

ANATOMY AND MORPHOLOGY OF *PSILOPHYTON*
DAWSONII, SP. N. FROM THE LATE LOWER
DEVONIAN OF QUEBEC (GASPÉ) AND
ONTARIO, CANADA

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ABSTRACT

For the first time a species of *Psilophyton* is described from petrifications. The specimens come from Early Devonian (Emsian) calcareous cobbles on the Gaspé Peninsula near Douglastown, P. Q., Canada. Compression specimens, occasionally petrified by iron pyrite, from along Abitibi River near Coral Rapids, James Bay Lowlands, Ontario, Canada, show identical anatomy and morphology. Epidermis, stomata, thick- and thin-walled cortical cells, phloem, and a centrarch xylem strand are recorded for branches of several orders; details of branch traces and of dichotomies in lesser axes are reported. Larger axes bear closely and spirally arranged vegetative branches in zones alternating with spirally arranged but alternate and distichous fertile branch systems. The latter usually branch six times and are three-dimensional because successive dichotomies occur 90° around the stem from one another. Each of the first two apparent dichotomies is two close divisions which would result in three axes. However one of the three aborts. This leaves an apparent dichotomy with a strange stump near its axil. The ultimate fertile branches terminate in fusiform sporangia whose walls resemble epidermal and cortical cells of the axes. Vascular tissue extends into the base of the sporangia. A thin membrane surrounds the mass of isospores which resemble most closely the spore-genus *Retusotrilites*. Dehiscence of sporangia is longitudinal along one side.

The vascular strand is terete, has one central protoxylem when not branching, and is massive compared to that of *Rhynia*. Annular and spiral elements occur in the protoxylem and scalariform elements in the metaxylem. The latter are characteristic because interconnections between the scalariform bars, formed by secondary wall material, outline thin areas of wall that thus simulate pits. The vascular strand is large and complex in the area of profuse vegetative branching and the traces to fertile branch systems are distinctively rectangular strands in transverse section. No leaves are present but some of the smaller vegetative branch systems as well as lesser laterals on some of the stemlike branch systems could be interpreted as precursors of leaves. The height of the plant and its base are unknown.

Psilophyton dawsonii, n. sp. is placed in the Trimerophytina and represents anatomically and morphologically the best known species in the subdivision. It is considered to be far more highly evolved than *Rhynia* and adds significant details for use in analysis of the plexus from which younger groups such as the coenopterids and progymnosperms could have evolved.

INTRODUCTION

The generic name *Psilophyton* and all the concepts that it connotes came to be almost synonymous with Devonian Flora and the origin of land plants. *Psilophyton* has been used as the type of several taxonomic categories, e.g. *Psilophytales*. It has given substance to hypotheses widely used in morphology, e.g. the telome theory of Zimmermann (1930). Yet, until 1967 (Hueber and Banks, 1967) its principal species, *P. princeps*, was not represented by a type specimen, several different kinds of axes were attributed to the species, and the connection of sporangia to larger axes was uncertain. Similarly there was no useful information concerning its anatomical structure. In 1968 Hueber described *P. princeps* in some detail and the present material permits us to describe a new species for which we can combine in one account the details of both its gross morphology and its anatomical structure. Hueber's work and our new, extensive discoveries should remove any remaining doubt as to the

exact vascular structure and the morphological complexity of this historic genus.

All types are on deposit at Cornell University Paleobotanical Collection (CUPC), Geological Survey of Canada (GSC) and National Museum of Natural History (U.S. Nat. Mus.).

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in the Halle Collection in the Section for Paleobotany of the Swedish Museum of Natural History, in the Lang and the Croft and Lang Collections of the Department of Paleontology, British Museum (N.H.), in the Dawson Collection of the Redpath Museum, McGill University, in the Stockmans Collection of the Institut Royal des Sciences Naturelles de Belgique, Brussels, in the Department of Paleontology, National Museum of Prague, and in the Geological Museum of the University of Oslo.

Leclercq wishes to express her thanks to Cornell University for her appointment as Visiting Professor for three months in 1963. This permitted her to begin the study of the anatomy of *Psilophyton dawsonii*, n. sp., as revealed in serial peels of calcareous cobbles from the Gaspé Bay area and to carry on the study at the University of Liège.

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HISTORICAL SURVEY

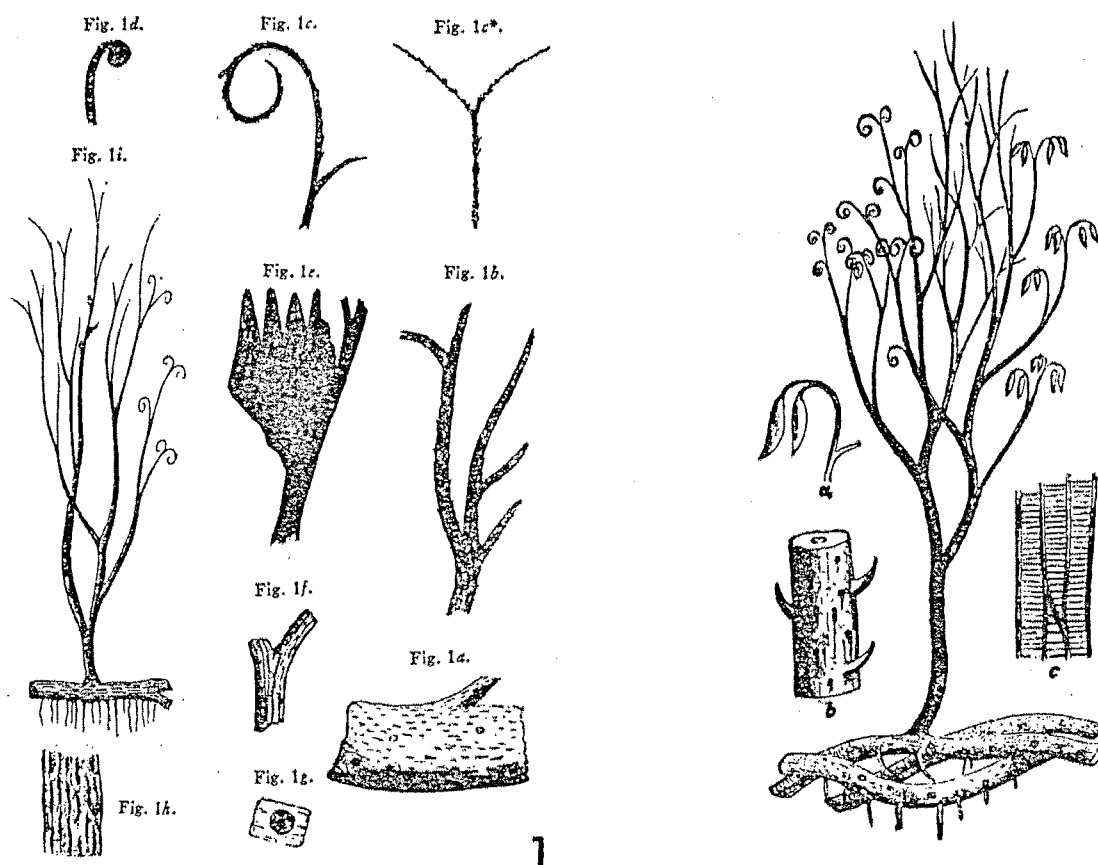
The genus *Psilophyton* was erected by Dawson in 1859 for Devonian fossils found on the Gaspé Peninsula, Quebec, Canada. He described two species, *P. princeps* and *P. robustius*. The latter has proved to be different. It is now in part *Trimerophyton robustius* Hopping (1956). In 1871 Dawson described a new variety which he named *P. princeps* var. *ornatum* (now *Sawdonia ornata* (Dn.), Hueber, 1971, a member of *Zosterophyllophytina* Banks, 1968, and no longer a *psilophyte*). These specimens of 1871 came gradually and informally to represent the type of the species *P. princeps*. Four arguments supported this interpretation. First, Dawson's original description and restoration (Text-fig. 1) united diverse organs without proof of their organic connection. Second, in 1871 Dawson provided satisfactory illustrations of spine-bearing axes, and he had originally described *P. princeps* as spiny. Third, in 1871 Dawson described terminal sporangia of *Psilophyton* which were well enough preserved to be accepted as sporangia by most workers although they were not attached to the new large spiny axes. Fourth, in 1870 Dawson had published a new, more reasonable, reconstruction of *P. princeps* (Text-fig. 2) which has been copied by many subsequent authors.

In 1895 Solms-Laubach analyzed critically the then current status of studies on *Psilophyton*. He pointed out

that neither the fructifications described in 1859 nor those of 1871 were attached to spiny stems. He noted also that the few anatomical details Dawson had recorded for the stems came from unattached fragments and should not be regarded as belonging to *Psilophyton*.

In 1905 White studied the Upper Devonian flora of Perry, Maine, and also some of Dawson's collection from the Gaspé Peninsula (Lower Devonian). He concluded that the spiny stems described and illustrated as *Psilophyton princeps* var. *ornatum* (Dawson, 1871, pl. 9, figs. 97-101) should be regarded as the type of *P. princeps*. He examined the unattached fructifications described by Dawson (1871, pl. 9, figs. 102, 103, 105-108) and found punctate areas on the sporangium-bearing axes. These impressed White as representing the bases of spines. Therefore, unlike Solms-Laubach, he united the terminal sporangia Dawson (1871) described as "Fructifications consisting of naked, oval spore-cases borne usually in pairs on slender curved pedicels, either lateral or terminal" with the spiny axes. That is to say he united all the organs illustrated by Dawson on plate 9, 1871, under the epithet *P. princeps* var. *ornatum*. Dawson believed the fertile axes belonged to his original *P. princeps*. White's suggestion, followed by many subsequent workers, meant the elimination of the variety *P. princeps* var. *ornatum* and the definition of *P. princeps* as a plant with numerous large spines rather than the slender, distant ones described originally in 1859 by Dawson. We shall show subsequently that White had good reason to believe that *P. princeps* bore both spines and paired terminal sporangia. The evidence will show, however, that he was not correct in associating the paired terminal sporangia with the stems Dawson had named *P. princeps* var. *ornatum*.

Halle (1916) continued the analysis of *Psilophyton* with a careful study of poorly preserved fossils collected in Lower Devonian strata at Røragen, Norway. Like Solms-Laubach he rejected Dawson's description of anatomy because the partially petrified specimens were not parts of spiny stems. For the same reason he rejected the unattached organs that Dawson had called rhizomes. We found three specimens labeled rhizome of *Psilophyton* by Dawson. These bear numbers 3203, 3205, 3206 in the Redpath Museum, McGill University. They are not connected to any axes of *Psilophyton* but they do have all the characteristics of *Taeniocrada dubia*. The late Dr. Kräusel, who also studied Dawson's collections, as well as European materials, agreed in 1959 at X International Botanical Congress, Montreal, that Dawson's rhizomes should be referred to *T. dubia*. Halle also rejected the paired, terminal sporangia on the ground that one must find actual spines on the reproductive



Text-figures 1, 2. — Text-figure 1 (left) Dawson's original drawings and reconstruction of *Psilophyton princeps*, 1859. Text-figure 2 (right) Dawson's revised reconstruction of *P. princeps* first published in 1870.

axes, not simply scars of spines. Thus, following Halle's paper, *Psilophyton princeps* was reduced to a spiny, vegetative axis that branched dichotomously.

Halle was constructive in his analysis. He compared the Røragen material with some specimens from the Gaspé Peninsula and concluded that Dawson's fertile axes bearing terminal sporangia (e.g. Dawson 1871, pl. 9, fig. 102) had no spines and were striated vertically whereas the axes of *Psilophyton* were unstriated and spiny. Halle, therefore, erected a "provisional" category, *Dawsonites arcuatus*, for the reception of axes from Gaspé, Røragen, and Matringhem, France (Bertrand 1913), that bore narrow obovoid, or short-fusiform, terminal sporangia, usually 3 to 5 mm in length, on slender, curved branches. The ultimate branches terminated a system of bifurcating lateral branches. Even more important was Halle's perceptive and convincing argument that these fertile axes foreshadowed the morphological pattern found among early prefeens.

In 1931 Lang began to contribute to this problem with his usual care and skill. First, he studied specimens from the Gaspé Peninsula which had been labeled *Psilophyton princeps*. Among the material he found some axes with longitudinal ridges (like *Dawsonites*) and occasional spines (like *Psilophyton*) that seemed to bear terminal sporangia (like *Dawsonites*). Lang considered these specimens to be identical to Halle's *Dawsonites* but he called them *Psilophyton* because they bore spines. This choice agreed with the suggestions made by White but not with those of Halle. As will appear below, Lang became more attached to the use of *Dawsonites* as his work progressed. Lang examined axes of many sizes, from large, spiny ones to smooth, slender, repeatedly dichotomized ones bearing terminal sporangia. He was successful in studying small bits of carbon removed from sporangia. They revealed (Lang, 1931, pl. 28, fig. 24) a carbonized outer wall and an inner, thin, translucent layer which surrounded the spores. The inner layer reminded him

of the persistent tapetum found in *Rhynia* and *Horneophyton*. Spores extracted from the sporangia ranged from 60 to 100 μ in diameter, were smooth, and were characterized by a darkened triangular area around the small trilete scar. In the same paper Lang described the detailed structure of the spines of *Psilophyton princeps* var. *ornatum* [now *Sawdonia ornata* (Dn.), Hueber, 1971], although he referred to them as *P. princeps*.

A year later Lang (1932, pp. 509-510) again reported sporangia with an outer wall and an inner, translucent layer. They came from Lower Devonian (Upper Siegenian) rocks in Scotland. The spores were somewhat larger, ranging from 75 to 100 μ in diameter. They were smooth or slightly papillate and showed some thickening around the trilete scar. Lang recognized that the fossils might be regarded as terminal parts of *Psilophyton* or as belonging to Halle's provisional genus *Dawsonites*. It is significant that this time Lang did not place them in *Psilophyton* as he had done the year before.

Lang's next contribution was made in collaboration with Croft (Croft and Lang, 1942). They described fertile axes from the Early Devonian (Siegenian) of Wales, some of which were smooth and some longitudinally striated. Both kinds bore lateral branches that subdivided several times and terminated in pendant sporangia. The fossils fitted Halle's diagnosis of *Dawsonites* and bore out the latter's prediction that numerous sporangia terminated the fertile branching system although Halle had not seen large numbers of sporangia. Croft and Lang's specimens (e.g. fig. 17, 18 on pl. 10) obviously provide a good illustration of Halle's concept of *D. arcuatus* (cf. Pl. 22, fig. 50). The authors also demonstrated that the wall of the sporangia consisted of an outer carbonaceous and an inner, translucent layer (cf. Pl. 23, fig. 52). This was the third time that such a sporangial wall had been associated with *Psilophyton* (or *Dawsonites*). Spores in these sporangia were in the smaller size range, 50 to 85 μ in diameter and were smooth. Croft and Lang in the same paper, described specimens bearing both spines and lateral sporangia under the epithet cf. *Psilophyton princeps*. Re-examination of these specimens by one of us (F.M.H.) has resulted in the conclusion that two or three different plants are included in the description and that certainly the fertile specimen in their figure 12 (BMNH V26507) is neither *Psilophyton princeps* nor *Sawdonia ornata* (Dn.), Hueber, 1971. The morphological characteristics of its sporangia and of its emergences related it more closely to *Crenaticaulis* Banks and Davis, 1969, than to the other genera. A new name is required for this fertile specimen.

Stockmans (1940) used Halle's provisional name *Daw-*

sonites in the restricted sense for monopodially and dichotomously branching axes that bore sporangia terminally, often pendant, on lateral branching systems. His specimens were collected at four Lower Devonian (probably Emsian) quarries and were clearly referable to *D. arcuatus*. Specimens from a fifth quarry he called *Dawsonites* sp. with the comment that they resembled *D. jabachensis* Kräusel and Weyland (1935) as well as *D. arcuatus*. In addition Stockmans provided good evidence that *Dawsonites* also occurs in early Middle Devonian strata. He illustrated (pl. 14, figs. 2-5) plants from two quarries and referred them to *Dawsonites* sp. but gave no further description because his monograph was concerned with Lower Devonian strata. We consider these to be good examples of *D. arcuatus*.

In 1930 (p. 75) Kräusel and Weyland used the name ?*Dawsonites* sp. for a narrow axis that bore two rows of (?) sporangia laterally. Dorf (1933, p. 246) suggested that this German material might be placed in *Bucheria* [now *Rebuchia* (Dorf), Hueber, 1970]. Both Halle (1936, p. 22) and Høeg (1942, p. 65) agreed with Dorf's suggestion. Kräusel and Weyland (1948, p. 91) agreed that *Dawsonites* was not intended to include spikelike fructifications. Earlier (1941, p. 54) they had remarked that their ?*Dawsonites* sp. might fall in the same group as *Barinophyton* or *Pectinophyton* and that it resembled *Zosterophyllum* as well. Certainly it is no *Dawsonites* and it has been relegated to doubtful species under *Rebuchia* (*Bucheria*) by Høeg (1967, p. 266).

In 1933 Kräusel and Weyland (p. 39) described another axis from the Middle Devonian Srbsko beds of Bohemia. It bore kidney- or club-shaped sporangia laterally along one side. They compared the specimen with *Taeniocrada*, *Zosterophyllum*, and *Hostimella racemosa* of Lang (1925) but rejected all three possibilities. Instead they chose to use Halle's provisional name *Dawsonites* in a wide sense to include almost any sporangia whose affinity is unclear. Thus they named their plant *Dawsonites bohemicus*. This use of the generic name marked a sharp divergence from the concepts of Halle and Lang. Obrhel (1961, p. 35) reexamined the type specimen of *D. bohemicus* and argued convincingly in favor of its reassignment to *Zosterophyllum* or *Gosslingia*. He chose the former name and made the recombination ?*Zosterophyllum bohemicum* (Kräusel and Weyland), Obrhel.

Kräusel and Weyland (1935, pp. 185-186) described a new species of *Dawsonites*, *D. jabachensis* from the upper Lower Devonian of Jabachtal near Lockmar in the Rhineland. In 1962 they described additional specimens from the Lower Devonian of Alken on the Moselle. They stressed the resemblance of its flat, ribbon-like branches, the arrangement

of its sporangia, and its general organization to *Taeniochrada*. Yet they separated it from *Taeniochrada* because of the longitudinal striations on some branches and the structure of its sporangia. In our opinion it shares with *Dawsonites* only the terminal position of its sporangia. It differs sharply from *Dawsonites* in its lack of a lateral, dichotomizing fertile branch system. It also differs because its older branches are ribbon-like, its longitudinal striations are continued on to the sporangia, and its sporangia are single, not paired. We believe that a new generic name should be created for it.

In the same paper Kräusel and Weyland (1935, p. 186) assigned specimens from Lower Devonian (Siegenian) strata of Nellenköpfchen to *Dawsonites* sp. The plant consisted of a pseudomonopodially branching axis whose laterals forked only once. One lateral bore a single terminal sporangium. The inclusion of this material in *Dawsonites* also requires an unjustified broadening of Halle's concept. We suggest it be placed in another genus.

Høeg (1935) erected the species *Dawsonites ellenae* for sterile and fertile shoots from the Middle Devonian of Western Norway. Fertile shoots bore lateral clusters of rounded bodies (probably sporangia) that he interpreted as terminating the branches of several successive dichotomies. The sterile shoots bore laterals, recurved at the apex, rather comparable to those of *Aneurophyton*. Some spines were found on both sterile and fertile axes. Høeg was fully aware that he had to widen the limits of Halle's provisional genus but he preferred this to the erection of a new genus on limited material. We think, however, that a new generic category is indicated. One significant character separating *D. ellenae* from *Dawsonites* is its rounded sporangia.

Stockmans (1940) described a new species of *Dawsonites*, *D. minor*. Its lateral branches forked only one or two times before terminating in more or less spherical sporangia. As a result the sporangia appear to be grouped against the main axis. The shape of the sporangia and the paucity of divisions of its lateral branches distinguish it clearly from *Dawsonites* and, like *D. ellenae*, it would be better transferred to another genus.

Høeg (1942, pp. 31-32) compared some plants from the Upper (?) Devonian of Spitzbergen with Halle's *Dawsonites*. Their straight and longitudinally ridged axes bore repeatedly branched lateral axes some of which terminated in pendant sporangia. The shortness of the side branches; the fact that they fork immediately on leaving the main axis and that some of them terminate in flattened, leaflike tips while others terminate in "small clusters of simple, narrow sporangia" caused Høeg to suggest that his plants might represent a new genus related to Protopteridales. His

plate 8, figures 4, 7, 8 includes the most *Dawsonites*-like of his illustrations. It is wiser, however, to exclude them from this genus, as he did, unless subsequent collections yield more convincing evidence.

Ananiev (1957) described briefly and illustrated Lower Devonian plants from southwestern Siberia under the tentative name cf. *Protopteridium minutum* Halle. Ananiev stated that his fossils represented the kind of plant Halle had called *Dawsonites arcuatus*. However, certain axes produced sterile laterals that terminated in at least two successive dichotomies. These laterals resembled the sterile "pinnules" of Halle's *P. minutum*. In his choice of name Ananiev was probably influenced more by the sterile branchlets than by the resemblance of the fertile parts to the *Dawsonites* of Halle and of Lang. Without seeing the original material we can only agree that it resembles *Dawsonites*.

Obrhel (1961) described a new species of *Psilophyton*, *P. kräuselii*, whose lateral branches forked in an open, dichotomous manner like those of Dawson's *P. princeps* of 1859. Axes of *P. kräuselii* were delicate, villous throughout, and terminated by large clusters of recurved, terminal sporangia. *P. kräuselii* (studied by H.P.B., in Prague, 1968) seems to combine some elements of Dawson's 1859 description of sterile axes of *P. princeps* with the major features of Halle's provisional genus for fertile axes, *Dawsonites*. It appears to be the first published specimen to display all of the critical characteristics of the external morphology of *Psilophyton*. But it must be emphasized that no histological details of any sort have been obtained from this species, no cuticle, no epidermis, no spores, no vascular tissue.

Just as Obrhel's *Psilophyton kräuselii* demonstrated a plant with the essential features of Dawson's original concept of *Psilophyton*, so did the work of Hueber demonstrate that *Psilophyton princeps* var. *ornatum* can no longer be retained in the genus. Hueber (1964b) reported lateral sporangia on *P. princeps* var. *ornatum* from Dawson's type locality and from deposits along the Abitibi River, near James Bay at the southern end of Hudson Bay, Ontario, Canada. In the same year Hueber (1964a) reported an exarch protostele (figured in Hueber and Banks, 1967) in this variety of *Psilophyton*. In 1971 Hueber erected the name *Sawdonia ornata* (Dn.) for specimens usually referred to *P. princeps* var. *ornatum*. Additional evidence of lateral sporangia on *Sawdonia* was provided by Ananiev and Stepanov (1968) who illustrated fertile specimens (labeled *P. princeps*) from Siberia.

Two major characters, exarch protostele and lateral sporangia with distal dehiscence, are shared by *Zosterophyllum* (Edwards, 1969), *Gosslingia* (Edwards, 1970a), and

Crenaticaulis (Banks and Davis, 1969). Banks (1968b) suggested that plants with this combination of characters be placed in a new subdivision, the Zosterophyllophytina. Thus the spiny axes described by Dawson in 1871 as *P. princeps* var. *ornatum* and shown by Hueber (1964a) to bear lateral sporangia differ sharply from Dawson's original diagnosis of *Psilophyton* as a plant bearing terminal sporangia. Their new name, *Sawdonia ornata* (Dn.), Hueber, 1971, and their classification in Zosterophyllophytina emphasize this distinction.

Returning to *P. princeps*, Hueber and Banks (1967) restudied available original material of Dawson at Redpath Museum of McGill University, Montreal. They selected a neotype for *P. princeps*. The specimen bears spines and lateral branch systems terminated by pairs of sporangia. It was illustrated by Dawson in 1871 as figure 103 on plate 9. We may recall that Halle (1916) and White (1905) had observed only scars of spines on fertile axes and not the spines themselves. This one observation led Halle to erect the new taxon *Dawsonites* and led White to the belief (now seen to be an error) that the terminal sporangia should be associated with the spiny axes called *P. princeps* var. *ornatum* by Dawson in 1871 (= *Sawdonia*). The spines of the two taxa are markedly different. Hueber (1968) showed those of *P. princeps* to be blunt-tipped and terminated by a cuplike depression. Lang (1931, pl. 27, figs. 3-12) showed the spines of *Sawdonia* (his *Psilophyton princeps* var. *ornatum*) to be glandular tipped. Hueber and Grierson (1961) found identical spines on *Sawdonia* (their *P. princeps*) in Upper Devonian rocks in New York. Hueber and Banks (1967) illustrated a terete, centrarch protostele for *Psilophyton*. *Psilophyton* with its centrarch xylem strand and lateral branch systems terminated by clusters of sporangia is sharply distinct from *Sawdonia* which has lateral sporangia and an exarch xylem strand. Banks (1968b) used these characters in distinguishing a new subdivision, Trimerophytina (for *Psilophyton* and *Trimerophyton*). It is completely different from Zosterophyllophytina.

Hueber (1968) demonstrated a membrane inside the sporangial cavity of *Psilophyton princeps*. Maceration released this membrane as a sac (cf. Pl. 23, figs. 53-55). The sac corresponds to the inner, translucent layer of sporangium that Lang demonstrated on three occasions (1931, 1932, and, with Croft, 1942). *Psilophyton princeps* can now be regarded as a clearly defined plant.

Andrews, Kasper, and Mencher (1968) recently described another species, *Psilophyton forbesii*, based on smooth main axes that bore spirally arranged lateral branch systems which forked equally or unequally. One fertile branch

system was found near the sterile specimens. The authors assumed it belonged with the sterile axes and so illustrated it in their reconstruction. Unfortunately their material yielded neither histological nor anatomical details nor additional morphological data.

Banks (1968a) studied specimens collected at Røragen (Halle, 1916) that were identical to axes Halle had called *Hosimella*. Halle suspected that these axes were terminal parts of his *Psilophyton goldschmidtii* and Banks demonstrated the probable correctness of this view by finding a terete, centrarch xylem strand in some of them. Thus anatomy typical of *Psilophyton* has been found both in Norway and in Canada.

Ananiev and Stepanov (1968) reviewed the status of the generic name *Psilophyton* prior to receipt of the paper by Hueber and Banks (1967) which established a neotype specimen to validate the species *P. princeps*. Like White (1905) they urged the selection of Dawson's (1871) sterile axes, *Psilophyton princeps* var. *ornatum*, as the type of *P. princeps*. However, their specimens from Siberia were richly covered by lateral sporangia like those reported by Hueber (1964b) and by Croft and Lang (1942). White, on the contrary, assumed that the spiny axes bore terminal sporangia. Hueber and Banks showed that terminal sporangia were central to Dawson's concept of his genus. Thus according to International Rules of Botanical Nomenclature the selected neotype should bear terminal sporangia. We suggest, therefore, that the excellent specimens of Ananiev and Stepanov be transferred to *Sawdonia ornata* (Dn.), Hueber, 1971, and be placed in Zosterophyllophytina.

