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NEW FERTILE SPECIES OF *PSILOPHYTON* FROM THE DEVONIAN OF MAINE¹

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A B S T R A C T

A review of the history of the genus *Psilophyton* is presented. Two new species with sporangia in organic connection, *P. microspinosum* and *P. dapsile*, are described. They are compared with *Psilophyton*-like plants from Maine and other previously described fertile species of this genus. Evidence from several species in the Trout Valley flora confirms the concept of this taxon as presented by Hueber and Banks. Data based on all sporangium-bearing species of *Psilophyton* are outlined, certain evolutionary trends within the taxon are tentatively presented, and recommendations for the treatment of the numerous fragmentary species and future new species are suggested.

DURING THE PAST eight years, in the course of our study of the early Devonian Trout Valley Formation in northern Maine, we have made collections from several localities of fossil plants that fall within the limits of the genus *Psilophyton* as redefined by Hueber and Banks (1967). In view of the information that we now have, it seems appropriate to present this unit on *Psilophyton*, our chief objectives being to add to the content of the Trout Valley flora, to further elucidate the wide-spread and important Devonian genus *Psilophyton*, and to shed some light on the evolution of early land vascular plants.

Any consideration of the genus *Psilophyton* raises the specter of its long and complex history. The concept of the genus has been elusive since its inception over a hundred years ago by J. W. Dawson (1859). The source of the confusion has been the type species itself, *P. princeps*, which was originally described from fragments of several different plants. Over the years each succeeding author took as the "true" *P. princeps* one or other of the plants represented by the original fragments. With the eventual clarification of the type species, the meaning of the genus was likewise elucidated. We hope to contribute to this new understanding of the genus by the addition of two new fertile species from Maine as well as presenting additional data on other species.

Psilophyton is an important taxon for many reasons. It is one of the earlier described genera

of Devonian plants, many species have been assigned to it, and it has played a prominent part in botanical literature. In addition to its importance, and almost of equal weight, has been the confusion surrounding it. Because of this it is necessary to present here, in as succinct a manner as possible, a brief summary of the history of thought concerning this genus.

In 1859 J. W. Dawson described fossil plant remains from the shore of Gaspé Bay, Quebec, Canada. He placed some of these remains in a new genus, *Psilophyton*, with *P. princeps* as the type species. His reconstruction (1859) of *P. princeps* illustrates a plant with an erect dichotomizing axis terminating in straight or circinate curled branchlets. The upright portion arises from a horizontal "rhizoma" with "cylindrical rootlets." The fructification is stated as being in "lateral masses, protected by leafy bracts." However, Dawson had some doubt about the true nature of the reproductive organs.

Later, in 1870, Dawson modified his description and presented a second reconstruction of *P. princeps*. The major change concerned the fructifications. Dawson described and illustrated these organs as being "... oval sacs or spore-cases, borne gracefully on slender bending stalks." This new reconstruction (1870) clearly shows the reproductive organs as paired fusiform sporangia on ultimate recurved branchlets. This is the popular restoration which has appeared in numerous botanical texts over the years. This restoration was also important in formulating the concept of the genus in the minds of botanists during subsequent years.

The following year, 1871, Dawson presented a modified diagnosis of *P. princeps* and more substantial figures based on material collected the

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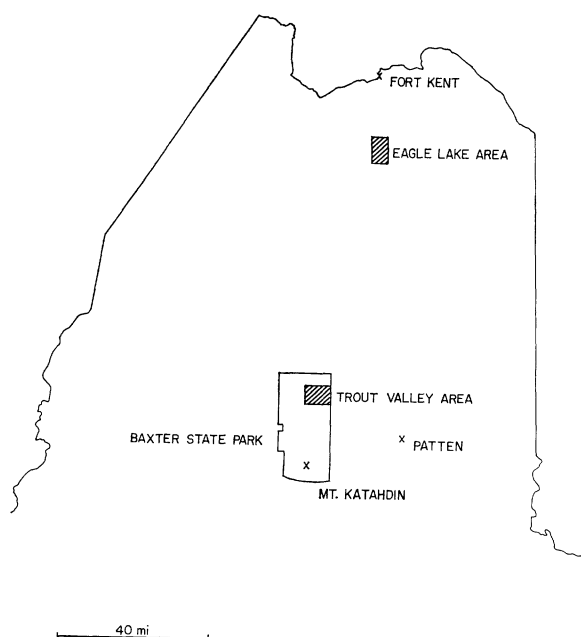


Fig. 1. Region of northern Maine, showing the Trout Valley and Eagle Lake areas from which fossil plants have been collected.

previous summer. It is at this point, however, that he introduced the fossil material called *P. princeps* var. *ornatum*: "In detached hand specimens I have no doubt that these plants would be regarded as specifically, perhaps generically, distinct from *P. princeps*; but the comparison of large numbers of nearly entire specimens forbids this conclusion. . . ."

