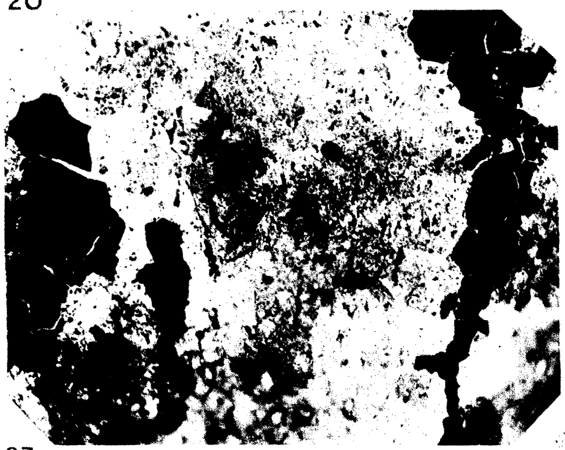
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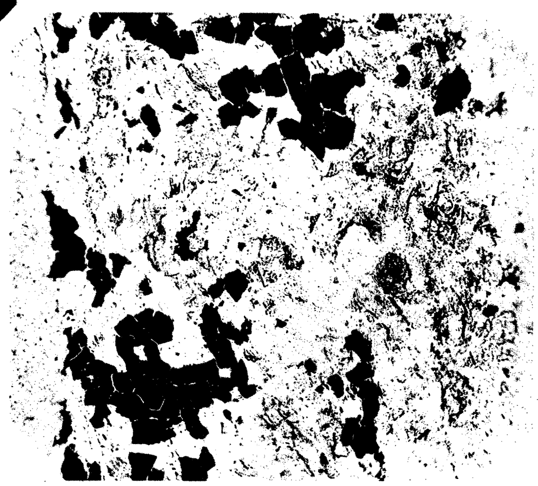
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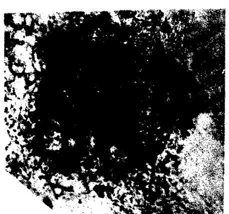
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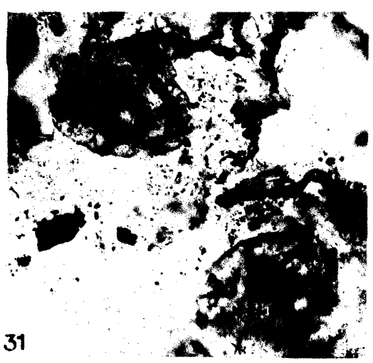
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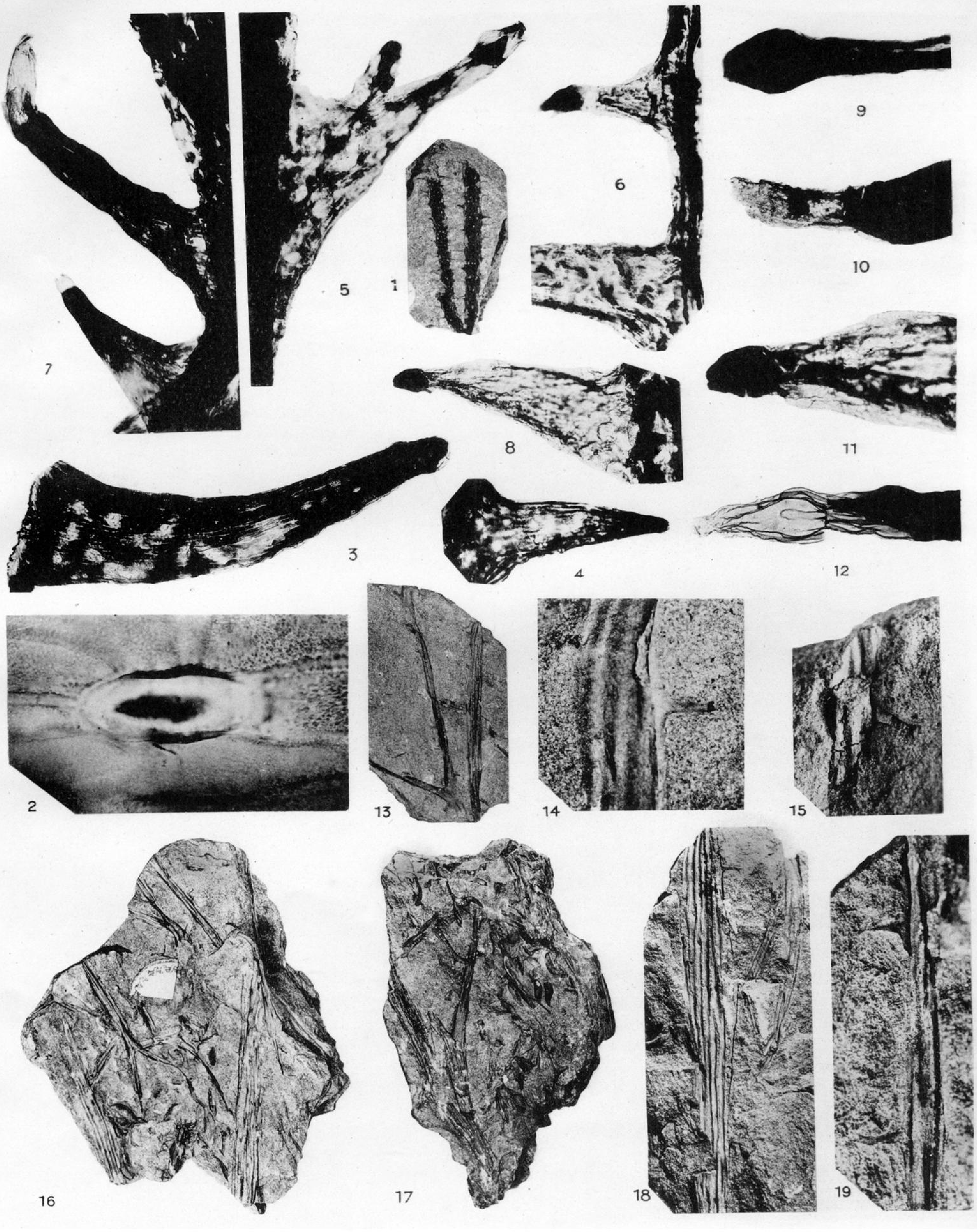