Numerous other species of *Psilophyton* have been named on the basis of sterile specimens. Some undoubtedly will be proven to belong to the genus and probably some belong to other genera. Our purpose has been to show that a) Dawson confused parts of two taxa representing two different subdivisions, b) Lang and Croft and Lang similarly had specimens of the two subdivisions almost inextricably confused, c) that it has taken over one hundred years to secure enough data to clarify the true situation, and d) that one must have more than dichotomizing, spiny axes to identify a specimen of *Psilophyton* or of *Sawdonia*. We do not propose here an exhaustive analysis of all plants previously assigned to the genus.

LOCALITIES AND STRATIGRAPHY

Locality 1. Specimens in the Cornell University Paleobotanical Collection were obtained from various levels in the cliffs (Pl. 17, fig. 1) along the beach between Douglas-

town and Seal Cove (Anse aux Loups-Marins) on the south side of Gaspé Bay, Quebec, Canada. From the same general area we used an additional specimen in the paleobotanical collections of the United States National Museum that is recorded as USNM loc. 14251, a site 48°40'32" North and 64°20'8" West, Range I Bois Brulé, Douglas Township, Gaspé, Quebec, Canada. McGerrigle (1950) included a useful map of the area: Malbaie Sheet No. 665.

The fossiliferous horizons belong to the continental Battery Point Formation which is generally regarded as Emsian to early Eifelian in age (McGregor, 1967, 1973). The lower (older) assemblage is similar to Lower Devonian assemblages at other localities in the world. In the middle of the Battery Point Formation, with no evidence of a stratigraphic break, the lower assemblage is replaced rapidly by one containing species characteristic of Eifelian and Givetian strata in Scotland and the U.S.S.R. Similar rapid floristic changes during Emsian have been recorded at other localities (see McGregor, 1967, p. 179). It is not yet clear whether the upper part of the Battery Point should be regarded as early Middle Devonian (Table 1). Our fossils are associated with the lowermost part of McGregor's (1967) upper spore assemblage (McGregor, Geological Survey of Canada Report No. F1-7-1972-DCM pers. comm.) and, therefore, are probably from Lower Devonian, late Emsian strata. Nevertheless we must emphasize that their position is close to the Lower-Middle (Emsian-Eifelian) Devonian boundary because there is no proof that the abrupt change in composition of the spore flora coincides with the Lower-Middle Devonian boundary. McGregor (1967) suggested the interesting possibility that a new flora rather suddenly began to invade and displace the earlier flora. This floristic change could have occurred late in Early Devonian time or early in Middle Devonian time. It need not have occurred simultaneously with an Early-Middle Devonian boundary. The fossil plant remains occur in cobbles and boulders of clay that were laid down in coarse, water-deposited sands and pebble conglomerates. The sediments were subsequently consolidated then lithified by precipitation of calcium carbonate. It would appear, at the locality, that mineralization and resultant petrification of the plant remains took place after deposition of the cobbles and boulders and not prior to their removal from an earlier site of burial. The specimens in the USNM collection differ only in that the sediments enclosing the plant remains are a medium-grained sandstone rather than mudstone.

Locality 2. This locality has been assigned number 6435 in the records of the Department of Energy, Mines, and Resources of the Geological Survey of Canada in Ot-

tawa. It is near latitude 50°13' North and longitude 81°38' West on the Abitibi River, Moose River Basin, James Bay Lowland, Ontario, Canada. Precisely, the site is an eight to twelve inch stratum of micaceous, medium-to fine-grained sandstone on the west bank of the River, below Sextant Rapids, above Coral Rapids, and directly opposite the south end of a red outcrop, 400 feet in length, located on the eastern bank. Maps as references in locating the site are entitled "Southern Part of James Bay Lowland - Index Map of Fossil Collections" and Map No. 1952-1953 - Southern Part of James Bay Lowland" (geologic map) and are attached to Martison's report (1953) on the geology and petroleum potential of the area. This horizon is a part of the non-marine Sextant Formation which is considered to be middle to late Emsian age (McGregor, Sanford, and Norris, 1970) (Table 1) on the basis of dispersed spores.

The first identification of plant fossils from the Sextant Formation is found in Martison's report (1953, p. 30) where the late W. A. Bell is cited as identifying *Drepanophycus spinaeformis* Goeppert and sympodially branched, longitudinally striated stems probably conspecific with *Dawsonites arcuatus* Halle. The latter specimens were probably examples of our new *Psilophyton dawsonii*. Plant remains were found to be locally abundant at several horizons along the outcrops on the west bank of the river during field studies undertaken by McGregor and Hueber in 1961. Hueber (1964b) added *Sawdonia ornata* (his *Psilophyton princeps* of 1964b) to the floral list.

MATERIALS AND METHODS

In the early 1930's the late Professor L. C. Petry of Cornell University discovered calcareous cobbles embedded in the sandstone cliffs at Locality 1 (Pl. 17, fig. 1). His collecting, several trips by Banks to the same locality, and more widely ranging expeditions by Hueber in New Brunswick and Ontario have resulted in a good collection of *Psilophyton*. The present account is confined to two localities in order to keep its size manageable. Running more or less parallel through the limey clay cobbles and boulders are petrified parts of *Psilophyton*. Selected specimens were cut into blocks, numbered, and peeled serially using standard coal ball techniques. Where measurements were essential, as with sporangia, the blocks were ground on a Croft parallel grinder. Altogether several thousand peels have been made and examined.

Some axes were macerated out of the matrix using hydrofluoric acid which, because it does not dissolve the carbonates in the lumens of the cells, left small branches intact,

		STAGES	FORMATIONS	
		W. Europe	Moose R. Basin N. Ontario	E. Gaspé Quebec ¹
DEVONIAN	Upper			
			Long Rapids	
	Middle	Givetian		
			Williams Island	
		Murray Island		
		Eifelian		
	Malbaie			
				?
Lower	Emsian	Moose River	Battery Point	
		Kwataboahegan		
		Sextant		
	Siegenian	Stooping River	York River	
			Grande Grève	
				Cap Bon Ami
	Gedinnian	Kenogami River	St. Alban	
	Griffon Cove R.			
SILURIAN				

Table 1. Correlation chart showing the position of the Sextant Fm. at Abitibi River and the lower portion of the Battery Point Fm. on the Gaspé Peninsula. From McGregor, Sanford, and Norris (1970). ¹Modified from Boucot, *et al.*, (1969).

although often coated with insoluble whitish fluorides. These branches were then imbedded in bioplastic, a methyl methacrylate resin, as visual evidence that successive dichotomies were produced at right angles to one another (Pl. 17, fig. 5).

Other fragments were prepared by bulk maceration in concentrated hydrofluoric acid, washing, and clearing in Schulze's solution (HNO_3 and KClO_3). Clearing was also

carried out using hydrogen peroxide or dilute sodium hypochlorite (Pl. 23, figs. 53-55).

Both axes and sporangia were demineralized, embedded in paraffin and microtomed (Pl. 18, fig. 16, Pl. 19, fig. 24, Pl. 23, fig. 52).

Plants at the Abitibi River locality occurred as compressions in medium-to fine-grained sandstone with occasion-

al lengths of axis preserved by iron pyrite. Some were uncovered (Pl. 17, fig. 3) using steel needles under a binocular dissecting microscope at 10-30X magnification (dégagement of Leclercq, 1960). Petrified axes were embedded in plastic, sectioned, impregnated with resin, and ground. Grinding was carried to the level of 800 grit and the surfaces then polished with chromium oxide on a glass plate.

Sporangia were macerated from the matrix using concentrated (48%) hydrofluoric acid. After several washings through ten changes of water, some of the sporangia were stored in glycerine jelly and others were treated with Schulze's solution. Oxidation in Schulze's solution disintegrated the sporangium walls and freed the spore masses or, in the case of empty sporangia, freed the saclike membrane that surrounded the spore masses. Specimens were mounted as temporary mounts in glycerine jelly for the purpose of photography.

Photography was done on a Zeiss photomicroscope and a Leitz Aristophot.

DESCRIPTION

A. ANATOMY

1. Histology

Main axes are frequent in the Gaspé cobbles. In transverse section they are slightly compressed because the inner cortex has usually been lost by decay (Pl. 20, fig. 30). When living, the axes were certainly terete. A single, cylindrical strand of primary xylem and an outer, resistant cortex are always preserved (Pl. 20, figs. 30, 31), a narrow zone of phloem and a parenchymatous inner cortex occasionally (Pl. 18, fig. 18, Pl. 19, fig. 19).

The xylem strand when not branching consists of a single, central protoxylem surrounded by metaxylem (Pl. 20, fig. 30). Maturation is centrarch. Protoxylem consists chiefly of narrow spiral and scalariform elements (Pl. 19, figs. 21, 22, 25). Metaxylem tracheids are long, tapering, and approximately 60-80 μ in diameter. All walls are scalariform (Pl. 19, figs. 23-26). Sectional views (Pl. 19, figs. 27-28) demonstrate that the scalariform bars are bordered, hence that the tracheids have scalariform bordered pits. Between the scalariform bars the deposition of additional secondary wall material has outlined horizontal rows of circular, pitlike areas (Pl. 19, figs. 23-24). This additional wall material may even resemble vertical striations (the Williamson's striations of lepidodendrids) between the scalariform bars (Pl. 19, fig. 25) although this is not a frequent appearance. One or two rows (Pl. 19, figs. 23-24, 26) of pitlike

areas are frequent, three rows are seen rarely. The number of pitlike areas in a row varies from 10-14; usually the wider the tracheid, the more numerous the circular areas.

Phloem is only rarely preserved immediately centrifugal to the xylem. It is a uniform zone composed of two to six layers of thin-walled, narrow, tangentially elongated cells (Pl. 19, fig. 19). In longitudinal section they are vertically elongated, with slightly oblique end walls (Pl. 19, fig. 20). No sieve areas have been observed.

Inner cortex is best preserved in slender branchlets where it consists of narrow, thin-walled, loosely arranged parenchyma cells that are rounded or polygonal in transverse section and vertically elongate-rectangular in longitudinal section (Pl. 18, fig. 18).

The absence of inner cortex often results in a change of position of the xylem strand during fossilization. It may appear in an eccentric position (Pl. 20, fig. 34). Simultaneous twisting of the strand sometimes results in apparent changes in the orientation of the protoxylem strands and consequently of the emission of lateral branches.

The outer cortex is usually well preserved (Pl. 18, figs. 12-14). It is composed of large, thick-walled cells which in longitudinal section have transverse to slightly oblique end walls (Pl. 18, figs. 16, 17). It is thus collenchymatous in appearance. In some areas this thick-walled tissue is partially replaced by parenchyma (Pl. 18, fig. 12). Occasionally in such areas the cells appear to have disintegrated (Pl. 18, fig. 15). Often these areas are completely empty of cells or of cellular debris (Pl. 18, fig. 13). If we recognize various appearances of the cortex internal to the stomata as developmental stages (as in Pl. 18, figs. 12, 13, 15) it seems clear that substomatal chambers arise ontogenetically under the stomata whose guard cells can sometimes be recognized (Pl. 18, fig. 13).

Epidermis is rarely recognizable. In transverse section the cells are small and rectangular (Pl. 18, fig. 14). In longitudinal section they are longer than broad (Pl. 18, fig. 11).

The hypodermal nature of most of the outer cortex and the substomatal chambers suggest that the inner cortex functioned as assimilating tissue.

2. Dichotomy of the main axis.

Below a branching the xylem strand is terete and has a single, central protoxylem. In successively higher sections the protoxylem is divided equally, the two resulting strands are gradually further apart, the entire primary xylem is constricted, and finally there are two main strands each with its single, central protoxylem (Pl. 20, fig. 29). At a still higher level the axis itself is constricted and then separated into two equal branches.

3. Anatomy of fertile lateral branch systems.

The first indication that a main axis will produce a fertile lateral branch is a tangential increase in its protoxylem. Soon one strand of protoxylem is free in the primary xylem strand (Pl. 20, fig. 31). In successive sections this lateral protoxylem is further from the original strand (Pl. 20, fig. 32) and finally is free in its own metaxylem (Pl. 20, fig. 33). The protoxylem of the main axis remains elongated tangentially (Pl. 20, fig. 32) thus demonstrating that the next higher fertile branch will be produced on the opposite side of the axis, a distichous arrangement. The lateral structure is now a circular branch trace with one central protoxylem. Higher up the branch trace is rectangular in shape and its protoxylem has become elongated (Pl. 20, fig. 34). By the time the branch is free from the main axis its protoxylem strand has dichotomized twice (Pl. 20, fig. 35) and soon there are three separate xylem strands (Pl. 20, figs. 36, 37). These two dichotomies are expected to result in three branches and at first this seems possible (Pl. 21, fig. 38). However, at a higher level, one of the three branches usually aborts. In this case it is the central branch that is aborting (Pl. 21, fig. 39). Each of the two branches that remains again undergoes two close dichotomies and again one of the three resulting branches aborts (Pl. 21, fig. 40). The fertile branch system now consists of four equal branches. On a compression specimen that branches in this way one sees what appear to be two, successive dichotomous forkings often with a peculiar fragment of a branch between the arms of the dichotomies. (Pl. 17, fig. 4). We refer to these unusual branchings as *double dichotomies* in order to emphasize that two dichotomies do occur each time and to explain the appearance of an aborted branch between two fully grown branches. We have observed these double dichotomies so many times that we believe they represent the usual pattern for the first two divisions of the fertile branch system of *Psilophyton dawsonii*. It seems likely that in exceptional cases there is no abortion and three branches develop from the double dichotomy.

Higher on the fertile branch system all forkings are strictly single dichotomies at successively closer intervals until all branches are terminated by sporangia. The beginning of one such dichotomy is shown in figure 41, Plate 21. Transverse and longitudinal sections of the final dichotomy whose tips bear sporangia are shown in figures 42, 43, Plate 22. It is clear (Pl. 22, fig. 43) that a large vascular strand extends into the base of each sporangium. Counting each double dichotomy as one branching this last forking (Pl. 22, figs. 42, 43) is the sixth and six seems to be the usual number of successive branchings of the fertile branch system.

Several features of the lateral branching system must be emphasized. 1) The branch trace is always rectangular in outline while its surrounding cortex is still attached to the main axis. This enables us to recognize the base of a fertile system even when its distal branchlets and sporangia are not preserved. 2) The first two divisions of the fertile system are closely spaced "double dichotomies" usually characterized by the abortion of one of the three resulting branches. 3) Successive divisions (six in all) of the fertile system occur at right angles, producing a three-dimensional branch system. 4. Anatomy of vegetative lateral branches.

One specimen has provided an unusually well-preserved example of extensive vegetative branching (Text-fig. 4). A large axis dichotomizes near the base of the specimen and the two new axes continue without change in diameter to the apex of the cobble. Both new axes produce lateral vegetative branches, one of them (B) giving rise to seven branches in the short vertical distance of 13-15 mm. This burst of branching is described in Part 3b - branch B and illustrated by Text-figures 9-12. Its good preservation permits a brief discussion of anatomical changes associated with the vegetative branching.

The stele of branch B below the level of profuse branching has a single, small protoxylem strand. Higher up it is enlarged and then much enlarged (Text-figs. 9d-g; Pl. 24, figs. 65, 64, 68). Two zones of primary xylem are clearly evident, a large, peripheral mass of metaxylem tracheids and an inner group of smaller protoxylem elements (Pl. 24, figs. 64, 68). The outline of the protoxylem soon becomes irregular and its continuity is broken during the rapid development of branch traces (Text-figs. 9f, g; 10a-c; Pl. 24, figs. 64, 63).

Traces to the sterile branches are essentially like the xylem of the main axis, circular in outline and with centrarch maturation (Text-figs. 10a-e; Pl. 24, fig. 62). Some of them are followed in a long series of peels, some disappear after a few peels, and one (No. 7 in Text-figs. 10b-e) fades out before it reaches the outer cortex of the parent axis. The bundles follow a steep course outward and as a result several are included within the cortex of the main stem (Text-figs. 10b-d).

The chief interest in this type of branching is the striking modification of the terete, centrarch xylem strand. The usual modification is a tangential elongation of the protoxylem (Pl. 20, fig. 31) which is related to the production of branches alternately first on one side then on the other, a distichous arrangement, basically a spiral referable to a $\frac{1}{2}$ phyllotaxy. The modification found in the area of vegetative branching is a considerable increase in the size of the proto-

xylem and its angularity in transverse section (Pl. 24, fig. 64). This change in contour of protoxylem is associated with the production of a large number of lateral branches in a close spiral and within an extremely short vertical distance. The enlarged central mass of xylem (Pl. 24, fig. 65) is associated with the origin of traces to this large number of lateral branches and by the time all of them are free, the individual traces are much reduced in size (Pl. 24, fig. 62) although clearly different from the usual pattern found in the axis (Pl. 24, fig. 69). Only one strand issuing from this large central mass assumes the typical configuration for an axis in the area of fertile branching. That is the one that continues the main axis (B) above the region of vegetative branching. It is shown in Plate 24, figure 66 which can be compared with Plate 24, figure 69 and Plate 20, figures 30-32. Plate 24, figure 66 represents a level slightly higher on the plant than Plate 24, figure 62. Thus *Psilophyton dawsonii* branches in a tight spiral and a loose spiral (alternate, distichous arrangement) depending on the level at which it is studied.

Also noteworthy is the rapid decrease in diameter of branch traces in the area of vegetative branching. Many of them arise as fairly large bundles but diminish rapidly in size in the cortex. See for example trace to branch 6 on Text-figure 10c, d and e or trace to branch 7 on the same figures. The latter disappears altogether in the cortex leaving no external evidence of its presence.

A further modification of the terete centrarch xylem strand is the apparent radial alignment of some of the increased metaxylem. This is shown well in Plate 24, figure 63 on axis B and near the origin of traces 5 and 6. This simulation of secondary xylem is perhaps only associated with the large increase in extent of the xylem strand. Nevertheless it is a tendency worthy of note. Plate 24, figures 64, 65, 66, 69, are all made at the same magnification in order to demonstrate the extreme enlargement of the central xylem just below the level of rapid vegetative branching and to contrast this large size with the usual size in the region of fertile branching (Pl. 24, fig. 69).

Plate 24, figure 66 shows a terete xylem strand above the vegetative branching, with an elongated protoxylem strand and a free branch trace (left). Slightly higher the branch trace is contained in its own cortex, is rectangular, and has three protoxylem strands (Pl. 24, fig. 67). This is the first double dichotomy at the base of a fertile branch.

B. MORPHOLOGY

1. Fertile lateral branch systems; based on Douglastown, Gaspé specimens: holotype 190, paratype 191.

a. Gross

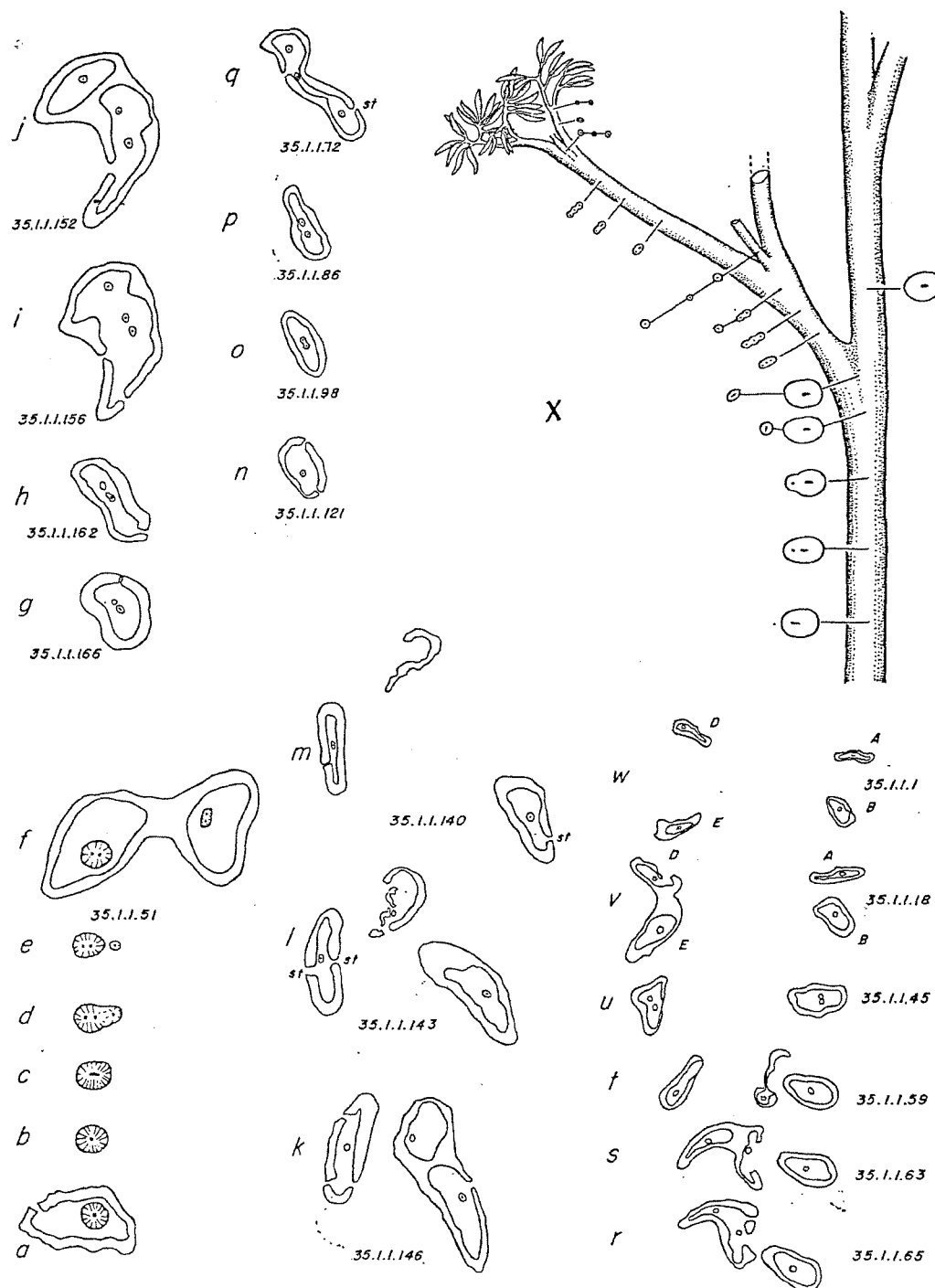
Our reconstruction (Text-fig. 13) shows a much-branched plant whose fertile lateral branches are produced alternately and distichously along the main axes. On the basis of serial peels we have reconstructed fertile lateral branches as three-dimensional systems with, usually, six successive divisions, hence seven orders of branch, the last of which are the short stalks of each sporangium. The first two divisions externally may resemble single dichotomies but as described earlier each one is in fact two closely spaced dichotomies of which only two branches develop. Sometimes the aborted remnant of the third branch can be seen between the two developed branches (Text-fig. 3x). Subsequent divisions are successively closer together and are dichotomous or slightly unequal. From the peels we conclude that these divisions occur at 90° angles to one another, resulting in a three-dimensional system. In order to confirm this we macerated some specimens in HF-HCl and extracted vegetative apices that retained two to four dichotomies. These were embedded in bioplastic (a methyl methacrylate resin) and photographed (Pl. 17, figs. 5, 6). All axes examined demonstrate that the plane of the dichotomies did in fact rotate 90° at each division.

There is of course much variation in the distance between successive dichotomies but Table 2 gives an approximation of the size of branching system.

b. Internal¹

Anatomically the production of a fertile lateral branch is indicated for the first time by a tangential enlargement of the protoxylem (Text-fig. 3c; 3x; Pl. 20, fig. 31). Slightly higher the new protoxylem is surrounded by its own metaxylem and a bulge appears on one side of the xylem strand (Text-fig. 3d; Pl. 20, fig. 32). Still higher a circular strand with a central protoxylem is free from the parent strand (Text-fig. 3e; Pl. 20, fig. 33). Slightly higher the new strand is located in its own axis. (Text-fig. 3f; Pl. 20, fig. 34) and it is rectangular in shape. The rectangular shape is partly the result of a tangential elongation of its protoxylem. The

¹ Text-figures 3, 5-12 are provided in order to supplement the reconstructions with anatomical details. Text-figures 5-12 are drawn to the same scale. Photographs of the peels were made at an enlargement of 20 times. Drawings were made from the photographs. These were reduced photographically. Thus all axes illustrated are shown in the same relationship to one another that they had in the peels and in the cobble except Text-figure 12 which is explained in the text and legend. Only the vascular strands and outer cortex are represented. Protoxylem is shown by a point or, if its size is greater, by an elongated solid line. Occasionally the number of protoxylem cells is much increased. This is shown by cross hatching and the surrounding metaxylem is then indicated by radial lines (see Text-figure 9).



Text-figure 3. Diagrams drawn from peels at successively higher levels from main axis to origin of fertile branches to sporangia. a) main axis; b-e) origin of trace to fertile branch, xylem only; f) with cortex; g-m) two dichotomies of trace followed by abortion of central

branch; n-t) similar "double dichotomy" of one of the two healthy branches in m — the other healthy branch divides similarly; u-w) first dichotomy of the two healthy branches in u (subsequent dichotomies omitted); x) reconstruction based on a-w.

Table 2. Length of successive axes of the fertile branch system and of sporangia.

structure	length (mm)
sporangia	3.0-4.2
axis 7 (in stalk of sporangium)	0.5-0.75
axis 6	1.5-2.0
axis 5	1.5-3.0
axis 4	3-5
axis 3	5-20
axis 2	5-20
axis 1 (up to the first double dichotomy)	up to 30

surrounding metaxylem is limited to two or three layers of cells. It must be emphasized that we have found this rectangular bundle repeatedly in sections at the base of fertile lateral branch systems. It is so constant that we are able to use it as an indicator of fertile branches even when the distal part of the fertile system was not preserved in a specimen. The rectangular bundle has a narrow, tangentially elongated area of protoxylem which divides into three separate strands. At higher levels first one and then the other lateral protoxylem group becomes a new bundle (Text-fig. 3 g-i; Pl. 20, figs. 35-37). Each of the three tiny new bundles is terete and centrarch. While still in a common cortex the distance between the two dichotomies is reflected by the distance between the three bundles. Shortly one, and then the other, of two axes becomes free (Text-fig 3k, l; Pl. 21, fig. 38). We refer to this pair of close branchings as a double dichotomy. At this point it is especially interesting to note that usually one of the three resulting branches diminishes in size and aborts. This phenomenon is illustrated in Text-figure 3 l and m; Plate 21, figures 39, 40. The aborted branch has been followed in one case for more than 5 mm but it is usually shorter. This may account for the failure to observe it on most compression specimens of *Psilophyton*.

We follow now the subsequent branching of one of the two remaining branches starting in Text-figure 3n. This branch, as well as the other which is not illustrated, divides in exactly the same fashion as before. The process of successive, close dichotomies (Text-fig. 3n-t; Pl. 21, fig. 40) followed by the abortion of one of the three resulting axes is repeated. The fertile system now consists of four slender axes (two of the four are shown in Text-figure 3x and one of the four in Pl. 21, fig. 41).