It appears from Dawson's own words that the material called variety *ornatum* had the misfortune of being neither similar enough to *P. princeps* to be called simply that nor distinct enough to be given a new binomial. This is where the confusion arose about the type species and hence about the genus. In his own diagnosis (1871) Dawson mentions this variation: "Leaves . . . in barren stems, numerous and spirally arranged; in fertile stems and branchlets sparsely scattered or absent. . . ." Later workers had to choose one or the other as the type material.

Solms-Laubach (1891) pointed out that Dawson failed to demonstrate organic connection between the "leafy sterile axes" and the "near-leafless fertile axes." He stated that of the numerous poorly preserved specimens assigned to *P. princeps* by Dawson—some even questionable as being plant—only the "leafy axes" with crozier tips of the variety *ornatum* possessed the tangible characteristics necessary for the identification of *P. princeps*. In short, Solms-Laubach chose the varietal form as being typical for the species.

David White (Smith and White, 1905) examined various material labeled by Dawson as *P.*

princeps from Gaspé Bay and Campbellton, New Brunswick. The material from Campbellton White called the "smooth type" and the material from Gaspé Bay, the "spinous type." White stated that the two were distinct plants and that the smooth type was erroneously referred to that species by Dawson. White held the "true" *P. princeps* to be spiny and best represented by the variety *ornatum*.

Halle (1916), using the argument that Dawson's description and reconstruction was based on fertile and sterile parts not found in organic connection, proposed in accord with White that the type material for the genus *Psilophyton* be the leafy axes figured as the variety *ornatum*. For the naked sporangium-bearing specimens described by Dawson, Halle set up a new taxon, *Dawsonites arcuatus*. From this point on most references in the literature to *P. princeps* meant the spiny axes of the varietal form *ornatum*.

Edwards in 1924 made a significant contribution to the understanding of the varietal form (called *P. princeps* by him) with cuticular studies. Lang (1931) discussed two types of axes under the name *P. princeps*: the "typical spiny stems" of the variety *ornatum* and the "relatively smooth, longitudinally grooved axes" with fusiform sporangia (the *Dawsonites arcuatus* of Halle). A year later Lang (1932) presented additional information on the spines and cuticular patterns of the variety *ornatum*.

In 1942 Croft and Lang made a major breakthrough. They described cf. *Psilophyton princeps* (the varietal form that is) as having lateral sporangia. This evidence was confirmed by Hueber in 1964. He macerated material from the Abitibi River, Ontario, Canada, which revealed globose sporangia in lateral position on axes of the variety *ornatum*. Following the nomenclature of Halle, this material was called *P. princeps*.

At this point a reevaluation was necessary. Dawson's concept of *P. princeps* and the historical one was that of a plant with spiny axes and terminal sporangia. The varietal form *ornatum*, which was taken to be the type for *P. princeps*, was now known to have lateral sporangia—a quite different plant. The problem was resolved by Hueber and Banks in 1967. They selected a neotype for *P. princeps* which had spiny axes and terminal sporangia. In a separate paper that same year Hueber described the true *P. princeps* in detail.

In 1968 Ananiev and Stepanov described the varietal form *ornatum* based on fossils from Siberia and presented a fine reconstruction of the spiny axes with their lateral globose sporangia. And in 1971 Hueber assigned a new binomial to the variety *ornatum* calling it *Sawdonia ornata*.