PLATE 27.

FIG. 1.—Well-preserved, flattened incrustation labelled by DAWSON "*Psilophyton princeps*, var. *ornatum*" from Gaspé, nat. size. (Kidston Collection, No. 107, Geol. Survey Museum.)
Figs 2–12 are from fragments derived from the matrix of this specimen.

FIG. 2.—Stoma and surrounding epidermal cells. × 400. (No. 814.)*

FIG. 3.—Spine (emergence) of fairly large size, partially macerated, showing complete tip and indications of cellular structure. × 50. (No. 691.)

FIG. 4.—Moderately small spine, partially macerated. × 50. (No. 814.)

FIG. 5.—Two spines of different sizes, attached close together on a fragment of stem; partially macerated. The longer spine has a swollen tip, that appears to be detaching a small, terminal cap. × 50. (No. 690.)

FIG. 6.—Portion of surface of stem on which are borne the base of a large spine and a complete, small spine, which, in spite of the fairly thorough maceration, retains a dark terminal region. × 50. (No. 829.)

FIG. 7.—Two spines of different size attached to a portion of stem-surface; partially macerated. The terminal regions of both are open, clear, cuticular tubes. × 50. (No. 827.)

FIG. 8.—Well-macerated spine of moderate size; the main lower portion is thoroughly cleared, but a persistent black mass remains in the dilated tip. × 50. (No. 812.)

FIG. 9.—Tip of unmacerated spine, showing the marked dilation. × 100. (No. 813.)

FIG. 10.—Tip of unmacerated spine, represented by an open, clear, cuticular tube, terminating the opaque, black, lower region. × 100. (No. 828.)

FIG. 11.—Tip of the spine shown in fig. 8; the dilated black tip has cracked on slight compression. × 100. (No. 812.)

FIG. 12.—Tip of spine, which, after maceration, contained a black mass, but this disappeared on treatment with alcohol, leaving a cavity within the clear epidermis of the dilation just behind the actual tip. × 100. (No. 833.)