From this level upward four successive dichotomies occur singly. The first of these subsequent dichotomies is illustrated in Text-figure 3u-w. At the level of 3w, there is a total of 8 small branches. The next dichotomy results in 16 smaller branches and we find usually a third forking which results in a total of 32 still smaller branches. Each of

the 32 dichotomizes into a pair of terminal sporangia. (Pl. 22, figs. 42, 43). Counting the first two closely spaced "double dichotomies" each as one, this means the fertile system often shows 6 successive forkings and bears 64 sporangia, arranged in 32 pairs. The number 64 can vary by any one of several minor changes. One dichotomy may be suppressed, a dichotomy may be added somewhere in the system, or one or more sporangia may abort. Finally, the number of sporangia would be increased markedly if the third branch at either of the first two double dichotomies were to develop rather than aborting. We have not actually observed these larger numbers but some specimens seem not to show abortion of a branch during the lower divisions and lead us to expect that the increased numbers may actually occur from time to time.

The histology of the smaller branches is similar to that described for the larger axis. Their xylem strands are still terete and centrarch. Their inner cortex is usually not preserved. When preserved it consists of narrow, thin-walled cells. Their outer cortex is reduced to two or three layers of hypodermal tissue and stomates and epidermis are often seen clearly.

The fusiform sporangia are borne in pairs on short stalks. They range from 3 to 5 mm in length and 1.0-1.5 mm in width. They widen from a narrow base and then taper distally (Pl. 22, figs. 43, 50, Pl. 23, fig. 51), sometimes to a point as though they were terminated by a spinelike beak which usually broke off during fossilization.

The distance between successive dichotomies of the fertile branching system is progressively less distally. Hence young sporangia often appear in close clusters (Pl. 22, fig. 44). As maturation continues the pairs of the clusters become somewhat more distant (Pl. 22, fig. 49). This ontogenetic change is reflected in the attitude and content of sporangia as well. Sporangia can be found on the broken surface of specimens from Douglstown, Gaspé (Pl. 22, fig. 50). These recurved, but not tightly recurved sporangia, still contain spores and represent the often figured attitude of sporangia of the genus. On Text-figure 13 however some fertile branching systems are shown terminated by sporangia in various attitudes, recurved, horizontal, and erect. This reconstruction is a faithful representation of empty sporangia that were revealed only in serial peels. The fact that all have dehisced and that they are no longer in tightly recurved groups leads to the conclusion that as sporangia matured and dehisced, they were borne in a more widely spread cluster. Specimens from Abitibi River to be described below confirm this conclusion.

Most striking is the resemblance of the anatomical

structure of sporangia to that of vegetative axes as shown by transverse and longitudinal sections just distal to, or at, the final dichotomy of the xylem at the base of the sporangia (Pl. 22, figs. 42, 43). One branch of xylem enters each sporangium. Clearly the ratio of diameter of xylem to diameter of axis is the same in the base of the sporangia as in large axes, and this xylem extends up to the sporogenous tissue of the sporangium. Similarly the sporangial wall itself (Pl. 22, figs. 44-48) is comparable to the cortex of the axes. The outer two or three layers of cells are hypodermal like the corresponding layers in the axis. The inner two to four layers are parenchymatous (Pl. 22, figs. 44-47) like the inner cortex of axes. Even stomata and substomatal chambers are like those of axes (Pl. 22, fig. 45). Epidermis is rarely observed but a cuticle-like layer is sometimes present.

Maturation of sporangia involves breakdown of parenchymatous wall layers (Pl. 22, figs. 44-48). Simultaneously the inner tangential walls of the innermost parenchyma break away as an intact membrane (Pl. 22, fig. 48). This membrane normally remains inside the sporangium, attached at either side of the region of dehiscence (Pl. 22, fig. 49), and often breaking opposite the region of attachment. Plate 22, figure 49 shows a cluster of four dehiscent sporangia more distantly arranged than the four immature ones shown in figure 44, Plate 22. The mature sporangia illustrate the dehiscence that is longitudinal along facing surfaces. This results in pairs of C-shaped, empty sporangia (Pl. 22, fig. 49).

Intact sporangia are found on compression specimens collected at the Abitibi River locality (Pl. 23, fig. 51). Some of these sporangia were demineralized, embedded in paraffin, and sectioned on a microtome. The sections revealed the same inner, translucent layer that Lang found in the sporangia from three different localities inside a thick carbonized wall (Pl. 23, fig. 52). In order to relate these two layers to the structure seen in petrifications, similar sporangia were macerated and thin sacs filled with spores were released from them. Full sacs are shown on figure 51, Plate 23, and at a higher magnification in figure 53, Plate 23, where both full and empty sacs are illustrated. Both were obtained from sporangia by maceration. Sporangia from Douglstown were macerated in the same way in order to compare plants from the two localities. Again we obtained both intact membranes containing spores and membranes that were free of spores (Pl. 23, figs. 54, 55). We believe that the cellular pattern on the membranes is that of the inner, parenchymatous wall cells of the sporangia. The anticlinal walls of these parenchyma cells broke down but

their inner tangential walls remained connected to form the sac. The sac may have been reinforced by deposition of end products of the disintegration of the tapetum.

Masses of spores, apparently representing all those found in one sporangium, are often abundant in the matrix (Pl. 23, fig. 57). It is not possible to determine whether they were released naturally by dehiscence or whether they were masses of immature spores freed by the decay of sporangial walls. The abundance of these spore masses is predictable when it is recognized that the sporangia are borne in masses of up to 64 or more, the number dependent on normal or abnormal branching of the lateral axis.

Spores occur variously in our material, some *in situ* in attached sporangia, some in masses that were released naturally from sporangia, and some removed from sporangia by maceration. Many of them, both inside and out of sporangia, have been compressed in a polar direction, resulting in a cup-shaped object with the firm proximal surface pressed against the distal surface. This compression can occur while spores are still arranged in a tetrad. As a result, the trilete mark appears to be on the distal surface (Pl. 23, fig. 60), where it is seen through the transparent distal exine.

The spores range from 40-75 μ in diameter. The equatorial contour (amb) is circular to subcircular (Pl. 23, figs. 58, 56). Contact areas are distinct, outlined by a simple trilete mark which extends $\frac{1}{2}$ or more the length of the radius. Its connection to the curvaturae is not obvious. Curvaturae usually follow the equatorial margin. The trilete mark is composed of three simple commissures, surrounded, or outlined, by a darkened triangular area (Pl. 23, figs. 58, 56, 59, 61), whose sides are variously straight or concave. The commissure is occasionally split open (Pl. 23, fig. 61).

The exine of the spores is smooth and unornamented. This statement requires some explanation. Within the sporangium, while the spores are still in tetrads some form of deposit is laid down on and around the spores (Pl. 23, figs. 59, 60 at C). This envelope appears to be minutely ornamented. However, it is not dispersed with the spores. Occasionally, for example, the envelope may break away from the spore as a thimble-shaped structure. This is illustrated (Pl. 23, fig. 58) in the case of a spore that has separated from a tetrad. Besides the spore, which now has a smooth exine, lies part of the envelope that formerly covered it. The envelope or thin membrane may be a perispore which is just as prominent between the spores (Pl. 23, fig. 59) as it is on them (Pl. 23, fig. 60 at C). It may be a product of tapetal fluids. In any case, the exine of the spores, once freed from the surrounding membrane, is smooth (Pl. 23,

figs. 56, 58) and the spores fit the *Infraturma Laevigati*. These spores if found as sporae dispersae would be placed in *Retusotriletes* (Naumova), emend Streel, 1967, and they are probably closest to *R. triangulatus* (Streel), 1967. Following Mortimer (1967) they would more likely be placed in *Phyllothecotriletes*.

Both Streel and Richardson examined the spores in our material and Streel published (1967) the illustration we use as figure 60, Plate 23, as well as one essentially identical to our figure 58, Plate 23. Richardson (1969) figured a *Retusotriletes triangulatus* from the Welsh Borderland on his plate 11-2 as figure 1 and commented (p. 211) on its resemblance to our spore without its perispore. When the perispore is still present he considered that our spores resemble *Perotriletes* which is illustrated on his plate 11-3, figure 7. This figure can be compared with our figures 59, 61, Plate 23. Richardson and Lister (1969, pp. 217-218) also commented on the resemblance of our spores to *Cyclogranisporites* sp. from the lower Battery Point Formation, Gaspé Peninsula, as illustrated by McGregor and Owens (1966, pl. 2, figs. 18, 19). Those figures compare favorably with our fig. 61, Plate 23. *Retusotriletes* sp., (McGregor and Owens, 1966, plate III, fig. 1) is the smooth type (perispore removed) that ours resembles most closely. Thus despite the vagaries of identification of spores, it seems that we can be relatively confident of our interpretation and identification.

2. Fertile lateral branch systems — Abitibi River

Our reconstruction of fertile branches of *Psilophyton dawsonii*, made from several thousand peels, receives striking confirmation from the discovery of identical branching systems preserved as compressions, partially pyritized, along the Abitibi River, northern Ontario, Canada. The fossils occur in a soft sandstone ideally suited to the uncovering technique of Leclercq (1960). Hueber demonstrated the production of fertile branch systems in an alternate, distichous arrangement along a main axis (Pl. 17, figs. 2, 3). On the proximal divisions of the fertile branch he found evidence of abortion thus indicating "double dichotomies" as on the Gaspé Peninsula. This feature is illustrated specifically by the abortion we found in Halle's Rörägen material (Pl. 17, fig. 4). Subsequent divisions of the Abitibi branches were single dichotomies and they occurred at a 90° angle to one another producing a three-dimensional system. This meant that as branchlets were uncovered, it was necessary to remove certain of them in order to uncover more deeply in the matrix. Where possible the sporangia that were removed were treated with HF and preserved in glycerine jelly. Fig-

ure 3, Plate 17, therefore, shows the end result, many branchlets and sporangia having been removed and counted before reaching the stage illustrated. Ultimate branchlets were terminated by pairs of recurved sporangia (Pl. 23, fig. 51) like those found on the Gaspé specimens (Pl. 22, fig. 50).

The anatomy of the Abitibi material is also identical to that from Gaspé. A portion of a series of sections preserved by pyrite is shown in Plate 17, figs. 8-10. Protoxylem, metaxylem, and branch trace all act exactly as in our Gaspé peels. Metaxylem tracheids (Pl. 17, fig. 7) show the same scalariform pitting and interconnections between the bars producing pitlike areas. The branch traces followed outward undergo two close dichotomies like those shown in figures 36-40, Plates 20-21, for Gaspé material.

Details of sporangia revealed by maceration and by microtome sections of paraffin embedded sporangia further confirm the identity of the two collections. Inside each sporangium is a thin membrane (Pl. 23, fig. 52) that can be released by maceration. The membrane proves to be a sac either full or empty of spores (Pl. 23, fig. 53). Our Gaspé peels shows the same membrane (Pl. 22, figs. 48-49) and our macerations disclose the same kind of sac (Pl. 23, figs. 54, 55).

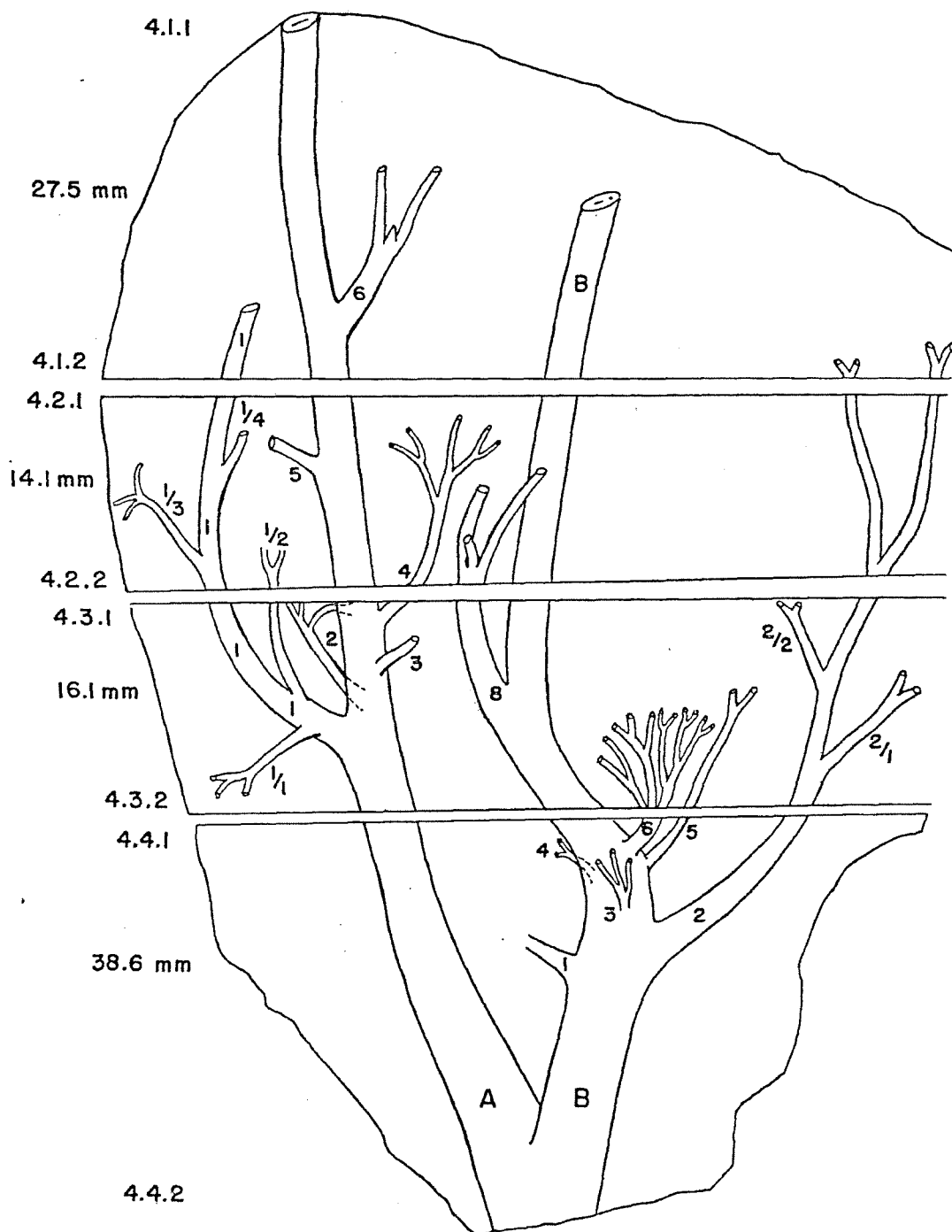
One difference between *P. dawsonii* on the Gaspé and at Abitibi River is the more marked incurving of the latter sporangia. They are also usually filled with spores. The majority of sporangia in the Gaspé specimens are empty. Hence we explain the difference in attitude and content of sporangia as indicative of an age difference, an ontogenetic feature. Streel (personal communication) has seen spores from both Gaspé and Abitibi River material. Without any information about the attitude and apparent age of the sporangia he suggested that the spores from Abitibi River were younger than those from the Gaspé. Therefore, on the reconstruction (Text-fig. 13) we have shown the more terminal fertile branches to have younger, more incurved sporangia (Abitibi River) and the more proximal ones (Gaspé) to be variously disposed, older, and presumably empty.

We regard the Abitibi River collection as providing unusual and striking support for our interpretation of the anatomy, morphology and habit of *Psilophyton dawsonii* that are based on the study of "serial" peels of *P. dawsonii* from the Gaspé Peninsula.

3. Vegetative lateral branching system: Douglstown, Gaspé. Specimen: paratype 192

a. Axis A.

We describe in detail a vegetative branching system



Text-figure 4. A reconstruction of the vegetative branching of *Psilophyton dawsonii* as found in specimen 192 from Gaspé Peninsula. Note the irregular spiral arrangement of the lower branches on both main axes and the alternate, distichous arrangement higher up on the axes. Branches 6 on axis A and 8 on axis B are both believed to be

bases of fertile branch systems. Branches are numbered and the order of their subdivisions is indicated by a slash, e.g. first branch of branch 1 is 1/1. Thickness of the four blocks is given in millimeters and the numbers of the cut surfaces are indicated on the left. Reconstruction not to scale but approximately $\times 3$.

found in specimen 192 for three reasons. First we have followed the system throughout the specimen. Second the specimen contains the most extensive vegetative system we have found and details of the vegetative branching *Psilophyton* have heretofore been unknown. Third, and most important, it bears the lower parts of fertile branching systems as well as the sterile. Specimen 192 was 10.24 cm in length. It was cut into four pieces (Text-fig. 4). The two main axes referred to as A and B are outlined in the sketch of the specimen.

At the base of the specimen there is a large axis which soon dichotomizes. Each of the axes produced branches so extensively and remains so large that we have designated them A and B in order to describe them separately.

Peels from the base of the specimen show an axis whose stele is in the process of dichotomizing (Text-fig. 5a). The stele in cross section is elongated and has two protoxylem strands. The metaxylem and cortex are identical to the same tissues in axes of the fertile branching system. Somewhat higher the amount of protoxylem is greater and both the stele, and then the axis, dichotomize (Text-fig. 5b-d). From this level onward we shall follow only axis A. Note however that the stele of axis B elongates quickly and soon shows three protoxylem areas (Text-fig. 5d). This demonstrates that axis B will branch soon and at a lower level than axis A.

The stele of axis A remains unchanged for more than 3.5 cm and then begins to branch. The successive lateral branches of axis A are numbered 1-6 (Text-fig. 4). Branchlets produced in turn by them are indicated by a slash, for example 1/1, 1/2, 1/3.

Text-figure 5g, from a higher peel, shows the stele of branch 1 free from that of axis A. It is smaller and is centarch. The first lateral of branch 1 curves downward. This is demonstrated by the appearance of ultimate sterile tips on the left side of Text-figure 5g. The several branchlets (a, b, c) at the apex of lateral 1/1 are produced by dichotomous divisions. In Text-figures 5h-j the curved stele of branch 1/1 is seen joining the stele of branch 1 which in turn is producing the vascular supply of its second lateral (1/2). In Text-figure 5k the stele of 1/2 is free and axis A has produced the vascular strand for its second lateral branch (2).

In Text-figure 6a axis A is giving rise to a third lateral (3). Meanwhile branch 2 has become free and has produced its first lateral, 2/1 which is bent downward from its insertion on 2. Its attachment to branch 2 will be seen in the next illustration. In subsequent peels the xylem of branch 2 dichotomizes, suggesting that it terminated in sev-

eral small appendages. Branch 1 and its second lateral are both well preserved.

In Text-figure 6b the union of branch 2/1 with its parent 2 shows that the former did in fact bend downward. Axis A and branches 1 and 1/2 have changed little from the previous figure. Branch 3 disappears quickly.

In Text-figure 6c we illustrate only the origin of a fourth lateral from axis A and the diminishing size of branch 2.

Text-figure 6d shows the stele of branch 4 free from the main stele although still within a common cortex. Branch 2 and its ultimate divisions have now terminated.

Text-figure 6e illustrates axis A, its fourth lateral, 4, and the second lateral produced by branch 1 which itself is now producing a third lateral, 1/3.

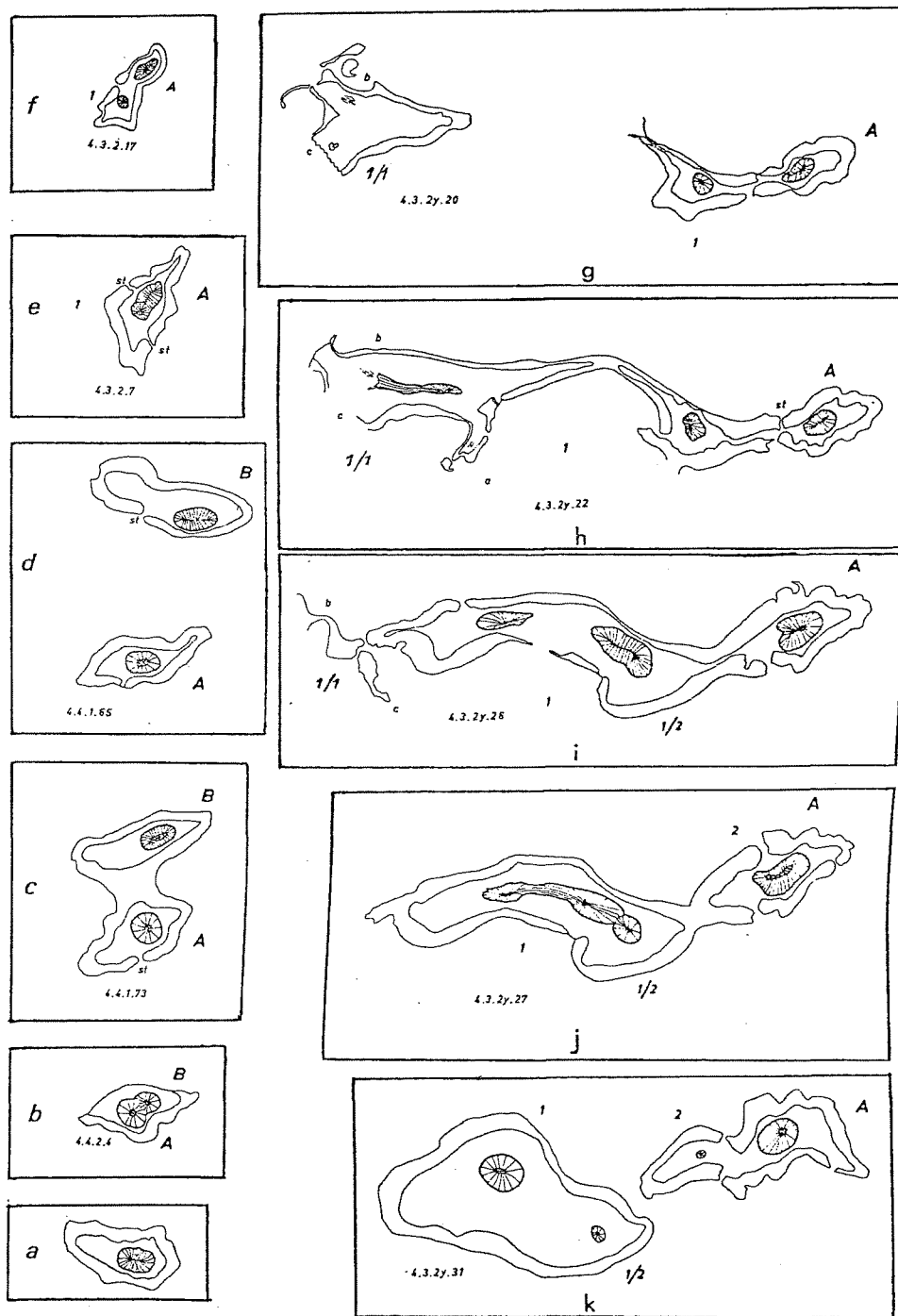
Text-figure 6f shows axis A little changed. Branch 4 is cut obliquely. Trace 1/3 is free from the stele of branch 1 and branch 1/2 is cut at a higher level.

In Text-figure 7a the main axis is unchanged. The third lateral, 1/3, from branch 1 is free and a bundle of a fourth lateral, 1/4, is free from the parent stele but is still within the same cortex. Branch 4 is in the process of rapid division. The stele of its first lateral, 4/1, has already divided and a trace to a second lateral branch has already been produced.

In Text-figure 7b axis A shows the first evidence of a fifth lateral branch. It appears as a bulge on the margin of the xylem. Branch 1/3 is well preserved and the profuse branching of 4 is clearly evident. Branch 4/1 has dichotomized into two small axes. One of these 4/1 b has two bundles. This indicates it will produce still another forking. Branch 4 itself now contains 3 bundles which will supply 4, 4/2 and 4/3.

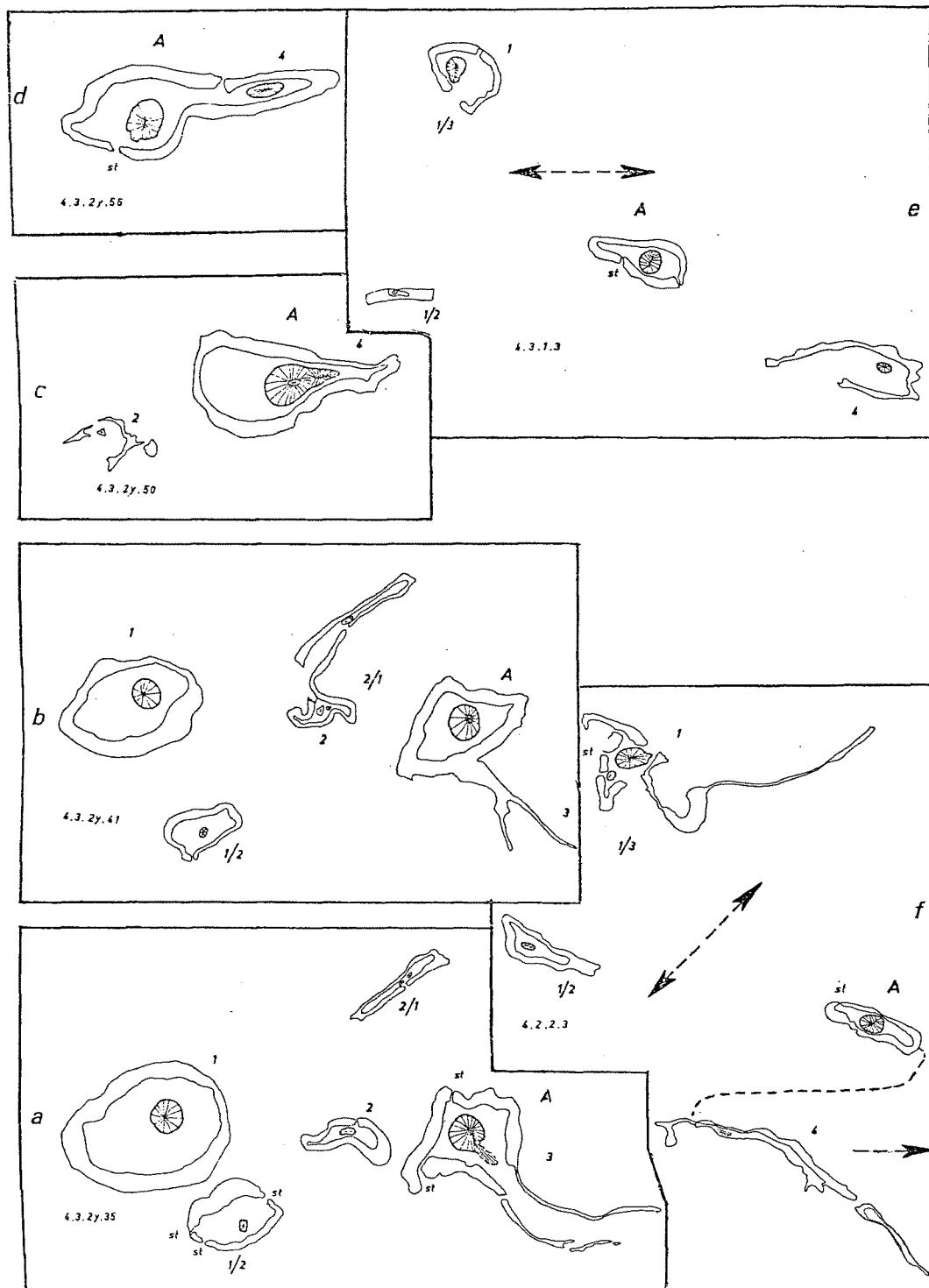
Text-figure 7c is taken near the termination of the sterile tips of branch 4 and its lesser branchlets. Branch 1/3 shows a division of xylem into three bundles that will soon appear in three sterile tips. Branch 1 is normal. Clearly its fourth lateral was preserved only for a short distance. Axis A and a small portion of its 5th lateral appendage are seen. Obviously this appendage bent downward quickly after its origin because here its stele has been cut twice, once in the cortex of axis A and once above axis A surrounded by a fragment of cortex.