This brief history of the genus *Psilophyton* and its type species will have to suffice. If nothing

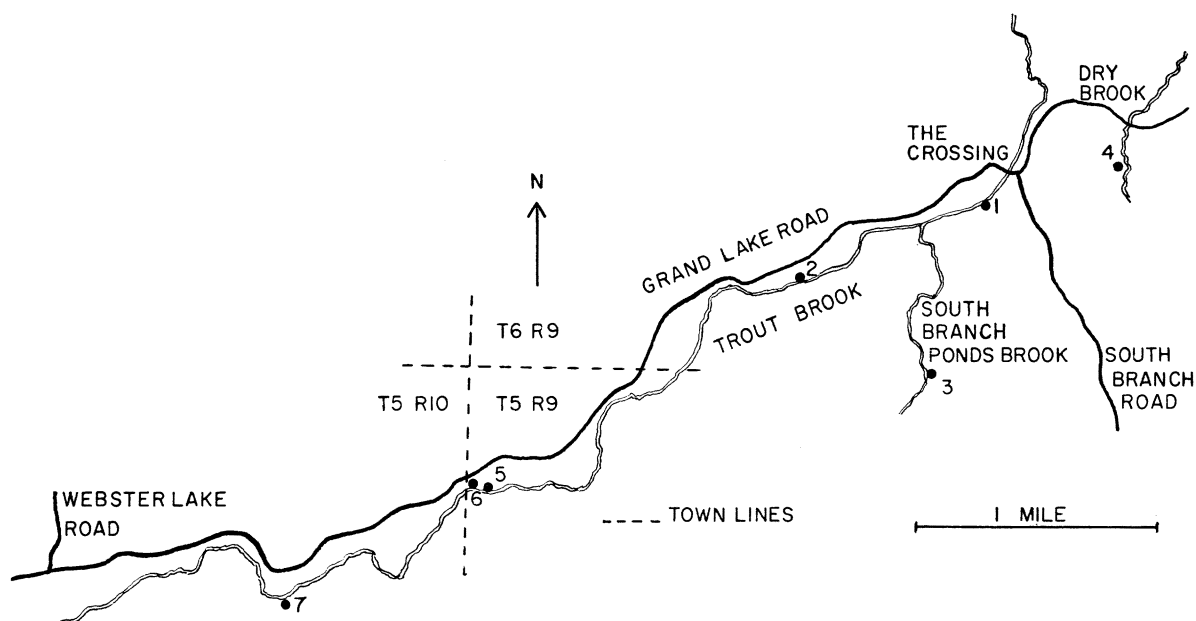


Fig. 2. Map of the Trout Valley area, showing fossil plant localities.

else it should convey the complexity of the puzzle and the number of workers responsible for putting the pieces together, all of which has taken more than a century.

LOCALITY AND STRATIGRAPHY—For the past eight years numerous specimens of several *Psilophyton*-like plants have been collected in northern Maine. These collections are from two areas: Trout Valley and Eagle Lake (Fig. 1). Figure 2 is a detailed map of the Trout Valley area and the localities listed below are sites at which species of *Psilophyton* have been uncovered. They all fall within a few miles of each other in Baxter State Park, Maine.

Locality #1: south bank of Trout Brook about 200 yards southwest (upstream) from the bridge at The Crossing, T 6N, R 9W, Traveler Mountain Quadrangle.²

Locality #3: east bank of South Branch Ponds Brook about 500 yards north (downstream) of its junction with Gifford Brook, T 5N, R 9W, Traveler Mountain Quadrangle.

Locality #5: north bank of Trout Brook about 150 yards east (downstream) of the Town Line between T 5N, R 10W, and T 5N, R 9W, Traveler Mountain Quadrangle.

Locality #6: north bank of Trout Brook about 25 yards east (downstream) of Town Line between T 5N, R 10W, and T 5N, R 9W, Traveler Mountain Quadrangle.

Within the Eagle Lake area (Fig. 3) there are two localities from which *Psilophyton*-like plants

have been collected. These sites are about 5.5 miles apart.

Locality #8: north bank of Red River about one-half mile west (upstream) of Red Ledge, T 15N, R 7W, Winterville Quadrangle.³

Locality #9: east bank of railroad cut about 50 yards north of point where tracks cross Fish River at Nadeau Thoroughfare, T 16N, R 7W, Eagle Lake Quadrangle.⁴

The localities of the Trout Valley area are all within the Trout Valley Formation. The sites from the Eagle Lake area are within the Fish River Lake Formation. Evidence for the ages of the two formations will be briefly outlined. The geology of northern Maine consists of numerous discontinuous intermontane basins which make correlation between formations, hence dating, very difficult.