FIG. 13.—Specimen of the longitudinally striated, relatively smooth type of axis from Gaspé, labelled *Psilophyton* by DAWSON. Nat. size. (Kidston Collection, No. 112; Geol. Survey Museum.)

FIG. 14.—Portion of the axis in the preceding figure, enlarged to show the longitudinal grooving or ridging and a distinct spine with a blunt tip. × $5\frac{1}{2}$.

FIG. 15.—Piece of grooved axis preserved as a solid cast, bearing a blunt-tipped spine. × $5\frac{1}{2}$. (Manchester Univ. Museum, No. LL180.)

FIG. 16.—Specimen from DAWSON, labelled "*Psilophyton princeps*, DAWSON, Gaspé (Fructification)." It shows longitudinally grooved axes of various widths, bearing occasional spines or punctate with their places of insertion; also a number of sporangia. Nat. size. (British Museum Coll., No. v 9464.)

FIG. 17.—Similarly labelled specimen showing axes and numerous sporangia. Nat. size. (British Museum Coll., No. v 3209.)

FIG. 18.—Portion of rather stout, longitudinally grooved axis, enlarged to show spines and the punctate appearance due to their places of insertion. × 2. (British Museum Coll., No. v 6301.)

FIG. 19.—Portion of more slender grooved axis, enlarged to show two spines projecting from the left-hand side into the matrix. × $5\frac{1}{2}$. (British Museum Coll., No. v 6339.)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