Text-figure 8a shows the union of the downwardly bent branch 5 to its parent axis (A). Branch 1 is well preserved and branch 1/3 shows one of the three xylem groups now free from the other two. The subsequent subdivisions of branch 1/3 are our best example of delicate, recurved or



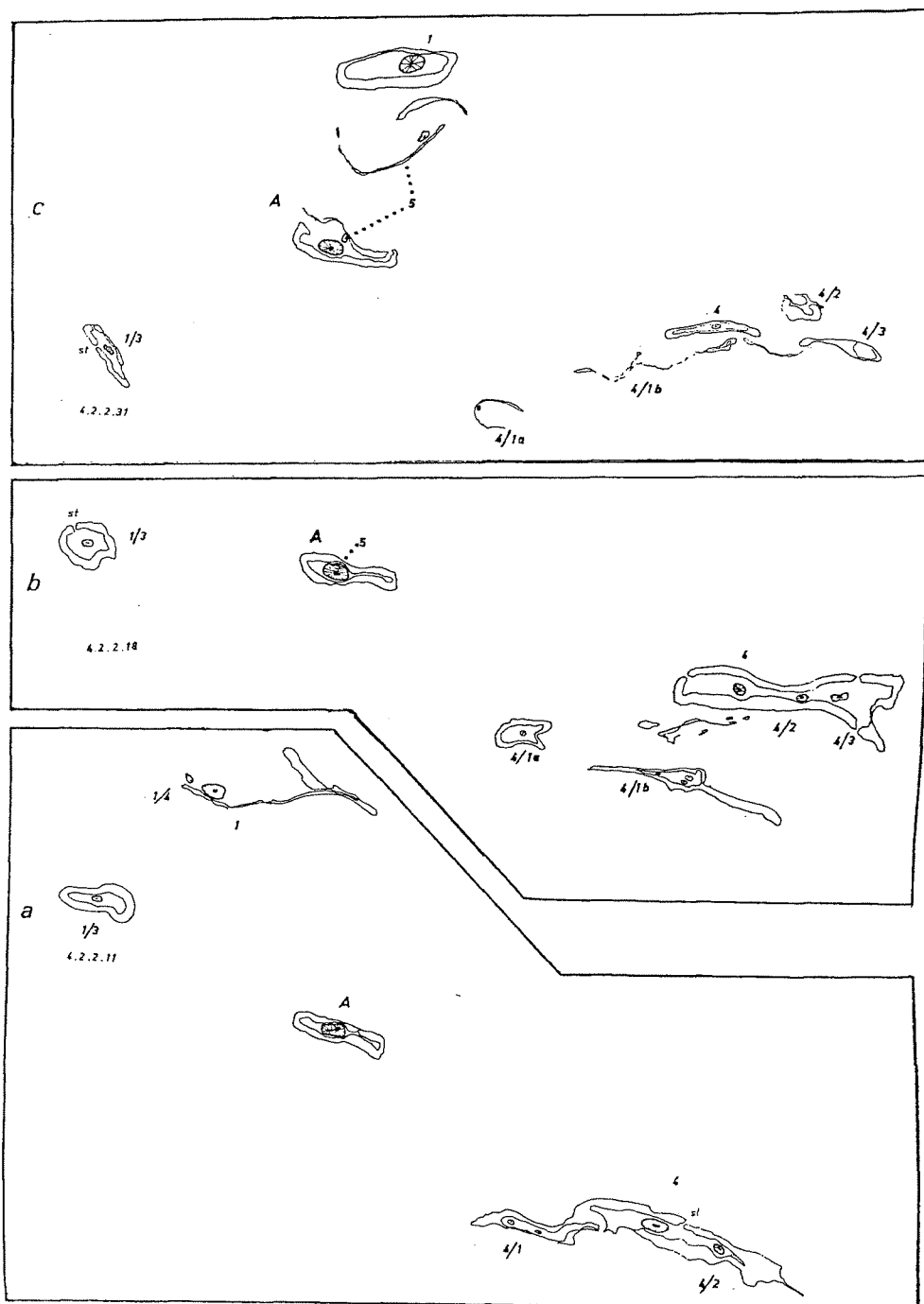
Text-figures 5-8. Selected peels, taken from base toward apex, illustrating details of vegetative branching of axis A (see Text-fig. 4). Text-fig. 5, a-k, lowest sections. Each diagram bears the number

of the peel from which it was made. Numbering on branches is as on Text-figure 4. st — stoma. See also footnote which applies to Text-figures 5-12. Full description in text; $\times 5$.



Text-figure 6. Selected peels, a-f, illustrating details of vegetative branching at a higher level than Text-figure 5. f has been rearranged

to fit the page. Description in text. All symbols as on Text-figure 5: $\times 6$.



Text-figure 7. Selected peels, a-c, from levels higher than Text-figure 6. Symbols unchanged. Description in text; $\times 6$.

straight, ultimate, sterile tips. Therefore, we have illustrated several successive peels in Text-figure 8h to show how branch 1/3 terminates in three slender, sterile divisions (1/3a, 1/3b, 1/3c). We believe this kind of branching characterized many of the ultimate divisions of the sterile branches. For example, in this particular series of peels, the endings of the branchlets produced by branch 4 (Text-figs. 7b, c) are the most similar to these terminations of branch 1/3.

Text-figure 8b shows axis A and the beginning of its sixth lateral branch. One sees only a slight bulge on one side of the stele. Branch 1 is still present.

In Text-figure 8c branch A is normal and branch 1 lies near the edge of the cobble, about to disappear outside it. Branch 6 now becomes particularly interesting (Text-fig. 8d) because its bundle has become rectangular, with three protoxylem strands like a bundle at the base of a fertile lateral branch system. For the first time axis A has behaved like a main axis bearing a fertile branch. Like a fertile axis, the rectangular bundle of branch 6 becomes three by two successive, close dichotomies (compare Text-figs. 8d-f with Text-figs. 3j, k).

Text-figure 8f shows axis A in the normal condition between branchings. Branch 6 now consists of three branchlets (6/1, 6/2, 6/3). The central branchlet is tiny and is in the process of aborting. The resemblance of this illustration to Text-figure 3k which is the first double dichotomy of an axis with attached sporangia (a fertile axis) is quickly apparent. It is most unfortunate that branch 6 now runs out of the specimen and can be followed no further. We are convinced however that branch 6 is in fact the first fertile lateral branch to be produced by axis A. Our conviction is based on the observation of this pattern of branching repeatedly in fertile branch systems of *Psilophyton dawsonii*. The branching illustrated in Text-figures 3i-m drawn from specimens 31 and 35 represents the pattern we have found to be constant in our specimens.

The final illustration, Text-figure 8g, is made from near the apex of the specimen. Only axis A which has been followed throughout the length of the specimen (10.24 cm) remains. Almost all of its branches were broken off at the time of breaking up and displacement of the masses of clay that contained the plant axes. However axis A was still vigorous at the top of the specimen. Its elongate protoxylem indicates the beginning of another branch that would have appeared at a higher level.

SUMMARY of branching of sterile axis A (Text-fig. 4, 13).

At the base of specimen 192 a typical centrarch xylem

strand dichotomizes. One axis, A, then soon produces four laterals in quick succession. Their precise arrangement is uncertain but they appear to be spiral. This may be related to the production of an unusually large central mass of protoxylem (Text-figs. 5d, e). This protoxylem condition is found only in regions of profuse and somewhat irregular branching. Higher up, alternate distichous branching appears as branches 5, 6 and a trace for 7 are produced at wider intervals. This arrangement is the one found in all of our specimens that contain only lateral fertile branch systems with sporangia in attachment. It is also typical of the compression specimens from Abitibi River that were uncovered by Hueber. Alternate, distichous branching also characterizes branch 1 which produces four laterals.

Interestingly, the first six branches of axis A are unequal in vigor. Branches 1 and 6 are both more vigorous than 2-5. Branches 2, 3, 4 and 5 are comparable in size to the laterals produced by branch 1 whereas branches 1 and 6 are more like major branch systems.

The sixth branch from axis A gives strong evidence that it is a fertile lateral axis. We were able to follow it up to its first double dichotomy. At this level one of its three branchlets aborts, exactly as in the fertile systems (Text-figs. 8d-f and 3j, k).

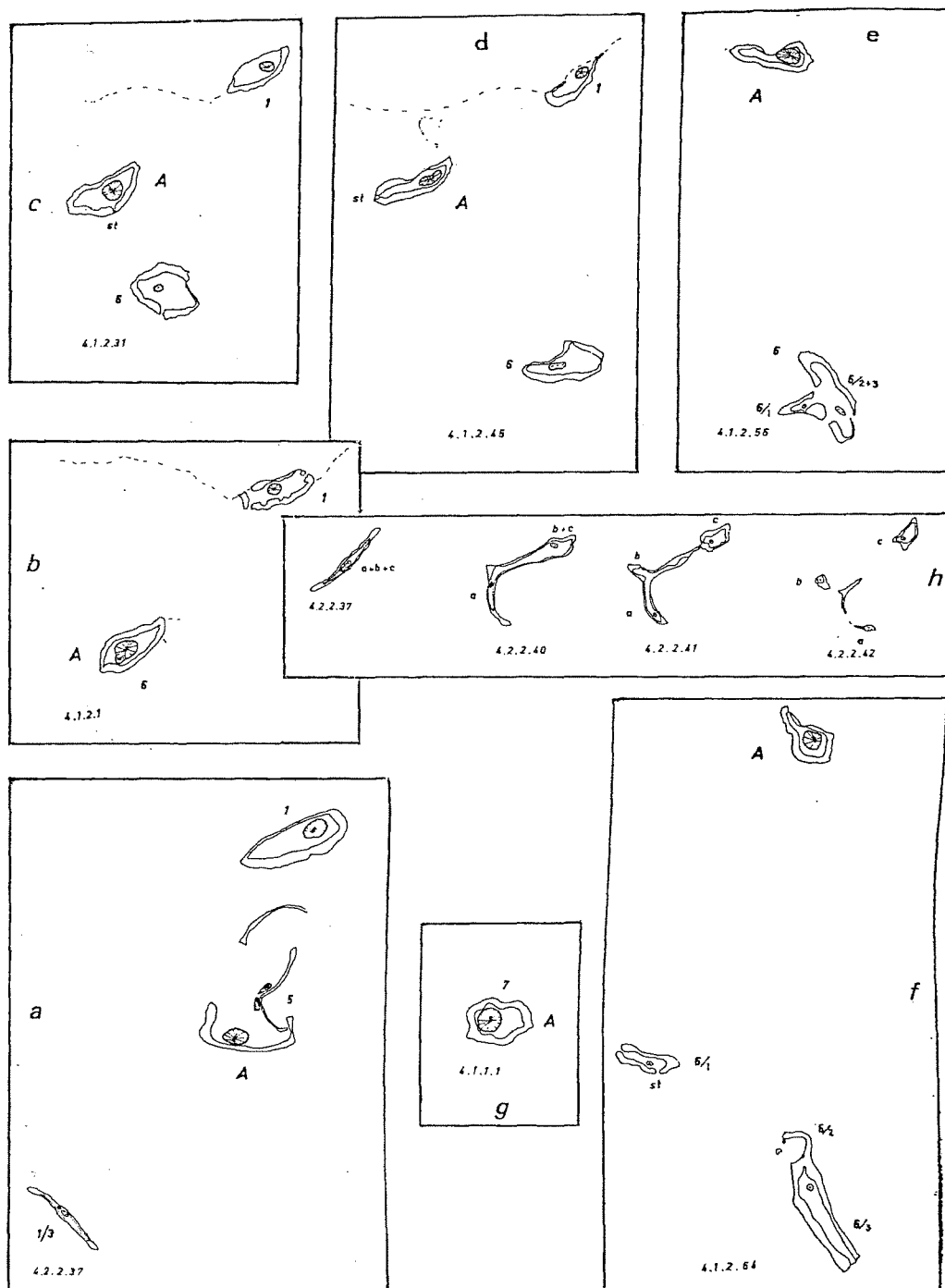
Axis A is still vigorous as the top of the specimen is reached and its protoxylem indicates the production of another (7) on the opposite side from branch 6, the alternate distichous arrangement which is usual for fertile branches.

We believe the above sequence demonstrates that large axes of *Psilophyton dawsonii* branched dichotomously, that at a higher level they produced a system of irregularly spirally arranged sterile branches terminated by sterile tips, and that still higher they bore fertile lateral branching systems. We note also that some laterals are more vigorous and branchlike whereas others are less vigorous and more leaf-like.

b. Axis B.

We showed the base of the sterile branching system in Text-figs. 5a-d and we followed axis B to a level just above a dichotomy. There it had three protoxylem areas. These demonstrate that axis B will soon produce lateral branches.

However, above this level, the xylem strand of axis B is suddenly absent and only fragments of its cortex remain. This situation is found in peels made over a distance of 4 mm. Then suddenly we find a naked stele with three protoxylem strands exactly like the stele seen below. Slightly higher in the specimen this naked stele is again surrounded



Text-figure 8. Selected peels, a-g, at a still higher level. Symbols unchanged. Description in text. Figure h shows several sections to illustrate the termination of a vegetative branchlet in three delicate apices; $\times 6$.

by normal cortex and the branch is again intact. We believe axis B was damaged and its stele broken but that it was held almost in place by the enclosing calcareous mud.

Text-figure 9a shows axis B above the break. It has three protoxylem strands. Higher up the stele is enlarged and the two lateral protoxylem strands become unequally distant from the central one. This is the first indication of a succession of lateral branches. Some of the fragments of cortex out of which the stele of axis B slipped are also shown.

In Text-figure 9b the origin of branch 1 is clearly visible as a large bulge on the left side of the xylem strand. The protoxylem of branch 2 is distinct on the opposite side of the stele.

Text-figure 9c shows stele B now surrounded by a considerable amount of broken cortex. Branches 1 and 2 are represented by xylem strands still enclosed in the cortex of axis B.

In Text-figure 9d the first lateral, 1, is seen to be completely free. It consists of a small, terete bundle and a narrow, broken cortex. Branch 2 is attached to the axis at an obtuse angle and therefore it appears, still connected, in several subsequent peels. The stele of axis B shows another bulge but one that is different from the usual type of emission of lateral bundles. The explanation will soon be apparent. At the same time the central group of protoxylem cells begins to be enlarged as shown by crosshatching.

Text-figure 9e shows the beginning of a profuse branching of the stele of axis B, and the starting point of a new behavior of the stele. Five branches (No. 3, 4, 5, 6, 7) of different sizes are produced in the vertical distance of only 2.5 mm. Here branches 1 and 2 are little changed. Axis B shows another new lateral trace, 3, which will be free slightly higher up. The stele of axis B elongates. Both its central area of protoxylem and its metaxylem are much enlarged (Pl. 24, fig. 68). For convenience we refer to this entire mass as B although very soon B and a cluster of branches will be separated out of the mass.

In Text-figure 9f, 10 and Plate 24, figs. 62-65 the striking features shown are the changes in size, form and structure of the stele of branch 3 which is enlarged. The stele is characterized by the enlargement of the central area of protoxylem, without the addition of parenchyma, surrounded by a peripheral zone consisting of large tracheids. Several small traces in the cortex arose by dichotomous divisions, an unusual origin when compared with branches 2 and 8 on Axis B and with branches 1, 4, 6 of axis A. On the side of the stele opposite branch 3 a bulge in the main stele repre-

sents part of the xylem of branch 4. The xylem strand of 4 apparently arched upward and then recurved. Evidence for this statement is provided by the trace of branch 4 that has been cut near the margin of the stem. Further evidence is the small strand of xylem that extends out of the main mass of xylem toward branch 4 (see Text-fig. 9g). Branch 4 is remarkably similar to 3. Both give rise to a cluster of tiny branchlets. Branches 1 and 2 in Text-figure 9f are little changed.

Particularly interesting at this point are Text-figures 9f, g, 10a, b, and Plate 24, fig. 63 because the massive xylem enlarges in a peculiar manner. Axis B is obviously bending to the left and is cut obliquely. Thus the xylem looks abnormally large. In addition the profusion of branches produced in a short vertical distance means that the large mass of xylem consists of the vascular strands of a number of branches. If this mass could be seen in three dimensions, it would be a compact mass with protuberances on all sides.

Text-figure 10a, Plate 24, fig. 63, show two new lateral bulges in the stele of axis B. They are numbered 5 and 6. Branch 5 already has its own centrarch protoxylem. Branches 3 and 4 are small and inconspicuous as is shown by the course of their bundles in Text-figures 10a-e. The curved mass of xylem of axis B is cut tangentially and is further attenuated.

Text-figure 10b shows the final separation of the bundles that comprised the large xylem mass called B up until this level. The strands to branches 4 and 5 are still in contact and a new trace has become obvious, trace 7. The xylem strand to branch 6 is apparent on the side of the stele of axis B. Branchlets from 3 are still attached to the axis.

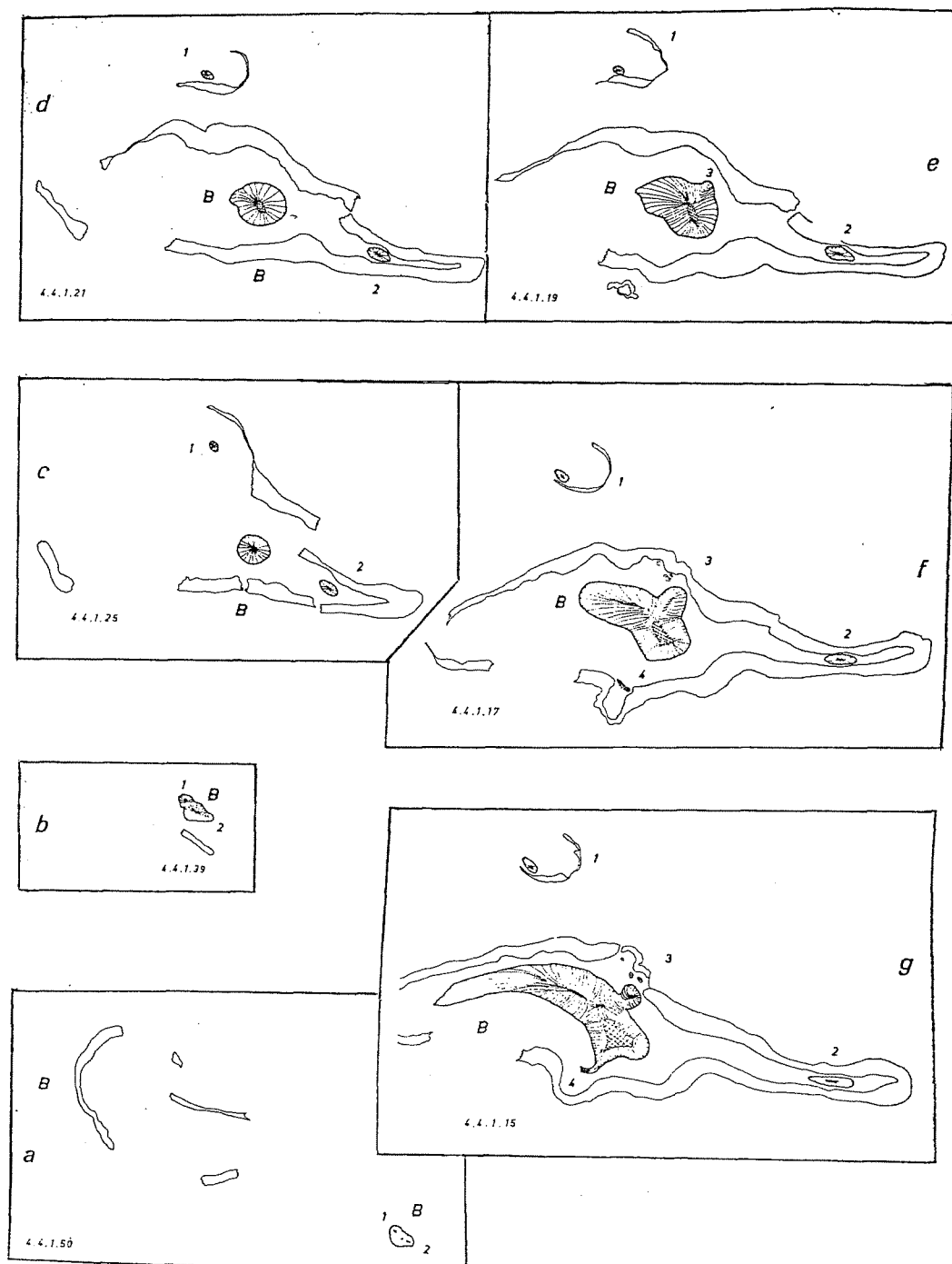
In Text-figure 10c, and Plate 24, fig. 62 nearly all the branch traces are free in a large cortical enclosure and axis B, which is upright again, is cut almost transversely.

In Text-figure 10d the insignificance of branch 7 is indicated by the diminution in size of its trace which terminates without ever having left the parent axis. All other branches are self-explanatory.

Text-figure 10e shows axis B separated from the complex of branches. Branch 2 is finally free from its parent axis B. Branches 5, 6 and 3 are still in attachment. Their steles are unequal in diameter; 5 is larger than the others.

Text-figure 11a shows axis B with its single protoxylem strand. Branches 5 and 6 are almost free from each other. Branch 2 continues vigorously while branch 3 ends in at least three small branchlets. From the above series it is evident that branches 3 and 4 terminated rapidly.

Text-figure 11b shows the stele of axis B in its more nor-



Text-figures 9-12. Selected peels, taken from base toward apex, illustrating details of branching of axis B (see Text-fig. 4). Text-figure 9, a-g, showing especially the enlargement of protoxylem (cross

hatched) and metaxylem (lined) below region of profuse vegetative branching. Symbols unchanged, description in text; $\times 6$.

mal condition about to produce a branch on one side. Branch 2 is vigorous. Branches 5 and 6 are now separated. Branch 3 is about to end.

Text-figure 11c shows axis B about to produce another trace that will be the vascular supply in branch 8. Branch 5 is reduced in size. Branch 2 is producing a small lateral which is cut obliquely. Branch 6 has subdivided at least three or four times into a tangle of small branchlets.

Before beginning the description of Text-figure 12 it is necessary to remark that the distance between the branches on the peels have become too great to continue illustrating them in their correct relationship to one another. We have therefore drawn the branches on Text-fig. 12 much closer together than they occur on the peel.

Text-figure 12a, Plate 24, fig. 66 show axis B with another alternate, lateral trace, 8. Two remnants of profusely branched 6 are still present but disappear shortly. Branch 5 is little changed. The xylem of branch 2 has produced a trace, 2/2, which is free. The first lateral of 2, 2/1, has now two traces following a dichotomy. Branch 2 produces a third lateral at a higher level. All of its lateral branches, 2/1, 2/2, 2/3 and branch 2 itself dichotomize once and then disappear. Therefore, we shall not illustrate the branch 2 complex again above the level of Text-figure 12a.

We shall now follow only axis B and its eighth lateral because 8 is certainly the most significant branch that axis B has produced.

Text-figure 12b, Plate 24, fig. 67 were selected to show branch 8 in the course of division into three branchlets by a pair of closely spaced dichotomies. One small trace is already free (the first dichotomy) but the other two traces are not yet separated. All are included in the same cortex. The outline of this xylem group is rectangular (more obvious at a lower level). This is the first emission of a rectangular trace by axis B. It recalls the rectangular bundle which identified branch 6 of axis A as a fertile lateral branch.

Text-figure 12c shows axis B and the three branches produced by the double dichotomy of its branch 8 (8/1, 8/2, 8/3). Of these three branchlets, 8/1 aborts, 8/3 runs out of the nodule, and 8/2 is seen in the next figure.

In Text-figure 12d axis B shows evidence of a ninth branch, to be produced alternately and distichously. Branch 8/2 has divided a second time by a double dichotomy. Its three bundles should soon be found in three new branchlets. This second double dichotomy repeats exactly the pattern we described as typical for fertile branching systems.

Text-figure 12e shows axis B still vigorous at the very apex of the nodule. No other branches are preserved at this level. The trace to lateral branch 9 is nearly free.

SUMMARY of branching of sterile axis B (Text-figs. 4, 13).

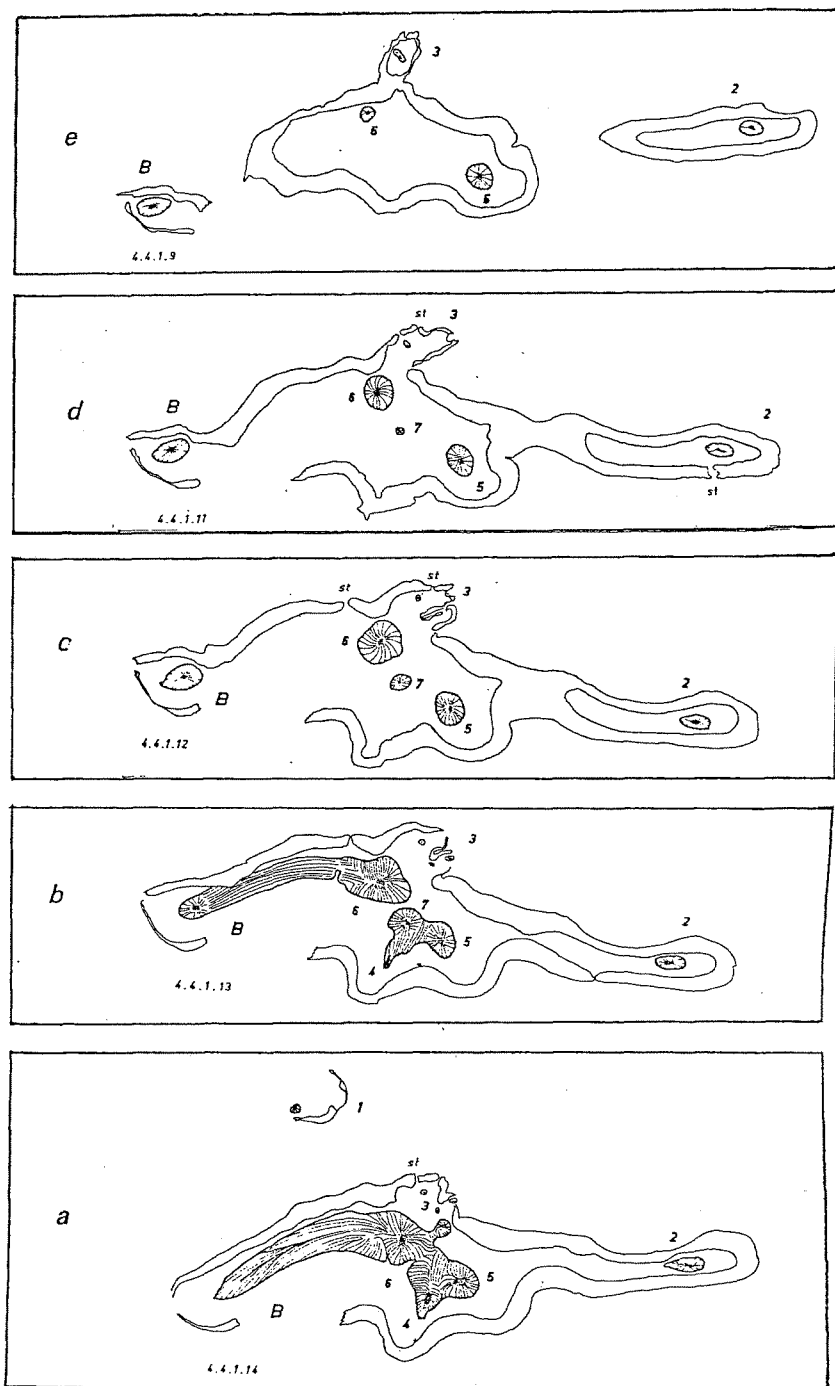
The second branch produced by a dichotomy at the base of cobble 4 also produces laterals spirally and in rapid succession. Like axis A the laterals produced by B are unequal in vigor. The small branches 3, 4, 5, and 6 were given off in a different manner from branches 1, 2, and 8 and over a very short vertical distance, 2.5 mm. At the same time the stele increased considerably in size, and became differentiated into two distinct tissue masses, a large central protoxylem and a surrounding metaxylem. This local behavior of the stele and the meaning of the lateral organs is not easy to elucidate. It might be presumed that they represented a first attempt to evolve a new function, *e.g.* that of adventitious roots, although their anatomy and mode of emission had not yet reached that of a true root. The behavior of the stele recalls that described by Benson (1911) in *Botryopteris antiqua* in the region of adventitious root formation. Thus these organs 3, 4, 5, 6 suggest another hypothesis just as did the small branchlet 1/3 on Axis A (Text-fig. 8a and 8h). We assigned a leaflike function to that branchlet although its delicate, terete, recurved or straight, ultimate tips had evolved neither the dorsiventral organization nor the expanded lamina typical of a leaf. Branches 2 and 8 are like major branch systems, one sterile, one fertile. Branch 8 is preserved through two double dichotomies that resemble in all respects the branching at the base of a fertile system. Higher up the vascular supply of a ninth branch is alternate and distichous as in our typical fertile branching systems in Gaspé specimens 190, 191 and Abitibi River compressions. Axis B is just as vigorous at the top of the specimen as it was at the base. Axis B tells the same story as Axis A, vegetative lateral branches below and fertile lateral branching systems above, and among the vegetative branches some suggesting the origin of leaves and others which might be interpreted as simulating adventitious roots.