The Trout Valley Formation was first described in a brief paper by Dorf and Rankin in 1962. The top of the formation is eroded and it unconformably overlies the volcanic rocks of the Traveler Rhyolite which, in turn, conformably overlies the Matagamon Sandstone. The marine fauna of the Matagamon Sandstone is of Becraft-Oriskany (= Siegenian of Europe) age (Rankin, 1965). This means that the Trout Valley Formation must not be older than Siegenian (Fig. 4). In a previous and more detailed treatment of the formation, Rankin (1961) correlated the Trout Valley Formation with marine beds of the Tomhegan Formation about 40–50 miles to the southwest. The age of the marine beds of the Tom-

² U.S.G.S. topographic map, 15 min series, 1955.

³ U.S.G.S. topographic map, 15 min series, 1928.

⁴ U.S.G.S. topographic map, 15 min series, 1928.

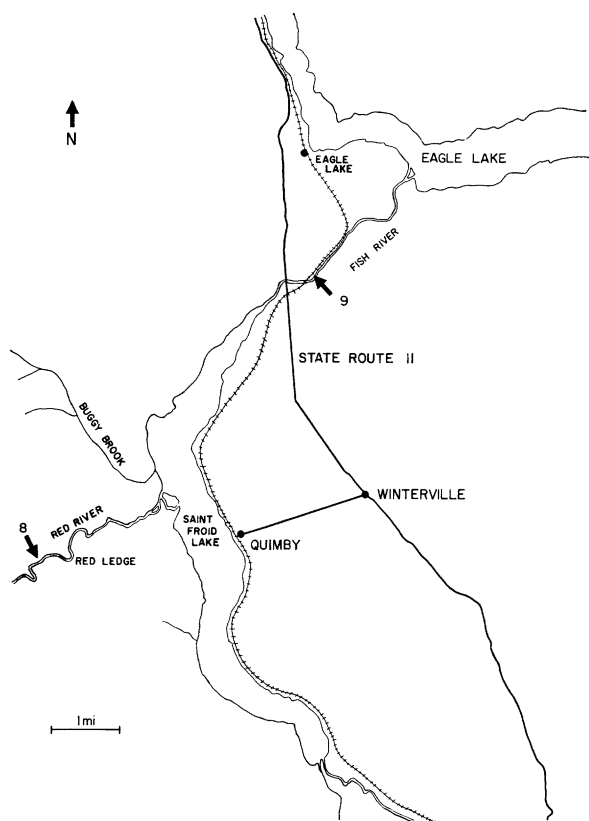


Fig. 3. Map of the Eagle Lake area, showing fossil plant localities.

hegan Formation has been given as Schoharie (= Emsian of Europe; Fig. 4). The basis of this correlation rests on the lithological similarities of the two regions. A more detailed review of Rankin's correlation has been presented in a previous paper (Kasper and Andrews, 1972).

Additional information is provided by the dating of the volcanic rocks. Bottino, Schnetzler, and Fullagar (1966) have proposed an absolute date for the Traveler Rhyolite as being 360 ± 10 million years old. However, the maximum range of this figure (370–350; Fig. 4) places the age of the Rhyolite, hence the Trout Valley Formation (if the time lapse between volcanism and deposition of the sediments was minimal), from earliest Middle Devonian to latest Upper Devonian (using the geologic time scale of Harland,

	STANDARD SECTION	AMERICAN SECTION
MIDDLE	359 GIVETIAN ---	HAMILTON
DEVONIAN	EIFELIAN 370	ONONDAGA
LOWER DEVONIAN	EMSIAN 374	DISCONFORMITY
		SCHOHARIE (ZONE B)
		ESOPUS
	SIEGENIAN 390	ORISKANY
		BECRAFT
	GEDINNIAN 395	NEW SCOTLAND
		MANLIUS-COEYMANS

Fig. 4. Chart modified from Pavlides et al., 1964; dates are in millions of years from the present (Harland et al., 1964).