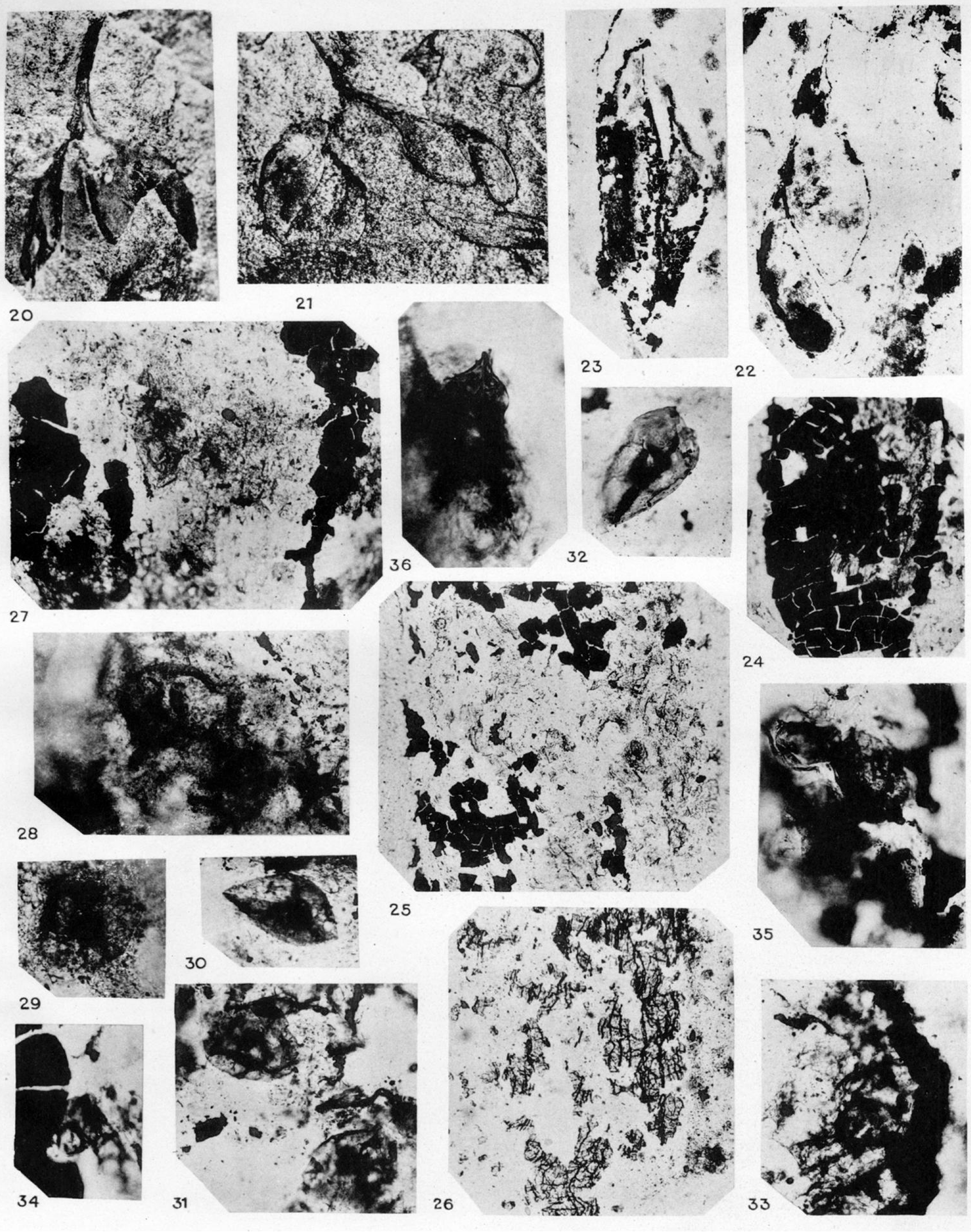

PLATE 28.

FIG. 20.—Group of sporangia borne on the slender terminal region of an axis; from the specimen shown in fig. 17. $\times 5\frac{1}{2}$. (British Museum Coll., No. v 3209.)

FIG. 21.—Group of sporangia which show the walls in outline, the cavities being filled with mineral material. $\times 5\frac{1}{2}$. (British Museum Coll., No. v 21107.)

FIG. 22.—Cellulose film-pull from the specimen in fig. 21, showing two complete sporangia and portion of another. Description in text. $\times$ 10. (British Museum Coll., No. v 21107 A.)

FIG. 23.—Similar film-pull from specimen in Manchester University Museum (No. LL180) showing two sporangia. Description in text. $\times$ 10. (No. 809.)

FIG. 24.—Portion of a sporangium from a film-pull, showing the fragmented outer black layer of the wall and, in the intervals of the fragments, remains of the brown layer. $\times$ 50. (No. 834.)

FIG. 25.—Portion of a similar film-pull, showing remains of the outer black layer and of the inner brown layer of the wall and a single spore. $\times$ 50. (No. 833.)

FIG. 26.—Portion of another film-pull, showing fairly extensive and well-preserved remains of the inner brown layer ("tapetum"). $\times$ 75. (British Museum Coll., No. v 21107 C.)

FIG. 27.—Portion of film-pull of sporangium, showing fragments of the black outer layer of the wall, indistinct traces of the inner brown layer and several flattened spores. $\times$ 75. (No. 809.)

FIG. 28.—One of the spores from the preceding figure, associated with others not in focus. $\times$ 200. (No. 809.)

FIG. 29.—Isolated spore from film-pull. $\times$ 200. (No. 809.)

FIG. 30.—Isolated spore, not completely flattened. $\times$ 200. (No. 810.)

FIG. 31.—Two spores associated with remains of the inner brown layer of the sporangial wall. $\times$ 200. (British Museum Coll., No. v 21107 A.)

FIG. 32.—Single clearly isolated spore from a film-pull of a sporangium. $\times$ 200. (British Museum Coll., No. v 21107 D.)

FIG. 33.—Portion of black outer layer of wall on the left; within this remains of inner brown layer and against this a single spore the brown wall of which is not compressed. $\times$ 200. (No. 818.)

FIG. 34.—Small uncompressed spore from a sporangium shown in fig. 23. On the right is a black fragment of the outer layer of the wall; adjoining this is the single spore associated with fragments of the inner brown layer. $\times$ 200. (No. 809.)

FIG. 35.—Portion of black outer layer of the sporangial wall, on the right. Within this traces of the brown inner layer of the wall and a group of some five uncompressed spores of different sizes, three of which are in focus. $\times$ 200. (British Museum Coll., No. v 21107 A.)

FIG. 36.—Well-preserved apical area of a spore, seen laterally as forced up into a beak-like prominence. The main area of the spore being at a lower level, is not in focus. $\times$ 400. (British Museum Coll., No. v 21107 B.)