DIAGNOSIS

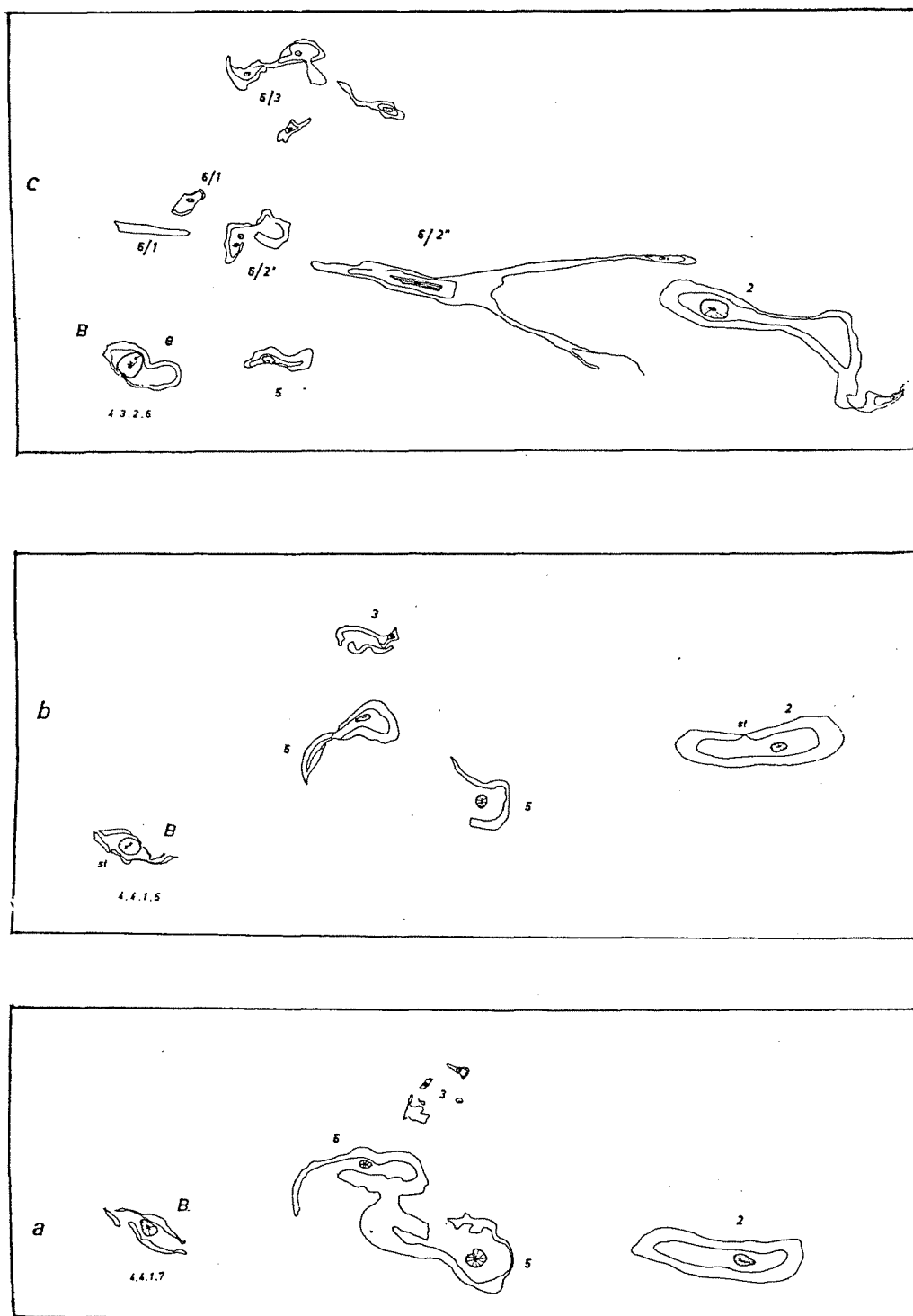
Genus *Psilophyton* Dawson, 1859

Diagnosis of Hueber, 1968, emended.

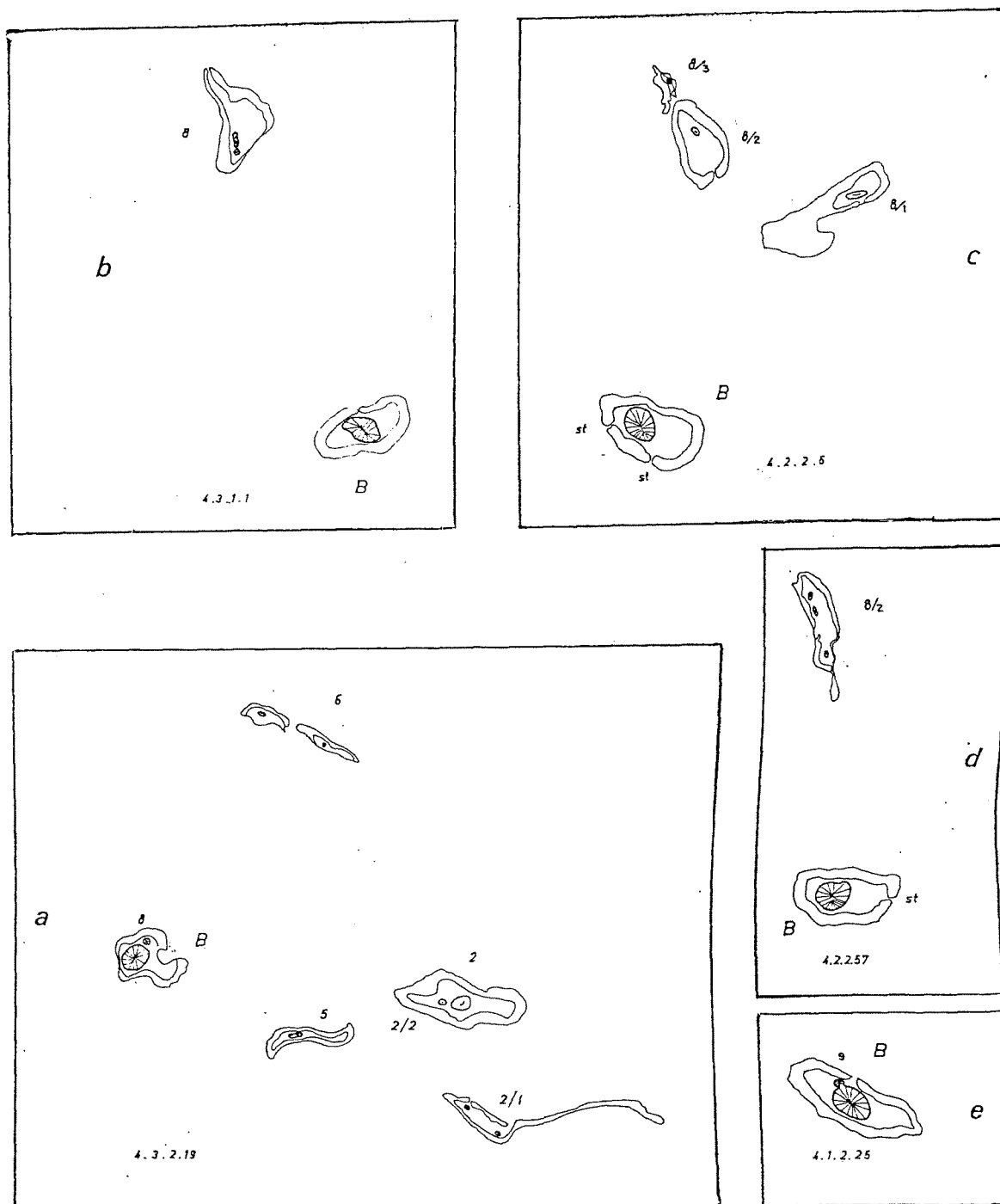
Stems branch dichotomously and laterally, the latter in an irregular, close spiral in zones of vegetative branching; fertile branches, in zones alternating with vegetative zones, more distant and alternate, distichous; lateral branches themselves branch either laterally or dichotomously with successive dichotomies each formed at right angles to the



Text-figure 10. Selected peels, a-e, of levels above Text-fig. 9. All symbols unchanged. Description in text; $\times 6$.



Text-figure 11. Selected peels, a-c, of levels above Text-figure 10. Symbols unchanged. Description in text; $\times 6$.



Text-figure 12. Selected peels, a-e, of still higher levels of vegetative branching. Symbols unchanged. Description in text; $\times$ 6.

other; axes naked or spinous, ridged or unridged, compressions may be marked by punctiform scars; sporangia elongate-elliptical, pendulous, paired, and borne terminally on repeatedly dichotomized lateral branches, total number per lateral branch large; dehiscence longitudinal along facing surfaces of paired sporangia; xylem a solid strand, centrarch; outer cortex collenchymatous except in areas of substomatal chambers.

Species *P. dawsonii*, sp. nov.

Characteristics as for the genus. Vegetative branches three-dimensional and of two sizes; terminated by slender, blunt tips in various attitudes; fertile branches usually dichotomize six times before terminating in clusters of approximately 32 pairs of sporangia 3.0-5.0 mm long by 1.0-1.5 mm in diameter, sporangial wall similar to stem cortex; at maturity consisting of an outer carbonized layer and an inner cellular membrane; both abortions of sporangia and of limbs of some dichotomies cause variations in total number; each of the first two apparent dichotomies is actually two closely spaced dichotomies each of which should result in three branches but one of the three aborts leaving a stump between the two remaining limbs. Protostele relatively large, $\frac{1}{4}$ the diameter of the stem; centrarch; becoming massive with several enlarged protoxylem areas and many radially aligned tracheids at the level of vegetative branching; in the area of fertile branching protoxylem branches alternately and distichously foreshadowing a similar arrangement of lateral branches; trace to fertile branch at first terete, soon characteristically rectangular; xylem all tracheids, scalariform pitted to modified scalariform resembling rudimentary circular pits; phloem and inner cortex parenchymatous, outer cortex collenchymatous with substomatal chambers; epidermis of small boxshaped cells; spores, 40-75 μ in diameter, smooth, with darkened areas around commissures, curvaturae; spores resemble the dispersed spore genera *Retusotriletes* or *Phyllothecotriletes*; young spores surrounded by a minutely ornamented layer (? perispore) which breaks away with age.

Holotypes: Cornell University Paleobotanical Collection Number 190, Plate 20, figs. 30, 31, 33-37; Plate 21, figs. 38, 39; Plate 24, fig. 69 (loc. No. 31).

Paratypes: CUPC No. 191, Plate 18, figs. 11, 17, 18; Plate 19, figs. 27, 28; Plate 20, fig. 32; Plate 21, figs. 40, 41; Plate 22, fig. 43 (loc. No. 35); CUPC No. 192, Plate 17, figs. 5, 6; Plate 18, figs. 12-14; Plate 19, figs. 19, 20, 22, 25, 26; Plate 24, figs. 62-68 (loc. No. 4).

CUPC No. 193, Pl. 22, fig. 50; Pl. 23, figs. 54, 55.

CUPC No. 194, Pl. 18, fig. 16; Plate 19, fig. 24; Pl. 20, fig. 29; Plate 22, figs. 42, 49 (loc. No. 13).

CUPC No. 195, Pl. 19, fig. 21; Pl. 23, figs. 56-61 (loc. No. 21).

CUPC No. 196, Pl. 22, fig. 48 (loc. No. 23).

CUPC No. 197, Pl. 19, fig. 23 (loc. No. 32).

CUPC No. 198, Pl. 18, fig. 15 (loc. No. 34).

Geological Survey of Canada No. 32719, Pl. 17, fig. 2 (loc. No. 6435).

GSC No. 32720 and slides a-e, Plate 17, figs. 3, 7-10; Plate 23, fig. 51 (loc. No. 6435).

GSC No. 32721, Plate 23, fig. 52 (loc. No. 6435).

GSC No. 32722, Plate 23, fig. 53 (loc. No. 6435).

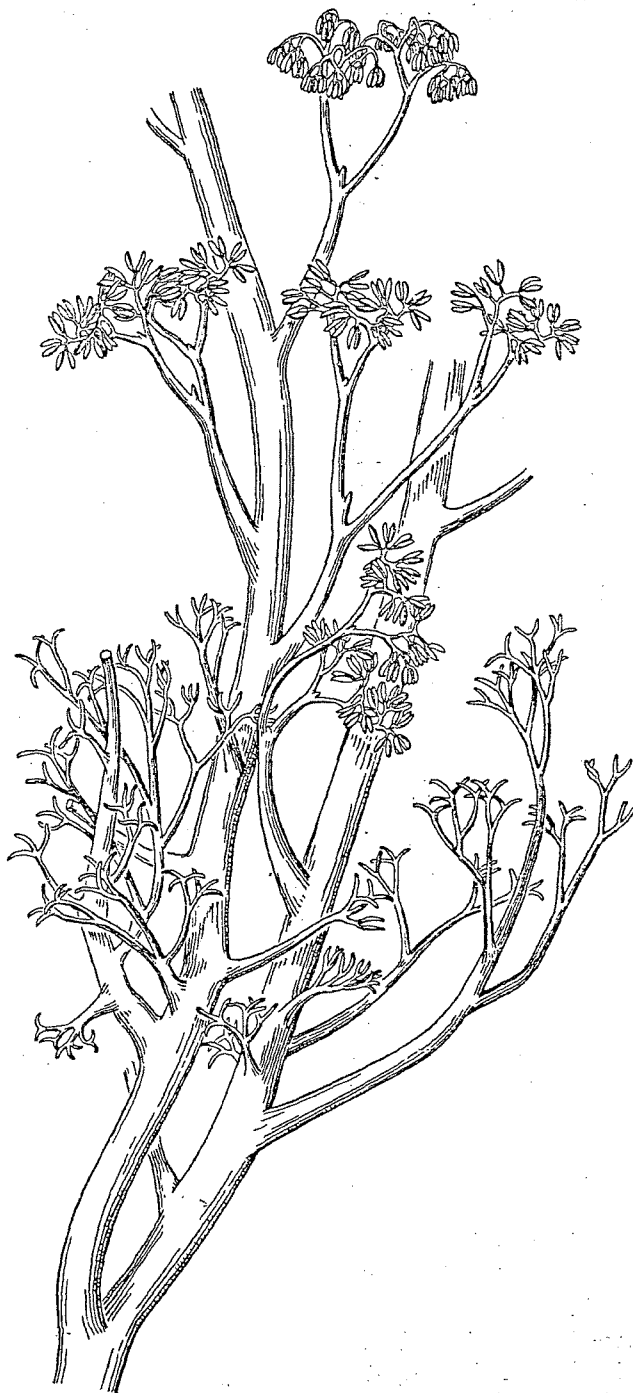
United States National Museum No. 175772, Pl. 22, figs. 44, 45 (peel 1.1.1.2), 46, 47 (peel 1.1.1.1) (loc. No. 14251).

THE NAME *DAWSONITES*

Halle (1916) erected *Dawsonites*, as a provisional name for use until some worker discovered the true affinity of any fossil temporarily placed in it. He described his material as: "Sporangium-bearing branch-systems, dividing dichotomously, or differentiated into a sympodially formed main axis and bifurcating lateral branches. Ultimate branches slender and curved, bearing terminal capsules of a narrowly obovoid or short fusiform shape and usually 3-5 mm long." It is now demonstrated that *Psilophyton* was a plant bearing fertile systems like those described by Halle. *Dawsonites* is, therefore, to be maintained as a form genus when only a portion of a fertile system is found, and it can not be shown by techniques to be *Psilophyton*. We would use the name in a restricted sense as intended by Halle (1916) and as discussed by Lang (1931, 1932), and by Croft and Lang (1942), and Stockmans (1940), and not as used by Høeg (1935, 1967) and Kräusel and Weyland (1933, 1935).

COMPARISON OF *PSILOPHYTON DAWSONII* WITH OTHER SPECIES

The abundance of detail revealed by *P. dawsonii* contrasts sharply with the paucity of data for other species. Some anatomy is known for *P. princeps* (Hueber, 1968), but no other species has been described with the combination of vegetative and fertile branching and anatomy. The most extensive taxonomic treatment of *Psilophyton* and associated plants (Høeg, 1967 in Boureau's *Traité*) confuses *Psilophyton* and *Sawdonia* (*P. princeps* var. *ornatum*) although Høeg obviously recognized the need for a complete



Text-figure 13. Reconstruction of plant of *Psilophyton dawsonii* based on calcareous petrifications from Gaspé Peninsula and compressions from Abitibi River, Ontario. Vegetative branching, irregularly spiral, shown below, fertile branching, alternate and distichous, shown above. Some branchlets reduced and simulating small but un-

planated leaves; some branches more indefinite in length. Older sporangia shown more spread out, younger more incurved. First two "double dichotomies" of fertile branches indicated by aborted stum in angle of apparent single dichotomies.

taxonomic revision of these early plants that bore either terminal or lateral sporangia. Høeg's figures 196, 198-201, 207-209 are now recognized as *Sawdonia*, not *Psilophyton*. His figures 238-241 of *Dawsonites* illustrate *Psilophyton*-like fertile branches. Other species of *Dawsonites* in Høeg's survey do not, in our opinion, conform to Halle's definition of the genus. It is also possible, in view of the vegetative branching of our new *P. dawsonii*, that *Psilodendron* (Høeg, 1967, pp. 315-317) might be a species of *Psilophyton* if it were better understood.

P. dawsonii can be distinguished from *P. princeps* by its lack of cup-tipped spines, by its vegetative branching and by the size of its sporangia $3.0-5.0 \times 1.0-1.5$ mm *vs.* $7.5-8.0 \times 1.0-2.0$. Sporangia of *P. dawsonii* are larger than those of *P. kräuselii* which measure only $2.0-2.5 \times 0.5-0.6$ mm and the latter species is hairy whereas *P. dawsonii* is glabrous. Vegetative branching of *P. kräuselii* is not known.

The other species of *Psilophyton* for which the sporangia are perhaps known is *P. forbesii* (Andrews, Kasper, and Mencher, 1968). Both vegetative and fertile branches have been found and although the authors are uncertain of the point of attachment of the fertile, they reconstruct the plant with alternating vegetative and fertile regions. Should this interpretation prove to be correct then it is a growth habit with which *P. dawsonii* agrees. Both species are glabrous. *P. forbesii* is known only as compressions and in the absence of any anatomical structure or detail of the branching of fertile shoots and the number of sporangia they bear, we have no hesitation in designating our material as a new species.

Psilophyton arcticum and *P. rectissimum* (Høeg, 1967) are based on sterile material and are represented only by compressions. Both are spiny whereas *P. dawsonii* is glabrous. Whether the fertile parts and the anatomy of these two species if found would prove them to belong to the now more clearly defined *Psilophyton* is uncertain.

Despite the ease and certainty with which *P. dawsonii* can be distinguished from *P. princeps*, there are major similarities. Stems of both species can branch dichotomously. Fertile branches of both are produced alternately and distichously and branch dichotomously about six times before ending in a large number of paired terminal sporangia. Dehiscence in both is longitudinal along facing surfaces. Sporangia of both consist of an outer carbonized wall and an inner, separate membrane that resists oxidative maceration. So far as can be determined the protostele of *P. princeps* is like that of *P. dawsonii* though badly preserved. Collenchymatous cortex and substomatal chambers probably charac-

terize both species. There is little question that the two are natural members of one natural genus.

Now that we begin to understand Dawson's genus, it is interesting to note some of his unrecognized accomplishments. His description (1859) of the "fructification probably in lateral masses, protected by leafy bracts" has long been considered worthless (see Text-fig. 1e). For example Halle (1916, p. 15) called it an "obscure object". However these "obscure objects" are clusters of detached terminal sporangia of *Psilophyton* (Hueber and Banks, 1967, fig. 10; Hueber, 1968, figs. 16, 17). Similarly Dawson's various fragmentary descriptions of the anatomy of *Psilophyton* were discounted because they came from detached specimens of axis. Knowledge of the anatomy of our more complete specimens permitted a search for microscopic preparations made by Dawson and a study of them. Eight slides were found in the General Botany Laboratory at McGill University. They were repolished and covered at the National Mus. Nat. Hist. (U.S. National Museum). They now bear Redpath Museum number 12.534-Slides 1-8. They were made from specimens similar to our calcareous cobbles and the cortex they reveal is like that which we have found. Seven slides show apparent scalariform tracheids (as Dawson reported) but also circular, pitlike areas between the scalariform bars (not reported by Dawson), just as we have described them in our new material. One slide was illustrated in Hueber and Banks (1967, fig. 11). It should be emphasized that to date only normal scalariform tracheids have been found in *Sawdonia* (Hueber and Banks, 1967; Hueber, 1971).

Psilophyton goldschmidtii Halle (1916) requires special consideration because Halle carefully segregated several associated but unattached plants into the individual genera *Psilophyton*, *Dawsonites* Halle, 1916, *Aphylopteris*, and *Hostinella* even though he believed some of them might be parts of one plant. The stem of *P. goldschmidtii* bore lateral branches which dichotomized repeatedly at a wide angle and apparently always in one plane. The stems were spiny and basal parts of the lateral branches bore occasional spines. If this description is fully correct and if the species is ever found to bear fertile branches with terminal sporangia or to have *Psilophyton* anatomy, then *P. goldschmidtii* is clearly distinct from the several species described above. As yet it has neither sporangia nor anatomy nor is it proven that its lateral branches were flattened into a two-dimensional system.

The *Hostinella* described by Halle varied widely. Some specimens Halle considered identical to lateral branches but

because they were glabrous he cautiously excluded them from *Psilophyton*. However Banks (1968a) found a centrach xylem strand and tracheids identical to those of *P. dawsonii* in a *Hostinella* collected by O. Selling at Røragen, Norway where Halle had collected. This suggests that some of the Norwegian *Hostinella* is *Psilophyton* and possibly *P. goldschmidtii*. A careful search at Røragen is essential for the discovery of a specimen of *P. goldschmidtii* with both sporangia and anatomy.

The *Aphyllopteris* described by Halle looks to us much like lateral branch systems of *Psilophyton* from the Gaspé now that branching patterns in the genus are known to vary from dichotomous to pseudomonopodial to lateral. Without further detail, however, it is probably necessary to continue to refer them to *Aphyllopteris*.

The glabrous specimens for which Halle erected the name *Dawsonites arcuatus* are typical, in every respect, of the fertile lateral branches we describe for *P. dawsonii*. Lacking anatomy and attachment to main axis they must continue to be identified as *D. arcuatus* because they could be parts of *P. goldschmidtii* whose main axis is spiny whereas that of *P. dawsonii* is glabrous. However we have good evidence for the assertion that Halle's *Dawsonites arcuatus* is closely similar to the apical portion of a fertile branch system of *Psilophyton*. We borrowed several of his specimens including the one he illustrated (1916) as plate 3, figure 3. Uncovering of this specimen by Leclercq revealed the presence of an aborted branch in the axil of the first forking of the fertile branch system, (Pl. 17, fig. 4) and of many, not simply a few, sporangia borne in a large three-dimensional cluster just as they are borne in *Psilophyton*. *Dawsonites*, like *Psilophyton*, bore a three-dimensional, much dichotomized, fertile branch whose proximal forkings occasionally aborted and whose distal end was terminated by a large cluster of sporangia.

Ananiev and Stepanov (1969) described a *Dawsonites* from Western Siberia that fits both Halle's generic diagnosis and our interpretation of Halle's material. Successive dichotomies occur 90° round the stem from one another and some divisions look like trichotomies. The latter might be comparable to the "double dichotomies" that we found near the base of fertile lateral branches.

Halle's (1916) *Psilophyton princeps*, on the basis of epidermal structure and morphology of its spines, is *Sawdonia*.

Comments on characteristics of true *Psilophyton* as revealed by Lang and Croft and Lang from Scotland and Wales will be found in the Discussion.

DISCUSSION

PSILOPHYTON

It is now clear, over 110 years after the original description, why Dawson had so much trouble defining *Psilophyton* and why opinions on the most suitable specimen to use as holotype have varied. *Psilophyton* is both spiny (*P. princeps*) and glabrous (*P. dawsonii*). It may be found as compressions or as petrifications and they differ in appearance. It consists of both fertile branches and vegetative branches which are usually preserved independently. Its branching is three-dimensional so that only portions of the plant appear on any one split surface. It occurs on the Gaspé Peninsula or near strata containing other plants such as *Sawdonia*, *Grenaticaulis*, *Trimerophyton*, and *Taenioocrada* none of which was known, in present-day detail, to Dawson or subsequent workers for many years.