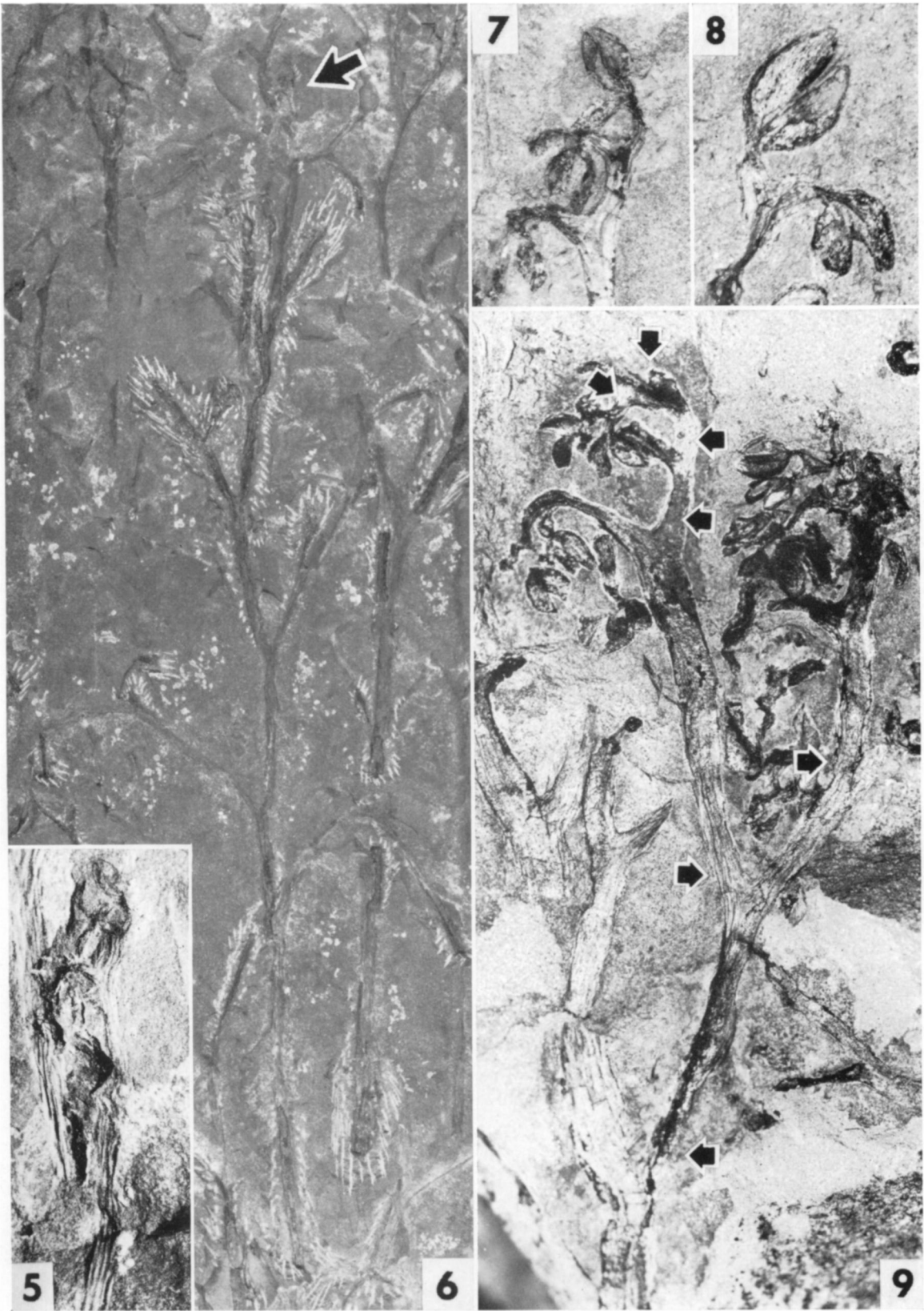
Smith, and Wilcock, 1964). This does little to pinpoint the precise age of the formation.

Finally, palynological studies (Andrews, Chaloner, and Segroves, 1972) from Locality #1 indicate that "The spores show closest agreement with assemblages of Emsian/Eifelian age from Europe, and from the upper part of the Battery Point Formation at Gaspé."

In short then, the Trout Valley Formation overlies marine sedimentary rocks of Siegenian age; it has been correlated lithologically with marine beds of Emsian age and spores indicate an Emsian/Eifelian age. In light of the above, the Trout Valley flora should be regarded as of latest Lower Devonian or possibly earliest Middle Devonian age (= Emsian or possibly Eifelian of Europe).

The two localities of the Eagle Lake area are both within the recently described Fish River Lake Formation, which consists of volcanic and sedimentary rocks (Boone, 1970). The sediments are composed of both marine and continental clastics. The marine fauna provides the evidence for dating the formation. Boone (1970) regards the Fish River Lake Formation "... chiefly as late Silurian, but with the upper siltstones and volcanics extending across the systematic boundary to the New Scotland time-stratigraphic horizon." New Scotland (= late Gedinnian of Europe) is early Lower Devonian (Fig. 4).