An apparent confusion of three, probably four, plants is seen also in Lang (1932) where he reported *Psilophyton* from Upper Siegenian strata in Scotland. His figures 17-22, 24, 33, 34, 36-70 on plates 2-4 illustrate *Sawdonia* whereas his figures 25-32 illustrate specimens which are, with present knowledge, best assigned to *Psilophyton goldschmidtii*. This action was alluded to by Lang. His figures 21, 23, 35 can not be assigned to either *Sawdonia* or *Psilophyton* and this is also the case with figures 72-77. In fact all of those fragments best would be considered as indeterminate vascular plant fossils or "kept apart as *Hostinella* sp." (Lang, 1932 p. 516). The paired sporangia illustrated in his figures 78-79 and the spores from the specimen in figure 79 that are illustrated in figures 80-82 are best kept with *Dawsonites arcuatus* as Lang suggested. The *sporodites* in his figures 83-86 are of the same type as those obtained directly from the sporangia and, therefore, are easily kept together with *D. arcuatus*. Essentially, Lang maintained an excellent order among the plants he examined particularly when one takes into account the state of knowledge of Devonian plants at the time, as well as the nomenclatural confusion associated with them. Croft and Lang (1942) faced the same problem with their identification of cf. *Psilophyton princeps* (figs. 8-15, pl. 9). Their plant bore lateral sporangia and its stem was ornamented with small spinelike protuberances. This latter characteristic led them to associate the plant with *Psilophyton*, but the position of the sporangia caused them to doubt the wisdom of identifying the plant unequivocally with *Psilophyton princeps*. The plant is neither *Psilophyton* nor *Sawdonia* as

should be restudied as it represents an ornamented form that belongs among the zosterophylls. Its sporangia are stalked and turned upward along the margins of the axis much as one sees in *Zosterophyllum* and *Rebuchia*. In their figures 16-19, plate 10 they illustrate specimens that may be fragments of *Psilophyton*. However, they wisely assigned them to *Dawsonites* and corroborated Halle's diagnosis of that genus in their description as they wrote: "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 pendant. The fertile branches arise laterally from broader axes and appear to have been radially arranged." All the features mentioned by Croft and Lang we have now confirmed in serial section and by uncovering three dimensional branch systems. Thus *Dawsonites* is similar to fertile branches of *Psilophyton dawsonii* but lacks main stems and vegetative branching.

Psilophyton has become at last a plant, not simply a fossil fragment. It was erect. Its main axis divided by equal dichotomy. It bore zones of vegetative lateral branches in an irregular spiral. Some of these branches forked dichotomously at varying intervals and finally terminated in slender blunt, sometimes recurved apices. Others were branched pseudomonopodially, bearing branchlets alternately and distichously. Some of the latter were elongate and some much shortened. The short branchlets even simulate precursors of leaves. In zones alternating with the vegetative branches fertile branching systems arose alternately and distichously. Branching of the fertile system was basically dichotomous. Usually six dichotomies, each at 90° around the axis from the preceding, resulted in a cluster of 64 terminal sporangia. However, the first two of these six dichotomies were unusual. Each was in reality two closely spaced dichotomies which would be expected to result in three axes. But one of the three axes aborted leaving two, thus simulating a single dichotomy. However, with care the stump of the aborted branch can be demonstrated. We have referred to this branching as a double dichotomy but count it as one when we say that the fertile system dichotomizes six times. Each sporangium has its own short stalk yet the sporangia always appear to be paired because intervals between dichotomies decrease steadily from base to apex of fertile branches. Sporangia are fusiform and dehisce longitudinally, a feature of many geologically younger vascular plants. Spores were smooth but characterized by *curvaturae perfectae* and by triangular darkened areas of the proximal surfaces along the commissures. Dawson suggested *Psilophyton* was rhizomatous and we have reason to believe him

correct although his "rhizomes" have since proved to be stems of *Taenioocrada* and our evidence is not yet definitive enough to publish.

Anatomically *Psilophyton dawsonii* is remarkably well preserved. Its main axes were characterized by a massive, terete xylem strand $\frac{1}{4}$ the diameter of the stem. Its maturation was centrarch. It dichotomized in typical fashion. At the level of vegetative branching both its protoxylem and its metaxylem enlarged remarkably and traces to lateral branches, consisting of both proto- and metaxylem, branched from the central mass in an irregular spiral. The traces were of varying sizes. The larger usually supplied the more extensive vegetative laterals. Like the main axis they were centrarch. Traces in the lateral branches divided dichotomously in the smaller branches and forked alternately and distichously in some of the larger. They become successively smaller toward the apices of all branches. Thus both morphologically and anatomically *P. dawsonii* is an extensive branching system. Despite the underlying uniformity of this branching system we suggest that the evolution of a distinction between major branches, leaves, and a rootlike function was underway. Organs that suggest large branches are laterals 2 and 8 on Axis B and 1 and 6 on Axis A (Text-figs. 4, 13). Organs that suggest the origin of leaves are illustrated on Text-figure 4 as branchlets 1/3 and 1/1 on branch 1 of Axis A and by extrapolation 2/1 and 2/2 on Axis B. Smaller organs are illustrated on Text-figure 4 as branchlets (?) 3, 4, and 6 on Axis B. Their mode of emission differs from that of larger branches and the stele of the stem changes markedly in size and shape while they are arising. This behavior recalls the stele of *Botryopteris antiqua* Kidston in the region where it produces adventitious roots (Benson, 1911). The slender, flexuous organs 3, 4, and 6 could not be followed to their apices and that portion of the reconstruction, Text-figure 13, is conjecture. Still another explanation of branches 3, 4, and 6 is that they were aphanoblasts.

Above the level of profuse vegetative branching the terete xylem strand of the main axis branched less often and supplied fertile branch systems. Its protoxylem first became elliptical, then a group of cells became free and ultimately was surrounded by its own metaxylem. Opposite this trace the same series of events resulted in a second, higher trace. Branches thus appeared on two sides of the axis only, an alternate, distichous arrangement. At the base of a fertile branch the branch trace was almost rectangular in outline. The constancy of this outline, observed more than a dozen times, gives us the assurance that we can

predict which branches were fertile even when they are without preserved sporangia. The rectangular trace soon dichotomized twice producing three strands, one of which aborted. The two remaining strands each repeated the two closely spaced dichotomies and again one of the three strands aborted. Subsequent divisions were normal, simultaneous dichotomies each 90° round the stem from the preceding. Thirty two apices resulted and each bore two stalked sporangia. A strikingly large vascular strand continued up into the very base of each sporangium.

Histologically the xylem was surrounded by phloem in which we have failed to find evidence of sieve areas. Phloem cells are vertically elongate and parenchymatous. The inner cortex when preserved is parenchymatous. Outer cortex was composed of thick-walled elongate cells whose end walls were transverse or slightly oblique, hence collenchymatous rather than sclerenchymatous. Underneath stomates some of the thick-walled cells were replaced by parenchyma that either disintegrated when young or was rarely preserved. In either case substomatal chambers resulted. The epidermis was small-celled and interrupted only by guard cells of which we have few details.

The anatomical resemblance of sporangia to small branches is striking. Sporangia consisted of an epidermis with guard cells and a hypodermis like that of branches. Substomatal chambers were produced as in branches, and the innermost layers were of parenchyma. During maturation many of the wall cells broke down but a membrane, probably consisting of the inner tangential walls of the innermost parenchyma, remained. In compression specimens the sporangial wall was reduced to an outer carbonized layer (remnants of epidermis and some hypodermis) and a free membrane surrounding the spores. Lang found these same two layers on three occasions (1931, 1932, and with Croft, 1942) and Hopping (1956) described two identical layers in *Trimerophyton*. Dehiscence was longitudinal and in a pair of sporangia was along surfaces that faced one another. Empty sporangia still contained the membrane hence we believe that it normally was not lost at dehiscence. Only when sporangia are chemically macerated does the membrane come out. Clusters of spores are often found in the calcareous pebbles. The clusters are the size of the inner sporangial membrane giving rise to the suggestion that they may have come out of sporangia as a mass rather than individually. Alternatively these masses may have been released by the decay of sporangial walls.

The xylem cells were annular, spiral, and scalariform. Typically however the secondary wall formed more than

just scalariform bars. It was deposited in various patterns between them as well. The result was a row or rows of circular areas between the bars or, occasionally, vertical connections between the bars. The circular areas seem to us to be homologous to pits.

CLASSIFICATION

The new understanding of the plants called *Psilophyton* necessitates a reevaluation of their taxonomic position. *Psilophyton* is still essentially a leafless plant bearing terminal sporangia, the classical definition of Psilophytales placed by Eames (1936) in the subdivision Psilopsida. Yet *Psilophyton* is a much more complex plant than *Cooksonia* or *Rhynia* both of which conform to the classical definition. Some examples of this increased complexity are the segregation of vegetative and fertile portions of the plant, the tendency toward pseudomonopodial branching that results in lateral branches, the differentiation of smaller (more leaf-like) from larger lateral branches, the restriction of sporangia to lateral instead of main axes, the profuse branching of the fertile branch system and the resulting mass of sporangia, the massive size of the xylem strand compared to the slender strand of *Rhynia*, the complex branching pattern of this strand in various parts of the plant, the more complex secondary wall structure of tracheids in *Psilophyton*. In other words *Psilophyton* can no longer be retained in a group designed for simple plants like *Rhynia*. Its closest relatives appear to be *Trimerophyton robustius* (Dawson) Hopping, 1956, and *Pertica quadrifaria* Kasper and Andrews, 1972. *Trimerophyton* consists of a pseudomonopodially branched axis that bears laterals in three vertical rows. The laterals branch quickly into three each of which again branches into three branchlets. The latter dichotomize and then terminate in clusters of erect sporangia whose mature walls, like those of *Psilophyton*, consist of an outer carbonized layer and an inner, thin membrane around the spores. Only fertile branches have been found but the tendency to fork into three parts recalls the two double dichotomies that we find in fertile branches of *Psilophyton*. Apparently, however, there was no abortion in *Trimerophyton*. The two genera are clearly distinct but equally clearly are closely related. Anatomy is unknown for *Trimerophyton*.

Pertica is also pseudomonopodially branched. Its laterals are borne spirally in four rows and show a tendency to be arranged in clusters of four (Kasper and Andrews 1972, fig. 8). All laterals branch dichotomously. Each dichotomy is at right angles to the next. Sterile branches terminat

in slender tips. Separate fertile branches terminate either in slender tips or globose masses of sporangia that radiate in all directions. *Pertica*, like *Trimerophyton*, was found only as compressions so that anatomy and histological details are unknown.

It has been recognized for some years that Psilophytales had become a meaningless category as one after another Devonian plant was placed in the order without due consideration of the variability found or on the basis of too restricted evidence. Leclercq (1954), for example, pointed out the existence of two discrete evolutionary lines among psilophytes, those with terminal and those with lateral sporangia. Hueber (1964b) expanded this suggestion by describing the longitudinal *vs.* distal dehiscence in the two groups. Banks (1968b) took the additional step of naming three subdivisions of vascular plants to replace the one subdivision Psilopsida (Table 3). For *Rhynia* and allied plants he suggested Rhyniophytina, plants with terminal sporangia, longitudinal dehiscence and centrarch maturation. Zosterophyllophytina included *Zosterophyllum* and allied genera with lateral sporangia, distal dehiscence and exarch maturation. For reasons given above, he added a third subdivision, Trimerophytina, for plants more complex than *Rhynia* but still with terminal sporangia (in large masses) and longitudinal dehiscence. *Psilophyton*, the only genus for which anatomy is known, has a large centrarch xylem strand. Elimination of Psilophytales was long overdue but these three new subdivisions are only a beginning of the classificatory changes that are required by plants in the Devonian flora. A picture of the many genera for which ultimately other subdivisions must be established can be obtained by studying the excellent account by Høeg (1967), in Boureau. The major hindrance to further categorizing is the paucity of data for the fossils in question. The same drawback is seen in Rhyniophytina. Only *Rhynia*, *Horneophyton*, and *Cooksonia* are really well characterized. The other genera listed lack many essential details and may ultimately have to be moved elsewhere.

Table 3. Classification. Three subdivisions of vascular plants (their characteristics given in text) designed to replace in part the now obsolete category Psilopsida. For other, as yet not reclassified, "psilophytes" see Høeg (1967). Some of the genera of Rhyniophytina may have to be transferred elsewhere when understood fully, *e.g.* *Hedeia*, *Yarravia*.

Division Tracheophyta

Subdivision — Trimerophytina Banks, 1968b

Psilophyton Dawson, 1859

Trimerophyton Hopping, 1956

Pertica Kasper and Andrews, 1972

Dawsonites Halle, 1916

Hostinella Stur, 1882 (in part, cf. Banks, 1968a)

Subdivision —

Rhyniophytina Banks, 1968b

Rhynia Kidston and Lang, 1917

Horneophyton Barghoorn and Darrah, 1938

Cooksonia Lang, 1937

Steganotheca Edwards, 1970b

Taenioocrada D. White, 1902

Hicklingia Kidston and Lang, 1923

Eogaspesia Daber, 1960

Hedeia Cookson, 1935

Yarravia Lang and Cookson, 1935

Subdivision —

Zosterophyllophytina Banks, 1968b

Zosterophyllum Penhallow, 1892

Gosslingia Heard, 1927

Crenatacaulis Banks and Davis, 1969

Sawdonia Hueber, 1971

(syn. *Psilophyton princeps*

var. *ornatum* Dawson)

Rebuchia Hueber, 1970 (syn.

Bucheria Dorf)

Bathurstia Hueber, 1972

STRATIGRAPHIC OCCURRENCE

The oldest plants proved to be vascular are *Cooksonia* Lang (1937) and *Steganotheca* Edwards (1970b). Both are found at the base of the Pridolian (Downtonian) (Banks, 1972), the youngest stage of Silurian. Both are naked, dichotomizing plants that bore terminal sporangia. Their basal parts are still unknown. Both are typical members of Rhyniophytina. The oldest Zosterophyllophytina appear to be Gedinnian (Banks, 1972). These two groups appear to be the only typical, proven vascular plants until about mid-Siegenian time when several additional groups appeared, as if a burst of evolution had occurred. One example of a new type is the genus *Krithodeophyton* Edwards (1968). It combines characteristics of two groups and perhaps belongs in the barinophytes. A second example is the lycopods which appeared for the first time in Siegenian and a third is a *Psilophyton*-like plant represented by fragments referable to *Dawsonites arcuatus* Halle which appeared in late Siegenian time in Wales (Croft and Lang, 1942).

Psilophyton in Norway, on the Gaspé Peninsula, in the State of Maine, and in Siberia is found in continental strata whose precise age is difficult to assess. It may be late Emsian or early Eifelian. In either case these more abundant collections are at most only a few million years younger than the earliest occurrence in the Siegenian of Scotland (Table 1) and it would be accurate to state that abundant *Psilophyton* occurs close to the Emsian-Eifelian (Lower-Middle Devonian) boundary. Presumably it persisted into later Middle Devonian but critical specimens and trustworthy evidence of the plant are sparse except in Stockmans (1940). We know no valid evidence of Upper Devonian *Psilophyton*. Carefully studied specimens reported as *P. princeps* such as those of Hueber and Grierson (1961) from the Upper Devonian of New York State are now referable to *Sawdonia ornata* (Dn.), Hueber and not to *Psilophyton*. All other records of late Devonian *Psilophyton* need equally careful analysis.

PHYLOGENETIC CONSIDERATIONS

Trimerophytina, represented by one genus (*Psilophyton*) whose morphology and anatomy are now well characterized and by two genera (*Trimerophyton* and *Pertica*) known only by their external morphology, demonstrate the evolutionary potential to continue the adaptive radiation of vascular plants on land that started with a burst in mid-Siegenian. Given the time-tested morphological dicta - overtopping, planation, webbing, recurving, reduction, and increased complexity - the trimerophytes represent a natural plexus at an evolutionary level whence such groups as coenopterids and progymnosperms might evolve as the flora of Eifelian and Givetian diversified.

The trimerophytes can only be regarded as an elaboration of the rhyniophyte level of evolution resulting from the interplay of overtopping and elaboration in both anatomy and morphology. Some of the still primitive characters of trimerophytes are the axis-like sporangial walls with many layers of differentiated cells and with stomata on their surface and vascular tissue continuing into the base of sporangia, three dimensional (non-planated) branching systems, retention of some dichotomous branching, and a solid proto-stele.

Certain characteristics of trimerophytes that are retained by, or modified in, younger groups are worthy of mention. Terminal, fusiform sporangia that dehisce longitudinally were abundant in Devonian strata once they appeared in trimerophytes. Banks (1970) illustrated this on his figures 5-9. The differences between the many genera (e.g. *Rachophyton*, *Pseudosporochnus*, *Calamophyton*, *Tetraxylopteris*, and *Archaeopteris*) in which they are found can all be accounted for by well-understood morphological changes and the similarities between them are sufficiently marked to suggest an elaboration on the evolutionary level represented by the trimerophytes.

Variability of branching patterns in trimerophytes provides a starting point for subsequent evolutionary modification. On the basis of our present knowledge, the main axis in all three genera branches pseudomonopodially and their laterals branch dichotomously, at least in part. Dichotomy is also known in the main axis of *Psilophyton*. The first two divisions of laterals in fertile branches of *Trimerophyton* produce three branchlets and the first two in *Psilophyton* result in strange abortions. Sterile lateral branches in *Psilophyton* are borne in a tight, irregular spiral whereas its fertile branches are loosely spaced and borne alternately and distichously. Laterals of *Trimerophyton* are borne tristichously, those of *Pertica* tetrastichously. Laterals of both *Psilophyton* and *Trimerophyton* are borne at an acute angle

and are elongate whereas those of *Pertica* are almost horizontal and obviously compact. Laterals of *Pertica* tend to occur in groups of four along the stem. Ultimate branchlets of both *Psilophyton* and *Pertica* are slender, often recurved, and are three-dimensional structures. *Psilophyton* bears laterals of two kinds, as mentioned earlier, some of which may simulate precursors of leaves, others which seem to be precursors of major branches rather than lesser appendages. The smaller appendages of *Psilophyton* and the sterile branches of *Pertica* both simulate the dichotomizing, three-dimensional ultimate appendages of some aneurophytes which are planated in other aneurophytes. Trimerophytes, it seems, were well provided with evolutionary potential if leaves evolved from branch systems as is usually hypothesized.

Psilophyton is the only trimerophyte whose anatomy is known. Both *P. princeps* and *P. dawsonii* are protostelic, the stelar type long held to be primitive. Current evidence indicates that it was the first type to appear in the fossil record. Equally acceptable is the hypothesis (Bower, 1930) that variously lobed steles evolved next, followed by dissected steles. The stele of *Psilophyton* is much enlarged over, and more complex than, that of the rhynia-type. Even the tracheids of *Psilophyton* can be interpreted as characteristic of a plexus whence evolution could have proceeded in several directions. The deposition of secondary wall in various patterns between the scalariform bars is seen as a stage in the evolution of circular bordered pits. Evolutionary derivatives of *Psilophyton* can be expected to have sharply defined circular bordered pits, as for example in the progymnosperms, or may retain only the scalariform type of pitting such as characterizes many ferns.

Some specific groups whose origin can be traced to ancestral forms represented by *Psilophyton*-like organisms are worthy of comment.

The evolutionary origin of coenopterid ferns has been uncertain although some workers have postulated that a dichotomizing "psilophyte" might serve as a prototype of a coenopterid such as *Botryopteris* whose stem stele and foliar bundle are little different in size. Morgan and Delevoryas (1954) suggested that the protostelic coenopterids *Botryopteris*, *Apotropteris*, *Anachoropteris* and *Tubicaulis* represented steps in specialization of petiolar traces from an original dichotomous branching system. *Psilophyton* can be regarded as an early step in such a series. It branches dichotomously and it also branches unequally. The rectangular strand at the base of its fertile branch could be regarded as an earlier step than either ad- or abaxially curved petiolar strands of coenopterids. Either of the curved strands could

have lost some metaxylem, leaving protoxylem in a peripheral position. Bulges on the stem xylem often precede the departure of petiolar traces in coenopterids. Similar bulges are found at the base of fertile branches of *Psilophyton* (Pl. 20, fig. 32), and even more markedly at the base of its extensive vegetative branching (Pl. 24, figs. 63-65). In the latter position one even finds radially aligned metaxylem as in *Zygopteris* (e.g. Baxter, 1952). The scalariform, multi-seriate scalariform (e.g. Delevoryas and Morgan, 1952) and circular pitted tracheids found in coenopterids can be derived from the scalariform and interconnected scalariform tracheids of *Psilophyton*.

Coenopterid ferns bear endogenously produced, diarch roots often in areas where both the number of protoxylem strands and the amount of primary xylem in the stem have increased noticeably (Benson, 1911). This anatomical change, also found in our vegetative Axis B in the region of profuse branching (Pl. 24, fig. 62-65) prompted our speculation that appendages 3, 4 and 6 (Text-fig. 4) might be precursors of rootlike organs rather than precursors of leaves as we have treated them earlier. At present this can be no more than speculation because appendages 3, 4, and 6 are neither exarch in maturation of xylem nor are they endogenous in origin. Yet it would hardly be expected to find such differentiated structure in a plant from the late Lower Devonian that is in the early stages of evolution. Coenopterids also often bear organs referred to as aphlebiae (Holden, 1930; Baxter, 1951, 1952) which have been variously called rootlets, secondary leaf pinnae, a delicate protective tissue, scale leaves and even reduced pinnules. Our appendages 3 and 4 may equally well represent precursors of these exogenously produced organs.

An extremely simple coenopterid such as *Rhabdoxylon* (Dennis, 1968; Holden, 1960) is little different from *Psilophyton* in its terete, protostelic, centrarch stem stele, and its unequal dichotomies that produce circular to ovoid petiolar strands with a single adaxial protoxylem group.

Psilophyton could even be thought to foreshadow the axillary branches found in some coenopterids if one accepted Baxter's (1951) suggestion that the leaf subtending an axillary branch "migrated" down the branch from an originally more distal position. In the vegetative system of *Psilophyton* some appendages on branches may be precursors of leaves which could undergo the phylogenetic "move" visualized by Baxter (e.g. branchlet 1/1 on branch 1 of axis A in Text-fig. 4). *Psilophyton*, in other words, displays several of the characteristics that one might envisage in a plant that was still "plastic" and at an evolutionary level somewhat below the coenopterids.

Delevoryas (1962, pp. 79, 80) outlined some of the reasons for not considering coenopterids to be ancestral ferns. However, trimerophytes were less advanced than coenopterids and not subject to the same difficulties. They were more "plastic" and, it seems to us, could still have evolved in the direction of ferns as well as of coenopterids but so far we can point to no Devonian ferns with which to test this hypothesis.

Progymnosperms were the other major group of Devonian plants whose origin might stem from plants at the trimerophyte level of evolution. The primary xylem of aneurophytes, the more primitive progymnosperms, was usually lobed protostele with several protoxylem strands and with varying amounts of parenchyma (Scheckler and Bonamo, 1971a, b). The latter became more abundant both ontogenetically as in *Tetraxylopteris* and phylogenetically as *Archaeopteris* until a mixed pith or a true pith was present. Thus the primary xylem of progymnosperms was somewhat advanced over that at the trimerophyte level. But the evolution of a cambium and secondary xylem, probably about Eifelian time, was the more striking advance found among progymnosperms. The resulting secondary tissues were markedly gymnospermous in character. Morphologically progymnosperms were an elaborate branching system, more elaborate than trimerophytes but marked by the same main axis and three-dimensional lateral branch systems that bore smaller ultimate appendages that were sometimes three-dimensional, sometimes planated. It is difficult to think of this system as more than an elaboration of the branching systems of trimerophytes. Certain lateral branches of aneurophytes were fertile. They dichotomized. They branched pinnately. They bore sporangia terminally and the whole system consisted of masses of sporangia. But again the planation of a fertile branch of a trimerophyte and the webbing of some of its members could easily result in the fertile system of aneurophyte such as *Tetraxylopteris* or *Protopteridium* (Bonamo and Banks, 1967; Leclercq and Bonamo, 1971).

SUMMARY

A new species, *Psilophyton dawsonii*, sp. nov., is proposed for specimens comprising petrifications and compressions from two localities in late Emsian-early Eifelian (late Lower-early Middle Devonian) sediments in Gaspé, Quebec and northern Ontario, Canada. The plant at all levels of branching is circular in cross section. As yet, the apex and base of the plant are not known. Maturation of the xylem in the centrarch, there is no secondary growth and the strand is circular in cross section in all parts except in the base and

lower branching levels of fertile branches. The protoxylem consists of narrow spiral and scalariform elements. The surrounding metaxylem tracheids have broad scalariform bordered pits in which additional secondary wall material has outlined one to three, most commonly one or two, horizontal rows of circular, pitlike areas. The number of pitlike areas in a row varies with the width of the tracheid. The phloem, rarely preserved, is centrifugal to the xylem strand and is composed of elongate cells with slightly oblique end walls in which no sieve areas have been observed. An inner cortex, which probably functioned as assimilating tissue, immediately surrounds the stele and consists of narrow, thin-walled, loosely arranged parenchyma cells. This tissue is followed by an outer cortex of thick-walled, collenchymatous cells which form a hypodermal layer that is continuous around the axis except at points where substomatal chambers have developed. There, directly beneath the stomata, the thick-walled cells are replaced by parenchyma which subsequently disintegrates and a substomatal chamber results. Epidermis is rarely recognizable but where it can be defined the cells are small and tangentially rectangular in cross section and vertically elongate in longitudinal section.

Branching of the main axis is into two equal parts, the xylem strand in both is terete. Fertile lateral branch systems are easily recognized in cross section by their distinctive xylem strand which is rectangular in outline. The first two divisions of the strand are closely spaced dichotomies, usually characterized by the abortion of one of the three resulting branches. Each of the remaining two branches, after elongation, again undergoes two close dichotomies in which one of the three resulting branches aborts. We refer to these branchings followed by abortion as "double dichotomies." Subsequent branching is strictly dichotomous and the distance between dichotomies decreases distally. A strand of xylem extends up to the sporogenous tissue of each of the sporangia which terminate the ultimate divisions. The sporangia form loose clusters consisting of 32 pairs with members of each pair arranged such that their lines of dehiscence are on facing surfaces. The number of sporangia in the clusters may be less as a result of abortion of a sporangium or suppression of a dichotomy. The number may be increased by the addition of a dichotomy in the system. Throughout the lateral branch systems the dichotomies occur 90° around the stem from one another, producing three dimensional structures. The fertile branches are produced from the main axis in alternate and distichous arrangement in zones which alternate with vegetative branch systems. The traces to, and xylem strand of, vegetative branches are circular in cross

section. The traces are produced spirally in relatively large numbers within an extremely short vertical distance. The plant is leafless but some of the vegetative branchlets with terete, delicate, recurved or straight, ultimate tips could be interpreted as precursors of leaves.

Spores isolated from the sporangia are 40-75 μ in diameter. Their exines are smooth. Curvaturae are present and they usually follow the equatorial margin of the spores. Commissures are outlined by darkened areas that may be straight or curved. The spores most closely resemble the spore genus *Retusotriletes*.

The fertile systems of *Psilophyton* are like those described by Halle, and for which he proposed the name *Dawsonites*. We maintain *Dawsonites* as a form genus when only a portion of the fertile system is found and can not be shown by technique to be *Psilophyton*.

Psilophyton dawsonii may be distinguished from *P. princeps*, *P. kräuselii*, *P. arcticum*, *P. rectissimum*, and *P. goldschmidtii* by its lack of spines or hairs which characterize the other species. The sporangia of *P. dawsonii* are smaller than those of *P. princeps* and larger than those of *P. kräuselii*. The glabrous species *P. forbesii*, for which sporangia are perhaps known, is not certainly enough described with regard to the arrangement and branching of its fertile shoots and the number of sporangia they bear to make meaningful comparisons with *P. dawsonii*.

The stratigraphic range of species of *Psilophyton* can not be clearly defined. The oldest *Psilophyton*-like fragments, referable however to *Dawsonites arcuatus*, are of late Siegenian age while the youngest well documented specimens are of Eifelian age. The plexus of *Psilophyton* spp. had its acme during Emsian-Eifelian time.

Phylogenetically *Psilophyton* and the other genera in the subdivision Trimerophytina (i.e., *Trimerophyton* and *Pertica*) demonstrate the evolutionary potential to continue the adaptive radiation of vascular land plants and serve as the source whence coenopterids and progymnosperms evolved.

ADDENDUM

Shortly after our paper was in press another, also in press, containing descriptions of two new species of *Psilophyton* came to our attention. The new species are *P. microspinosum* and *P. dapsile* Kasper, Andrews, and Forbes in "New fertile species of *Psilophyton* from the Devonian of Maine", *American Journal of Botany*, 1974. *P. dawsonii* is readily differentiated from *P. microspinosum* in that its axes

are not spinous and that its sporangia are pendulous rather than standing erect. Sporangia of *P. dawsonii* are larger than those of *P. dapsile*, 3.0-5.0 mm $\times$ 1.0-1.5 mm vs. 1.7-2.1 $\times$ 0.5-0.9 mm and are less abundant, approximately 32 pairs as opposed to possibly 256 pairs if the reported estimate of 256 pairs is substantiated. No anatomical detail is known for the species described by Kasper, *et al.*, and thus comparison with *P. dawsonii* is precluded.

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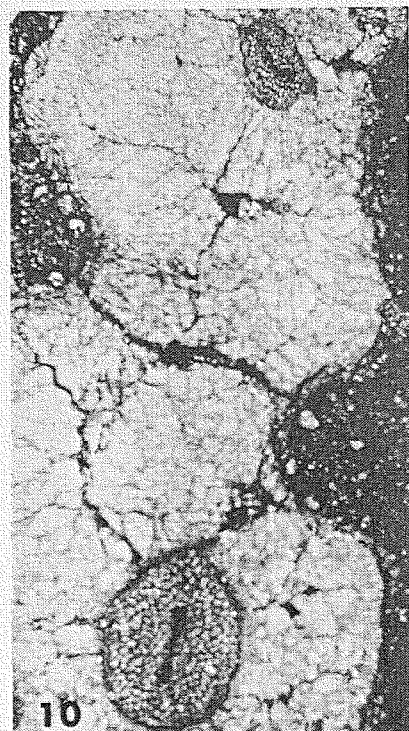
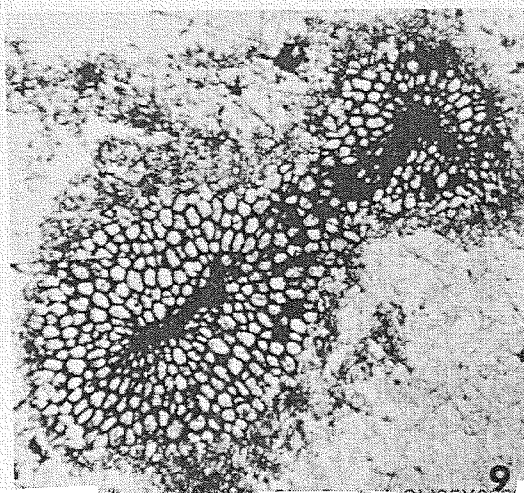
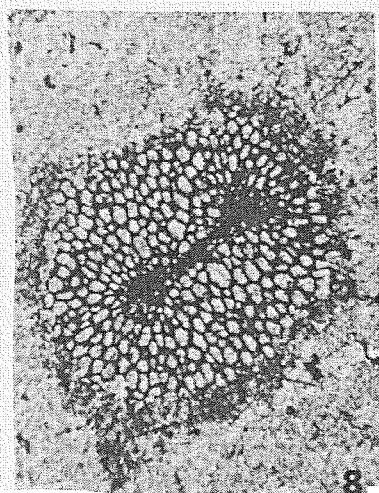
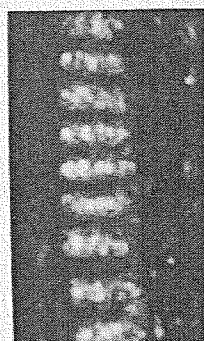
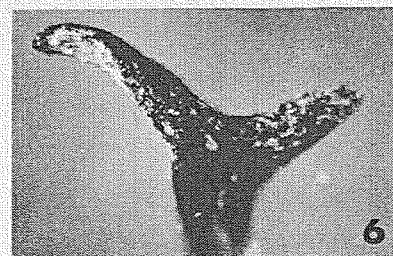
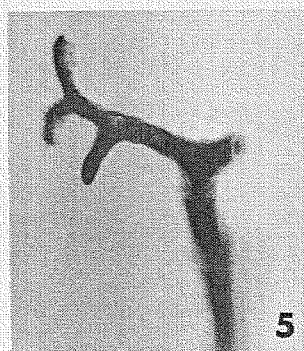
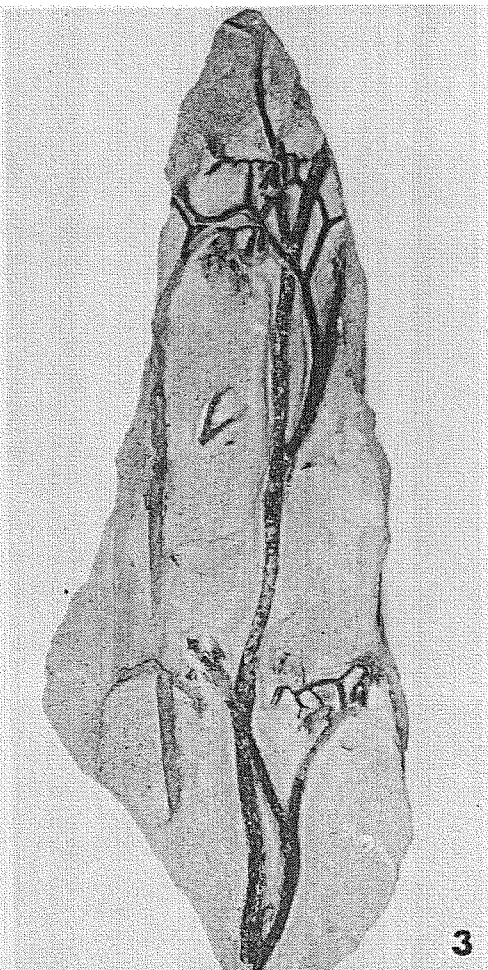
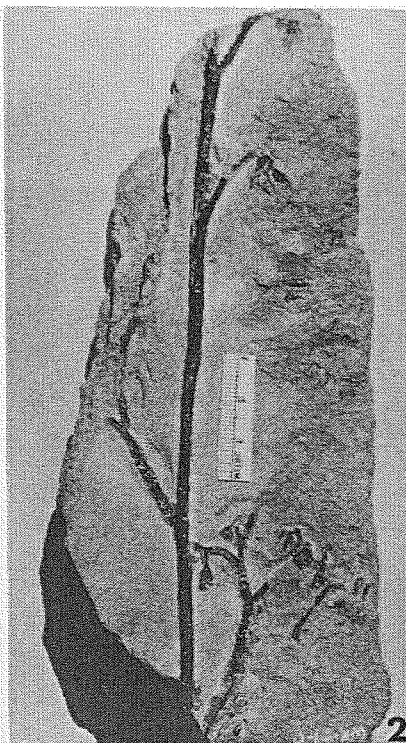
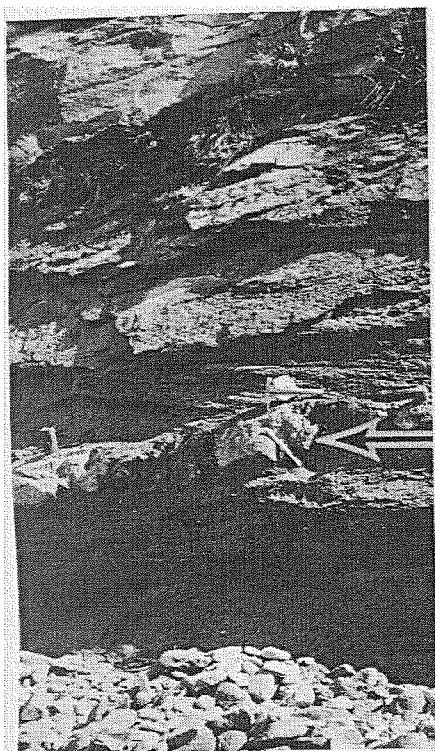
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PLATES

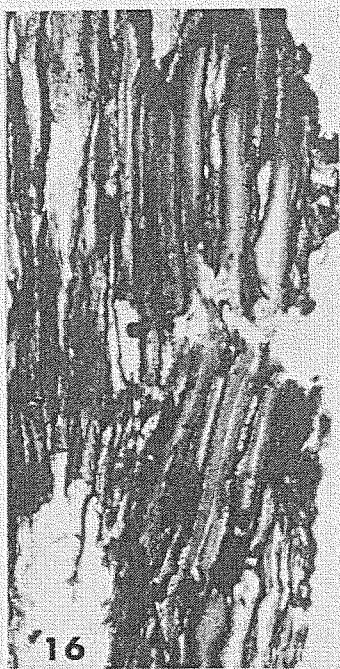
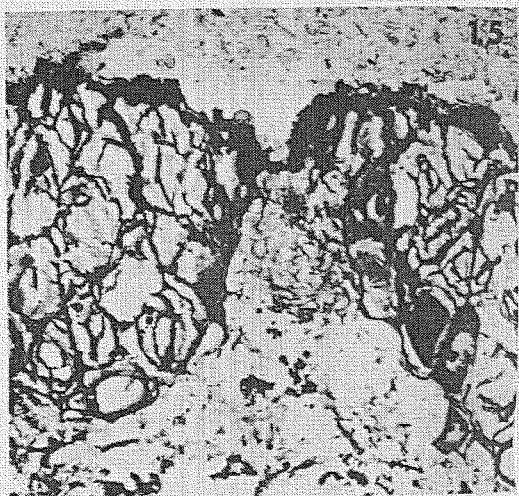
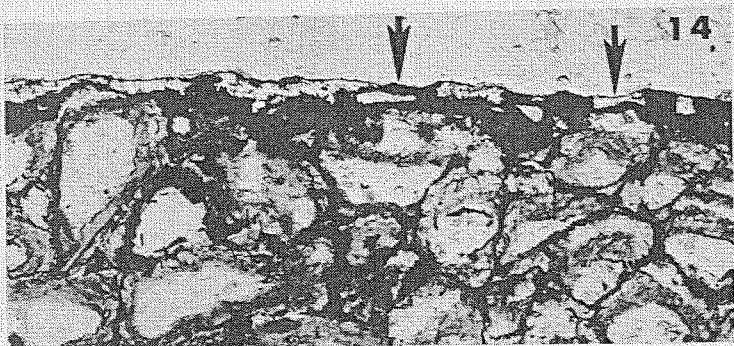
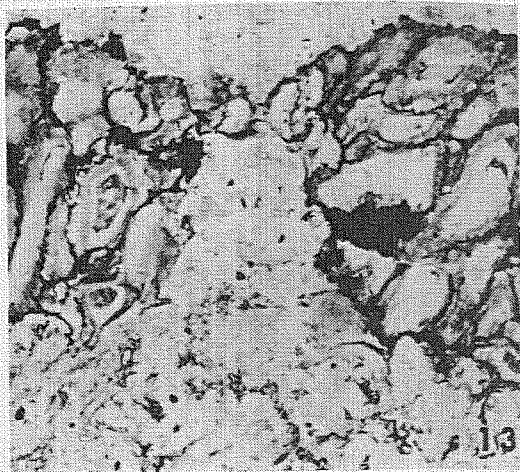
EXPLANATION OF PLATE 17

Figure	Page
1-3, 5-10. <i>Psilophyton dawsonii</i> , sp. nov.	105
4. <i>Psilophyton goldschmidtii</i> Halle	107
1, 5, 6. <i>P. dawsonii</i> from Gaspé; 2, 3, 7-10. From Abitibi River, Ontario; 4. <i>P. goldschmidtii</i> Halle from Røragen, Norway.	
1. Boulder (arrow) containing <i>P. dawsonii</i> in place in cliff east of Douglastown, P. Q. on Gaspé Peninsula; $\times 1/40$.	
2. Specimen from Abitibi River locality prior to uncovering by needles (GSC 32719); $\times 1/2$.	
3. <i>P. dawsonii</i> , sp. nov.	105
Final stage in uncovering, by F. M. Hueber with steel needles, of a fertile branching system that terminates in 64 sporangia. Specimen from Abitibi River (GSC 32720); $\times 2/3$.	
4. <i>P. goldschmidtii</i> Halle	107
Borrowed from the Halle Collection Swedish Museum of Natural History and uncovered by Leclercq to show an aborted branch (arrow) at first "double dichotomy" of fertile branch system; $\times 1$.	
5. Tips of sterile (vegetative) branch system macerated out of cobble and embedded in bioplastic. Three dichotomies are seen here to be at right angles to one another. Branch system was thus three-dimensional (CUPC 192); $\times 5.5$.	
6. Final dichotomy of vegetative branch system, also in bioplastic. Note that tips are tapering and rounded, not spinelike (CUPC 192); $\times 13$.	
7. One tracheid from pyritized axis at Abitibi River to show its identity to those from Douglastown; cf. Figures 23, 25, 26 (GSC 32720a); $\times 400$.	
8. Transverse section of xylem strand from pyritized axis (Abitibi River) showing division of protoxylem below attachment of a fertile branching system (GSC 32720b); $\times 70$.	
9. Same axis as Figure 8 higher up showing trace to fertile branch (GSC 32720c); $\times 70$.	
10. Same axis as Figures 8 and 9 showing xylem of main axis (below) and rectangular strand to fertile branch (above). Compare this series from Abitibi River with the series (Figs. 31-34) from Douglastown (GSC 32720d); $\times 30$.	



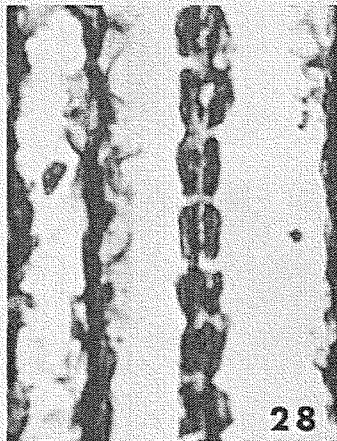
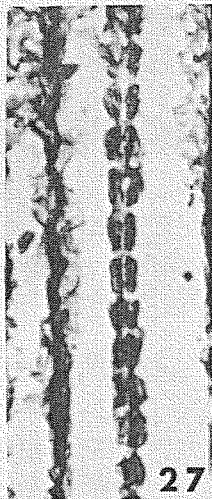
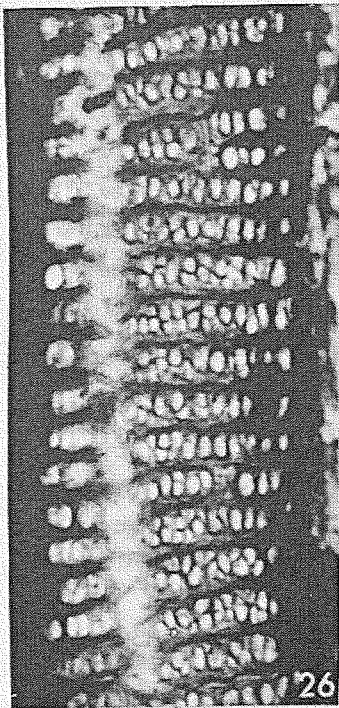
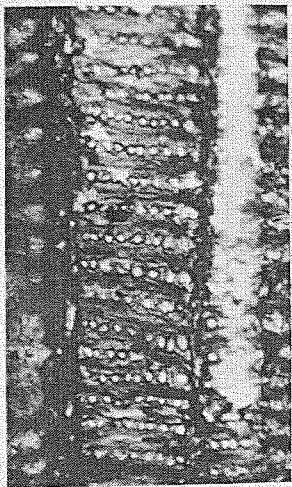
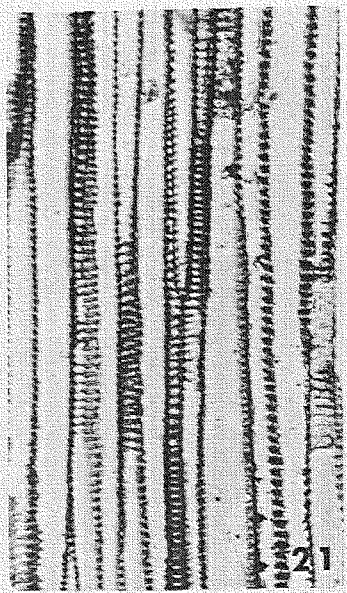
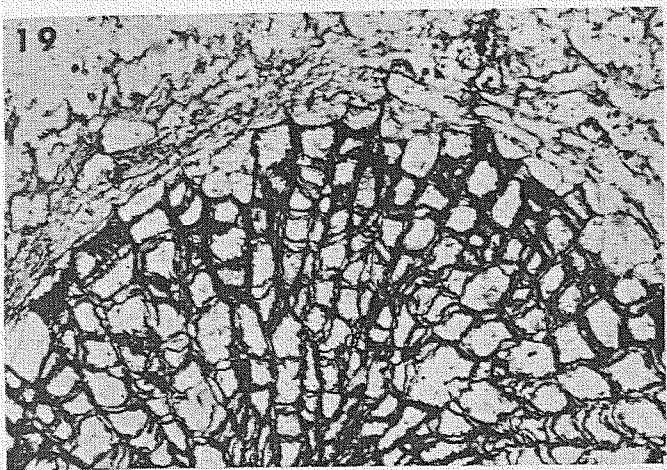
EXPLANATION OF PLATE 18

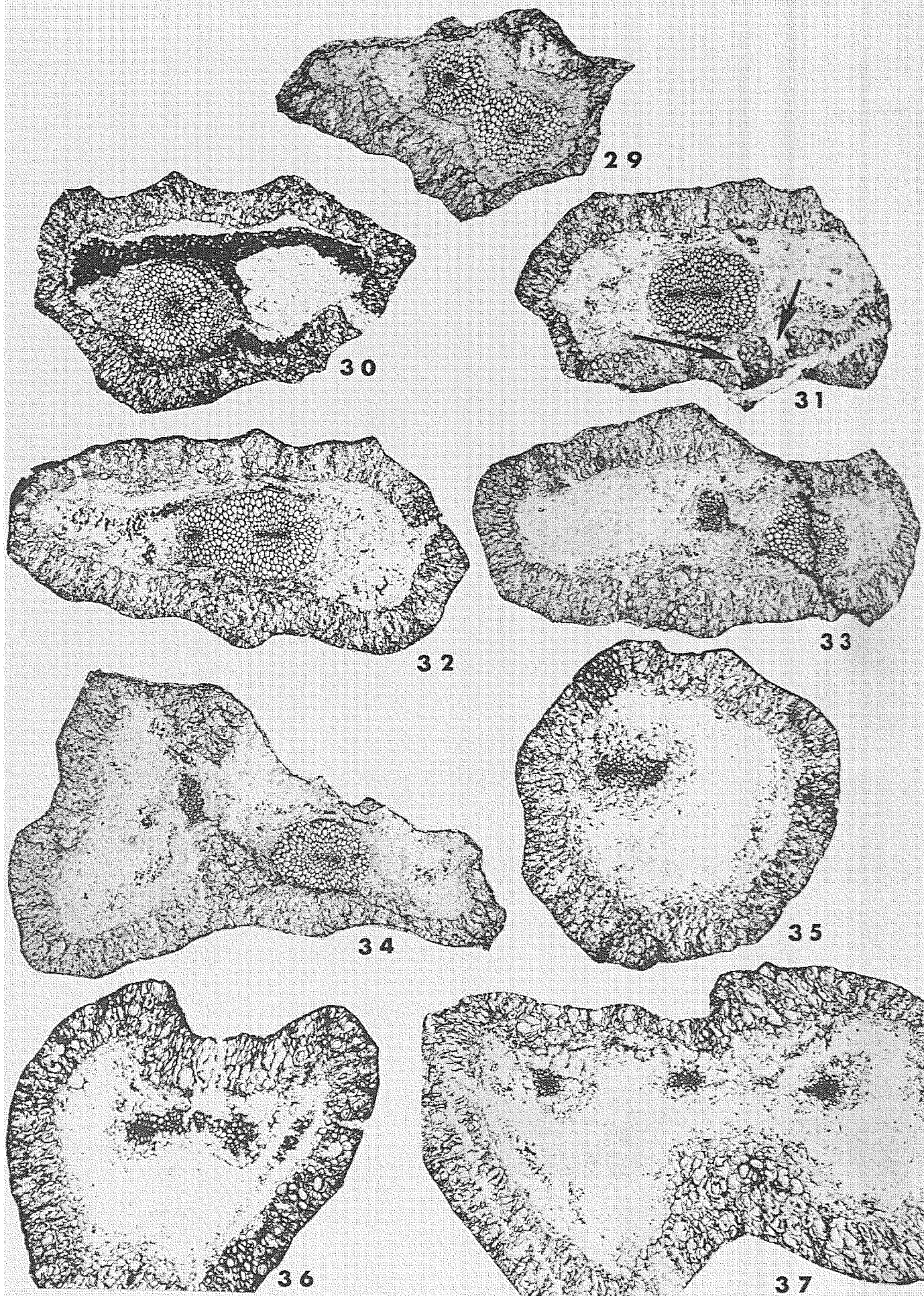
Figure		Page
11-18.	<i>Psilophyton dawsonii</i> , sp. nov.	105
	Histology.	
11.	Epidermis (arrow) in longitudinal section (CUPC 191 — slide 35.1.bY.4). × 180.	
12.	One substomatal chamber still filled with intact cells, some parenchymatous (arrow), some collenchymatous (CUPC 192 — slide 4.3.2Y.31); × 110.	
13.	Substomatal chamber below a pair of presumed guard cells (CUPC 192 — slide 4.4.1.3); × 140.	
14.	Epidermis (arrows) in transverse section (CUPC 192 — slide 4.3.2Y.35); × 145.	
15.	One substomatal chamber in which cells are disrupted and represented by debris (CUPC 198 — slide 34.3.1.13a); × 145.	
16.	Demineralized axis embedded in paraffin and microtomed. Several thick- walled collenchymatous cells well preserved (CUPC 194 — slide J1); × 100.	
17.	Collenchymatous (hypodermal) cells of outer cortex in longitudinal section, end walls transverse to slightly oblique (CUPC 191 — slide 35.1.1.17); × 105.	
18.	Inner cortex, parenchymatous cells in longitudinal section (CUPC 191 — slide 35.1.bY.4); × 140.	



EXPLANATION OF PLATE 19

Figure		Page
19-28.	<i>Psilophyton dawsonii</i> , sp. nov.	105
	Histology.	
19.	Phloem cells adjacent to xylem in transverse section (CUPC 192 — slide 4.3.2Y.35); $\times$ 110.	
20.	Phloem cells in longitudinal section (CUPC 192 — slide 4.3.L.7); $\times$ 280.	
21.	General view of xylem in longitudinal section (CUPC 195 — slide 21.3); $\times$ 150.	
22.	Spiral element in protoxylem, longitudinal (CUPC 192 — slide 4.3.L.8); $\times$ 450.	
23.	Metaxylem tracheid showing scalariform secondary thickenings and interconnections between them that outline pitlike areas (CUPC 197 — slide 32.3bL.18); $\times$ 360.	
24.	Scalariform pitted tracheid derived from a demineralized axis that was embedded in paraffin and microtomed. Note resemblance of this cell to that in Fig. 23 (CUPC 194 — slide F2); $\times$ 715.	
25.	Scalariform-pitted tracheid with interconnections between the bars simulating the Williamson's striations characteristic of some lepidodendrids (CUPC 192 — slide 4.3.L.7); $\times$ 450.	
26.	Scalariform-pitted tracheid showing two rows of pitlike areas between the bars (CUPC 192 — slide 4.3.L.4); $\times$ 610.	
27.	Sectional view of scalariform bordered pits, longitudinal section (CUPC 191 — slide 35.1.bY.15); $\times$ 770.	
28.	Sectional view of scalariform bordered pits, enlarged (CUPC 191 — slide 35.1.bY.15); $\times$ 1205.	