Fig. 5–9. *Psilophyton dapsile*. 5. Detail of sporangium-bearing axis, showing attachment to holotype (Fig. 6, arrow). $\times 4.2$. 6. Holotype, showing main axis branching dichotomously with some overtopping. Arrow indicates the location of attached sporangia. White striations are the needle marks resulting from excavation U.S.N.M. 192297 A. $\times 1.2$. 7. Sporangia enlarged (Fig. 6, arrow). $\times 7.3$. 8. Detail of loose sporangia showing the pairing. U.S.N.M. 192298 A. $\times 8.9$. 9. Specimen showing recurved branchlets with numerous paired sporangia. Arrows indicate at least seven successive levels of dichotomy. U.S.N.M. 192299. $\times 4.7$. Specimens in Fig. 7–9 photographed under xylol.



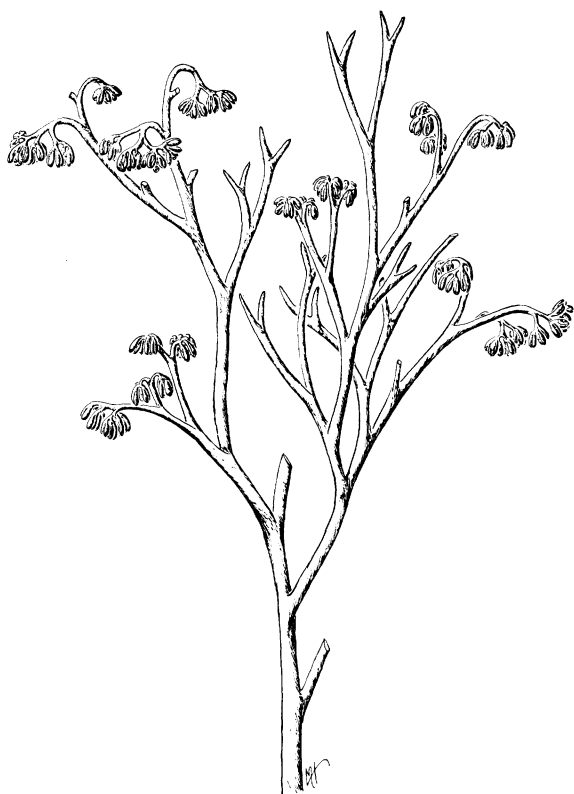


Fig. 10. Distal portion of *Psilophyton dapsile* about 1.2 $\times$; plants may have reached 30 cm in height.

MATERIALS AND METHODS—All the plants from the various localities are preserved as compression fossils. Unfortunately, the remaining carbon is amorphous and attempts at bulk maceration of the specimens causes total disintegration of the plant along with the rock matrix. As a result no cellular detail or spores have been preserved.

The main technique employed in treating this material has been that of "degaging," i.e., the excavation of the plant axes with needle and hammer under the dissecting microscope as they ramify through the rock matrix. In those cases where rather extensive uncovering was necessary, a Dremel Electric Engraver fitted with a steel phonograph needle was used. After preparation the specimens were usually photographed under xylol to mask the needle marks resulting from excavation. Those specimens photographed under xylol are so indicated in the captions.

FOSSIL PLANTS FROM THE TROUT VALLEY AREA:
Psilophyton dapsile sp. nov.—A narrow horizon a few inches thick at Locality #1 has yielded numerous specimens of a small profusely fertile plant. The plant consists of naked dichotomous axes with the ultimate branchlets bearing clusters of sporangia. The sporangia are extremely small and abundant.

The most informative specimen (Fig. 6, holotype) is approximately 17 cm long and 2.0 mm in diam at its widest. Although incomplete, it is interpreted as the main stem of the plant. The axes bear minute discontinuous striae and are without enations of any type. The striae are believed to be an artifact of compression rather than cortical fibers in this case. Several dichotomies occur in the main axis (Fig. 6), with some overtopping evident. The overall height of the plant is unknown because its basal portion is missing. In view of the small size of the axes and if the interpretation of the holotype as main stem is correct, it seems unlikely that the plant could have attained a height of more than 25 or 30 cm.