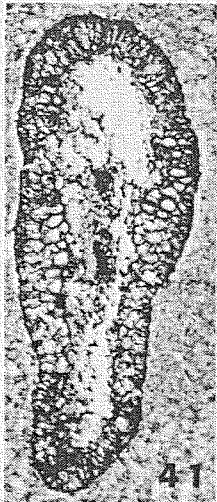
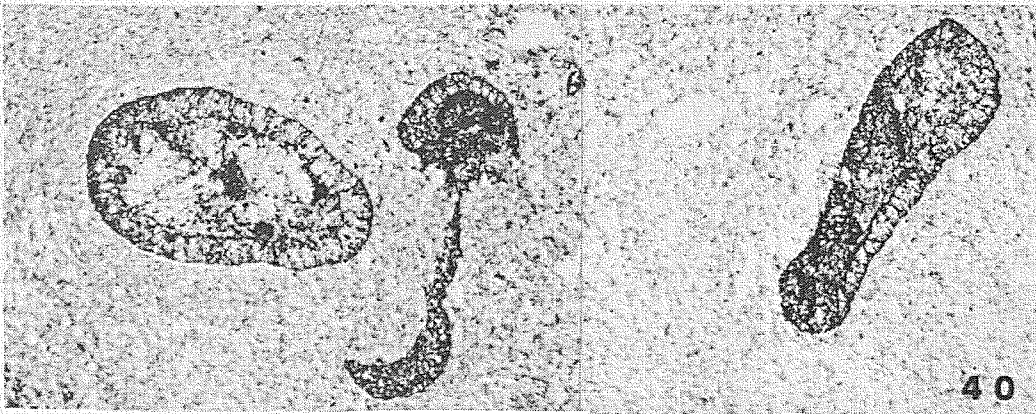
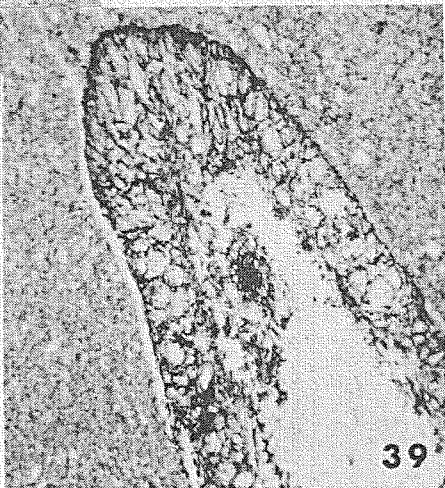
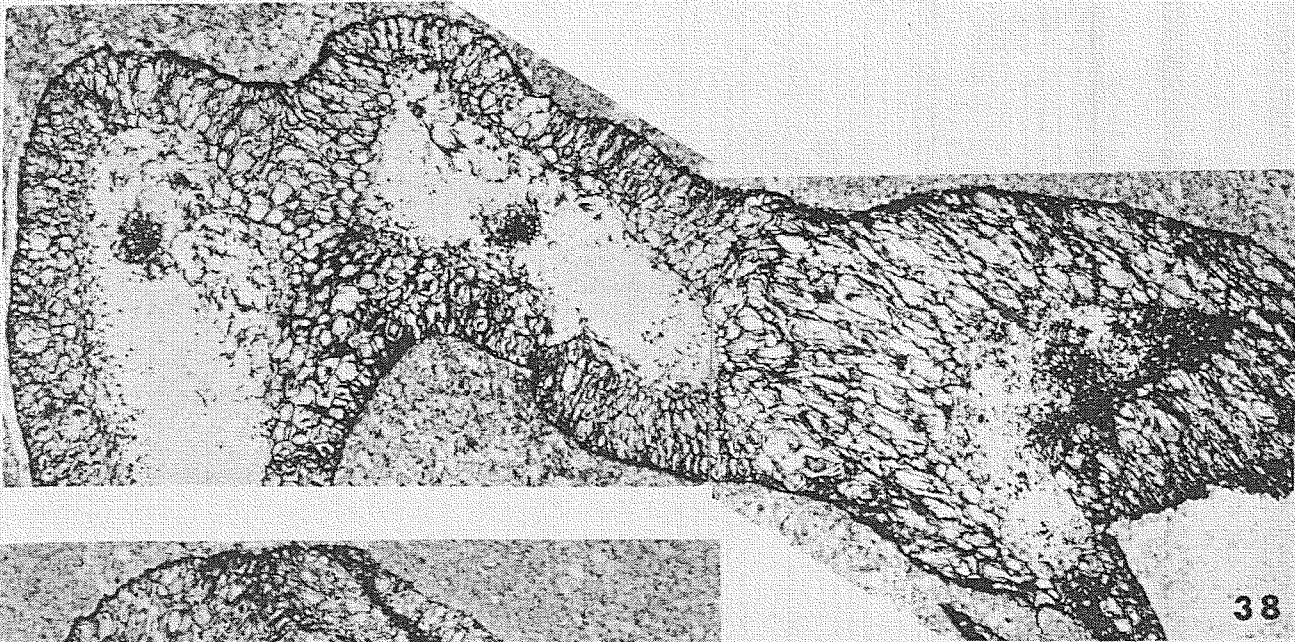


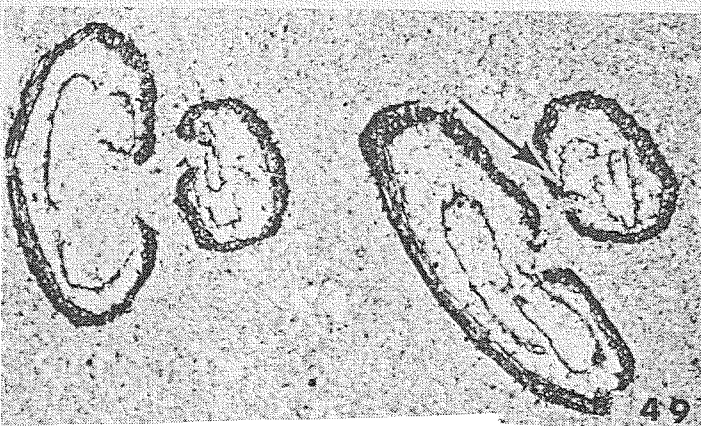
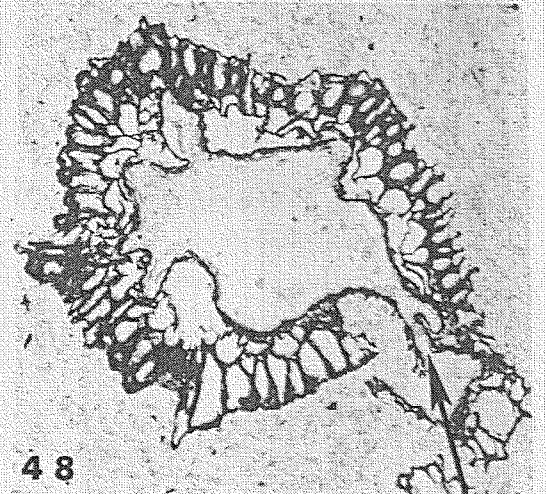
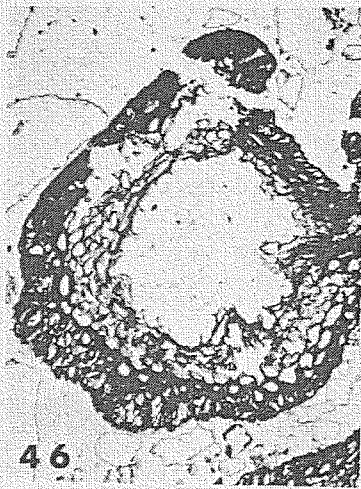
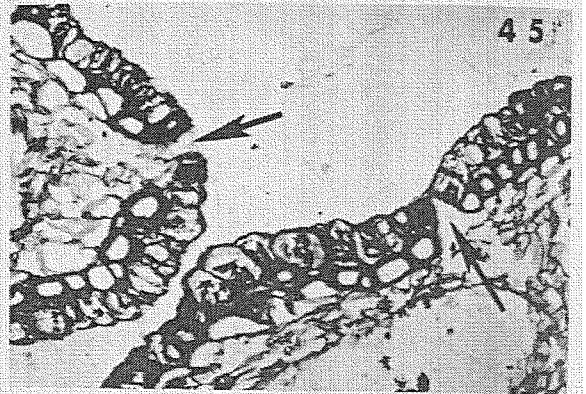
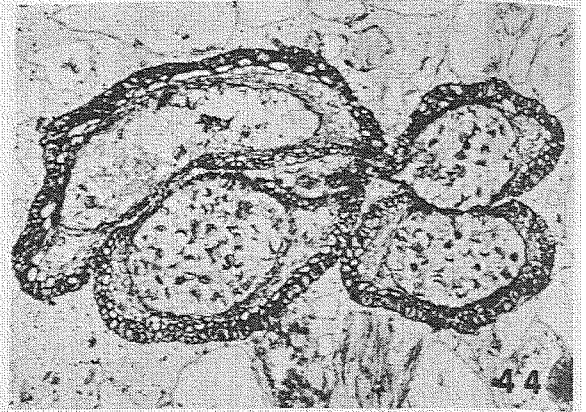
EXPLANATION OF PLATE 20

Figure		Page
29-37.	<i>Psilophyton dawsonii</i> , sp. nov.	105
	Series of sections of main axis and fertile branch system arranged from base toward apex.	
29.	Dichotomy in a main axis below a fertile branch. Each new xylem strand has one centrarch protoxylem strand (CUPC 194 — slide 13.23); $\times 30$.	
30.	Transverse section of main axis with one protoxylem strand at a higher level but still below origin of fertile lateral branch (CUPC 190 — slide 31.3.1.23); $\times 30$.	
31.	Main axis now with two protoxylem strands and xylem elliptical rather than terete. Arrows indicate substomatal chambers (CUPC 190 — slide 31.4.1.15); $\times 30$.	
32.	Xylem strand, at higher level, further attenuated. Trace to fertile branch is seen on left and protoxylem of main axis has elongated well below the level at which a second fertile branch will originate on the right (CUPC 191 — slide 35.1.1.86); $\times 30$.	
33.	Trace now free from xylem of main axis and becoming rectangular in shape (CUPC 190 — slide 31.3.1.151); $\times 30$.	
34.	Trace to fertile branch almost enclosed by its own cortex (CUPC 190 slide 31.3.1.172); $\times 30$.	
35.	Transverse section of proximal end of fertile branch system. Its xylem strand is rectangular (CUPC 190 — slide 31.3.1.80); $\times 30$.	
36.	Trace in fertile branch following two dichotomies of its protoxylem strand (CUPC 190 — slide 31.3.1.2); $\times 30$.	
37.	Fertile branch at higher level after xylem strand has dichotomized twice. The resulting three strands included in common cortex (CUPC 190 — slide 31.2.2.3); $\times 30$.	

EXPLANATION OF PLATE 21

Figure	Page
38-41. <i>Psilophyton dawsonii</i> , sp. nov.	105
Anatomy of lateral fertile branching system, continued from Plate 20.	
38. Each of the three xylem strands produced by first "double dichotomy" now enclosed by its own cortex (CUPC 190 — slide 31.2.2.50); $\times 30$.	
39. Three branches resulting from first "double dichotomy"; middle branch already aborting. Each of the two healthy branches will repeat the stages shown in Figures 35-39, producing a second "double dichotomy". Only the final stage of this second series is illustrated for one of the two branches, in Figure 40 (CUPC 190 — slide 31.2.2.135); $\times 30$.	
40. Result of second "double dichotomy" of one of the two healthy branches in Figure 39. Here the central branch is again aborting. The fertile system now consists of four strong branches like these in Figure 40 (CUPC 191 — slide 35.1.1.59); $\times 30$.	
41. One of the four branches which were present at the level of Figure 40 is shown here with two xylem strands resulting from its first dichotomy. Each strand will soon be found in its independent cortex, and each may dichotomize three more times producing a total of 32 slender axes. Each of the 32 may dichotomize a final (fourth) time and terminate in a pair of sporangia as shown in Figures 42, 43 (CUPC 191 — slide 35.1.1.86); $\times 30$.	





EXPLANATION OF PLATE 22

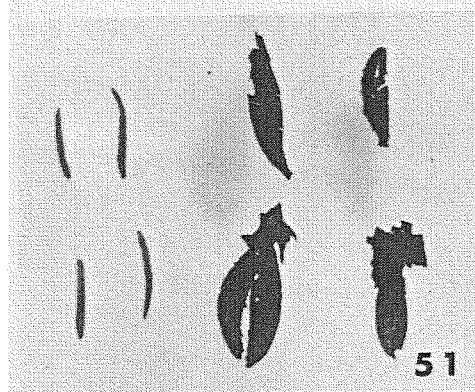
Figure		Page
42-49.	<i>Psilophyton dawsonii</i> , sp. nov.	105
	Structure and ontogeny of sporangia.	
42.	Transverse section showing the dichotomy at the base of a pair of sporangia. Note relatively massive xylem strands at this ultimate division and stem-like nature of sporangia (CUPC 194 — slide 13.23); $\times 70$.	
43.	Oblique longitudinal section of a pair of sporangia showing final (sixth) dichotomy of vascular strand at base of sporangia (CUPC 191 — slide 35.2.1.34); $\times 35$.	
44.	Group of four young sporangia (two pairs) containing spores and with both inner and outer "cortical" tissues still intact in some areas (USNM 175772, peel 1.1.1.2); $\times 30$.	
45.	Transverse section of parts of two young sporangia, each showing a probable stoma and stomatal chamber. Parenchyma cells here are beginning to break down (USNM 175772, peel 1.1.1.2); $\times 90$.	
46.	Transverse section of one entire young sporangium showing its intact outer collenchymatous and inner parenchymatous wall cells. Note resemblance to stem cortex (USNM 175772, peel 1.1.1.1); $\times 60$.	
47.	One end of sporangium in Figure 44 enlarged. In this older sporangium parenchyma has broken down along much of the lateral wall but remains intact at the ends (USNM 175772, peel 1.1.1.1); $\times 110$.	
48.	Mature, dehiscent (arrow) sporangium. Parenchyma cells now represented only by a membrane which is formed by the innermost tangential walls of parenchyma tissue. This membrane remained inside sporangia in nature but it can be removed from the fossil by maceration as is shown in Figures 53-55 (CUPC 196 — slide 23.30); $\times 90$.	
49.	Transverse section of old, dehiscent sporangia. Dehiscence occurs along facing surfaces. An empty pair resembles two letter C's. Membrane remains inside sporangia, attached near line of dehiscence (arrow) (CUPC 194 — slide 13.34.)	
50.	Result of splitting one calcareous cobble to expose paired terminal sporangia similar to those in Figures 43-49 (CUPC 193); $\times 3$.	

EXPLANATION OF PLATE 23

Figure

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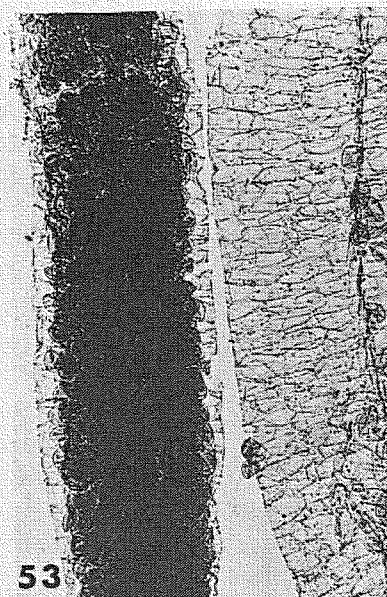
- 51-61. *Psilophyton dawsonii*, sp. nov. 105
- Sporangia and spores.
51. Sporangia (right) and membranes full of spores (left) macerated out of similar sporangia. All from Abitibi River, Ontario (GSC 32720e); $\times 3$.
 52. Sporangia (Abitibi River) demineralized, embedded in paraffin and microtomed. Outer thick wall and inner translucent membrane (arrow) both visible. This is identical to the two layers found by Lang (1931, pl. 28, fig. 24 and subsequent papers) (GSC 32721); $\times 30$.
 53. Two membranes isolated by maceration from Abitibi River sporangia; one is full of spores (GSC 32722); $\times 60$.
 54. One membrane full of spores isolated by maceration from a sporangium from Douglastown (CUPC 193 — slide 1); $\times 35$.
 55. One empty membrane isolated by maceration from a sporangium from Douglastown (CUPC 193 — slide 2); $\times 25$.
 56. Single spore with uncovered, smooth exine. Remnants of envelope (? perispore) in the background outside the spore. Thickened areas along commissure have concave sides. Amb nearly circular. Some evidence of curvaturae toward lower margin (CUPC 195 — slide 21.10); $\times 465$.
 57. Mass of spores found in the matrix amongst a cluster of sporangia (CUPC 195 — slide 21.2.3); $\times 45$.
 58. One spore with its outer covering removed revealing its smooth exine. The covering envelope whose surface is granular lies to the lower left. Thickened areas along commissures have straight sides and the amb is essentially circular (CUPC 195 — slide 21.10); $\times 675$.
 59. Single spore mostly covered by envelope. Thickened triangular areas with straight sides (CUPC 195 — slide 21.2.3); $\times 715$.
 60. One tetrad in which distal and proximal walls of each spore are compressed together so that trilete mark appears to be distal in position. A. Thickened proximal wall. B. Distal wall. C. The envelope (? perispore) which separates from the spore before dispersal (CUPC 195 — slide 21.10); $\times 500$.
 61. Single spore still partially covered by envelope. Commissure split open. Thickened area with concave sides (CUPC 195 — slide 21.2.3); $\times 515$.



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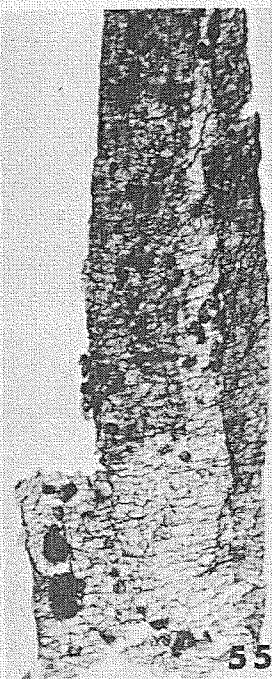
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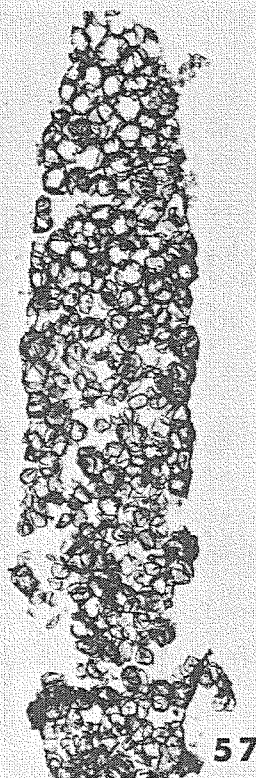
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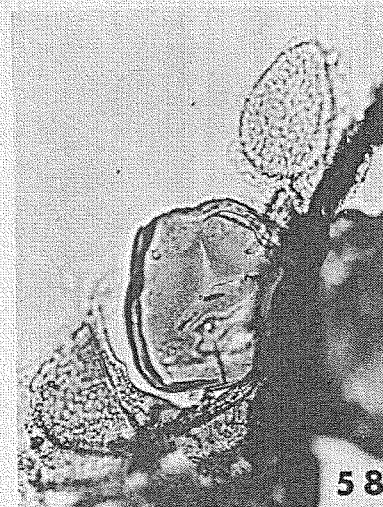
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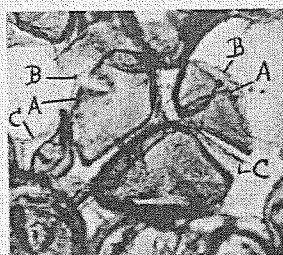
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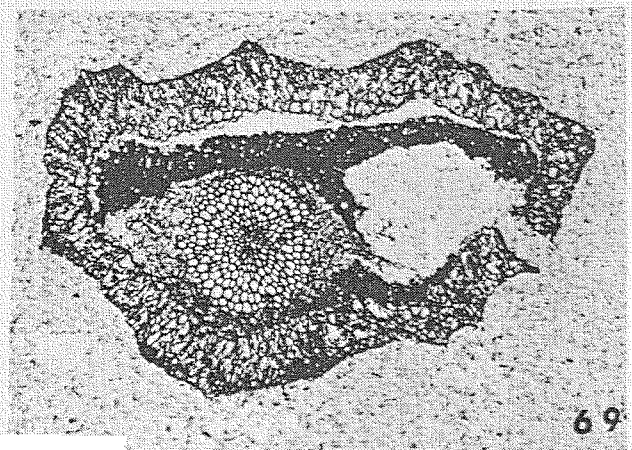
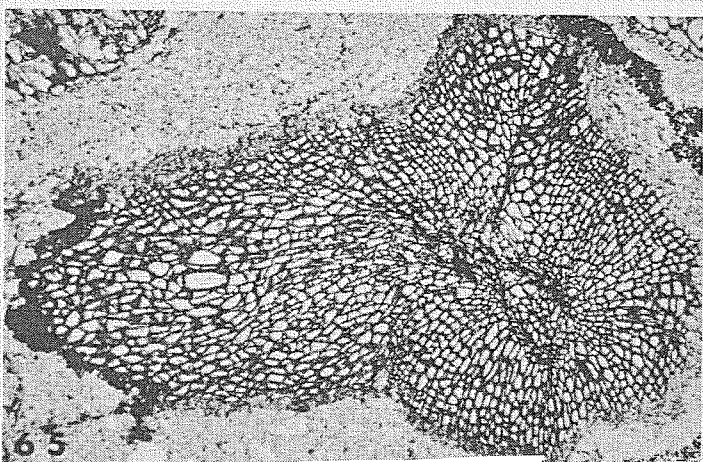
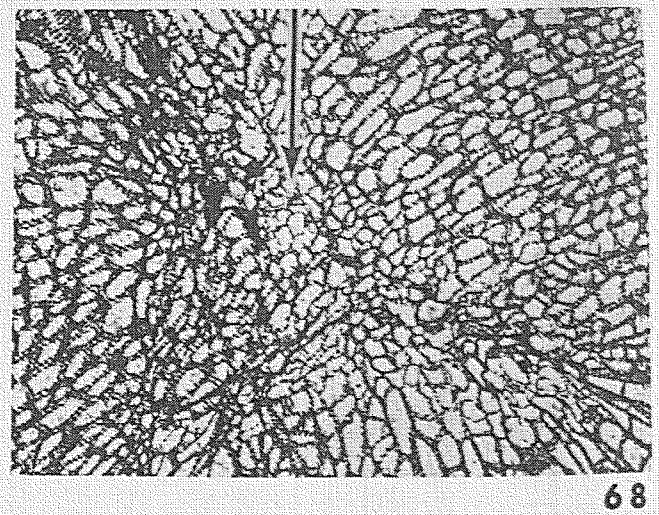
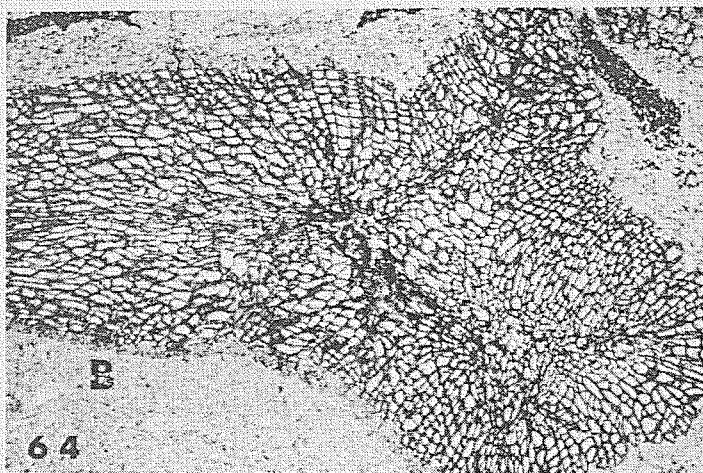
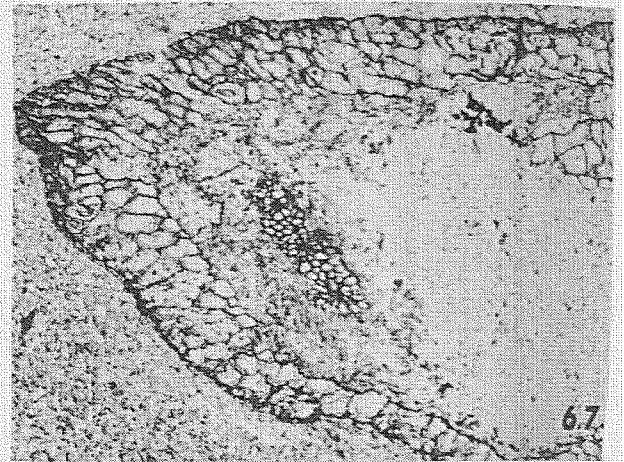
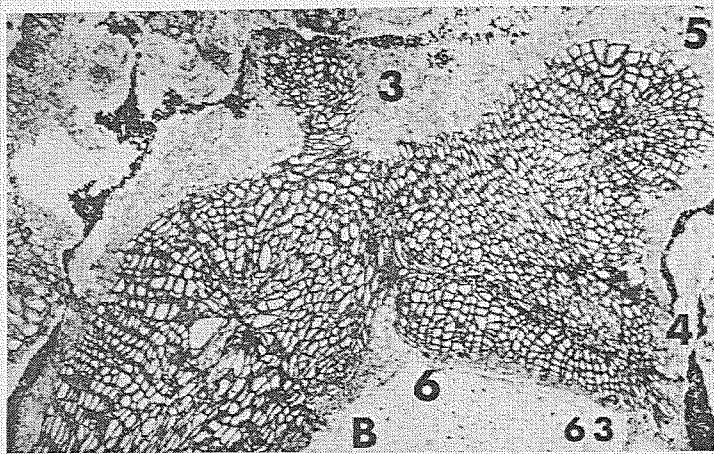
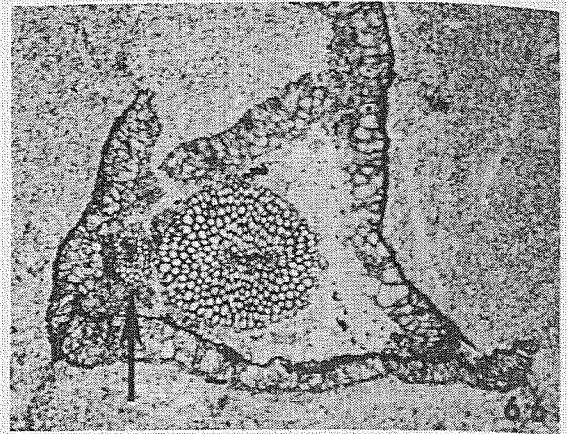
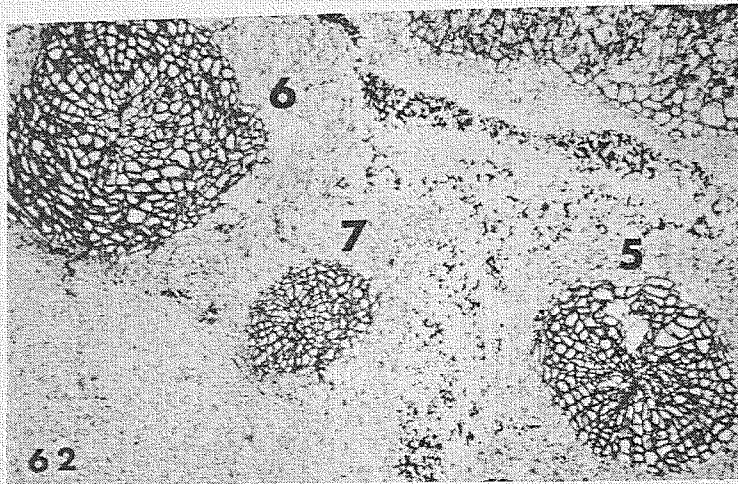
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61



EXPLANATION OF PLATE 24

Figure

Page

- 62-69. *Psilophyton dawsonii*, sp. nov. 105
- Anatomy of main axis in region of vegetative branching and up to the base of region of fertile branching.
- 62-65. Series of transverse sections from more distal toward more proximal end.
62. Vascular strands to vegetative branches 6, 7, and 5 (left to right) (CUPC 192 — slide 4.4.1.12); $\times 30$.
63. Lower level than Figure 62: shows origin of traces to sterile branches 3, 4, 5, 6. Xylem strand of main axis B bends downward at left. Note that some metaxylem simulates secondary xylem (CUPC 192 — slide 4.4.1.14); $\times 20$.
64. Lower level. Massive xylem strand with several large protoxylem areas. Xylem of main axis B is the large strand at left and branch 3 will be supplied by large mass at top right; remainder will eventually produce strands to branches 4, 5, 6, 7 (CUPC 192 — slide 4.4.1.16); $\times 30$.
65. Lower level. Large compact mass of xylem. Xylem of main axis is the mass at left, branch 3 at top, and branches 4, 5, 6, 7, will originate from the remainder (CUPC 192 — slide 4.4.1.18); $\times 30$.
66. Xylem strand of main axis B above the level of production of vegetative branches 1-7 (above Fig. 62). Note that xylem strand now resembles one about to produce a fertile lateral branch (cf. Figs. 31-33) and note the typical rectangular bundle to a fertile branch (arrow) on the left (CUPC 192 — slide 4.3.2Z.27); $\times 30$.
67. Transverse section of rectangular bundle, first seen in Figure 66, at a higher level now with three protoxylems and about to undergo a first "double dichotomy" (CUPC 192 — slide 4.3.2Z.52); $\times 50$.
68. Transverse section of a portion of Figure 64 to show one enlarged mass of central protoxylem (arrow) associated with the production of vegetative branches (CUPC 192 — slide 4.4.1.16); $\times 75$.
69. Transverse section of axis, also illustrated as Figure 30, below level of production of a known fertile branch system in the holotype. Compare the size of its xylem strand with that of the central xylem in the region of vegetative branching. Figures 64, 65 taken at the same magnification. Compare its size also with the axis in Figure 66 that we suppose will produce a fertile branch system above the level of vegetative branching (CUPC 190 — slide 31.3.1.23); $\times 30$.

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