The distal portion of the holotype (Fig. 6, arrow) is enlarged in Fig. 5 and shows an ultimate branchlet with a diameter of less than 1 mm bearing several sporangia. Although the carbon is missing, the remaining impression (Fig. 5) shows that this fertile branchlet is in organic connection with the main axis (Fig. 6). The sporangia (Fig. 7) are paired, elliptical in outline, and measure 1.7 mm long and 0.5 mm wide.

Another specimen, 3.5 cm long, illustrates how the fertile branches dichotomize quite profusely and bear numerous pairs of sporangia on the recurved ultimate branchlets (Fig. 9). The actual specimen shows seven levels of branching which are indicated in the photograph by arrows. The true nature of the left limb produced by the lowermost division is not known; it may be stem or part of the branch. Each limb of the next higher division, however, produces sporangia. Therefore, it may be assumed that there are at least seven dichotomies in this branch system: those indicated by the six uppermost arrows and an ultimate division producing paired sporangia. If all seven dichotomies produce fertile branchlets and if none of the sporangia abort, then the specimen could theoretically bear 128 sporangia or 64 pairs. This is a conservative estimate as the specimen is incomplete: some of the divisions may not have been uncovered, others may have been destroyed by excavation, and the lowermost dichotomy (Fig. 9) may also be a division within the lateral system. Most likely there were variations in the number of dichotomies in lateral branches, with the number of sporangia varying accordingly.

The paired arrangement of the sporangia is consistent (Fig. 7–9). However, one of the two may be hidden in the matrix or broken off by the initial cleavage of the rock. The sporangia are elliptical and measure 1.7–2.1 mm long and 0.5–0.9 mm wide (Fig. 7–9). They are smaller than the sporangia of any previously known species of *Psilophyton* and the exact number of sporangia on any branch system, although unknown and probably variable, appears greater in this plant than in other species.

Like most of the fossils in the Trout Valley Formation this plant is found, for the most part, as a pure stand. At one spot the specimens are so thickly matted as to make it impossible to distinguish individual plants on the rock surface. The specimens shown in Fig. 11 and 12 seem to be representative of the sterile portions. The dichotomies for the most part are equal, with a slight tendency toward overtopping. Tapering of the axis through the length of the longer specimen (Fig. 12, 6 cm) is unnoticeable. The irregularity in axis width, from 0.5–1.0 mm, is due to distortion brought about during preservation.

Figure 10 is a restoration of the aerial portion of the sporophyte as we believe it appeared during the Devonian. It is based on numerous specimens such as those shown in Fig. 6, 9, 11, and 12.

Psilophyton Dawson emend. Hueber and Banks, 1967; *Psilophyton dapsile* Kasper et al., sp. nov.

Diagnosis—Plants erect, perhaps 25–30 cm tall; axes branched dichotomously, naked, without emergences or punctiform scars, up to 2.0 mm wide; compressed sporangia elliptical, approximately 1.7–2.1 mm long and 0.5–0.9 mm wide, borne terminally in pairs on closely dichotomizing ultimate branchlets, very abundant, appearing in masses or clusters.

Holotype—Specimen in Fig. 5–7 (U.S.N.M. 192297 A).

Paratypes—Specimens in Fig. 8 (U.S.N.M. 192298 A), Fig. 9 (U.S.N.M. 192299), Fig. 11 (U.S.N.M. 192300), Fig. 12 (U.S.N.M. 192301).

Type locality—Locality #1 of this article.

Horizon—Trout Valley Formation; Schoharie (= Emsian of Europe), Lower Devonian.

Derivation of species name—From the Latin “dapsilis” meaning “abundant” with reference to the great number of sporangia.

Psilophyton microspinosum sp. nov.—The specimens on which this species is based were collected from Locality #6. The plants occur through a

vertical section of about 12 inches of a fine-grained, dark gray shale. The rust-colored mineralized compressions provide a strong contrast to the rock matrix. No other plants were found directly associated with them but immediately underneath this zone there is a rather dense mass of axes that can be assigned to the genus *Taenio-crada* and some broad axes about 2.0 cm in diam bearing short stout spines.

On most rock specimens, the main axes of *Psilophyton microspinosum* are aligned in nearly parallel rows, suggesting that they were growing in a dense stand and were buried in place (U.S.N.M. 192302, not figured). In spite of its relative simplicity the plant displays several distinctive features that set it apart from any previously described species.

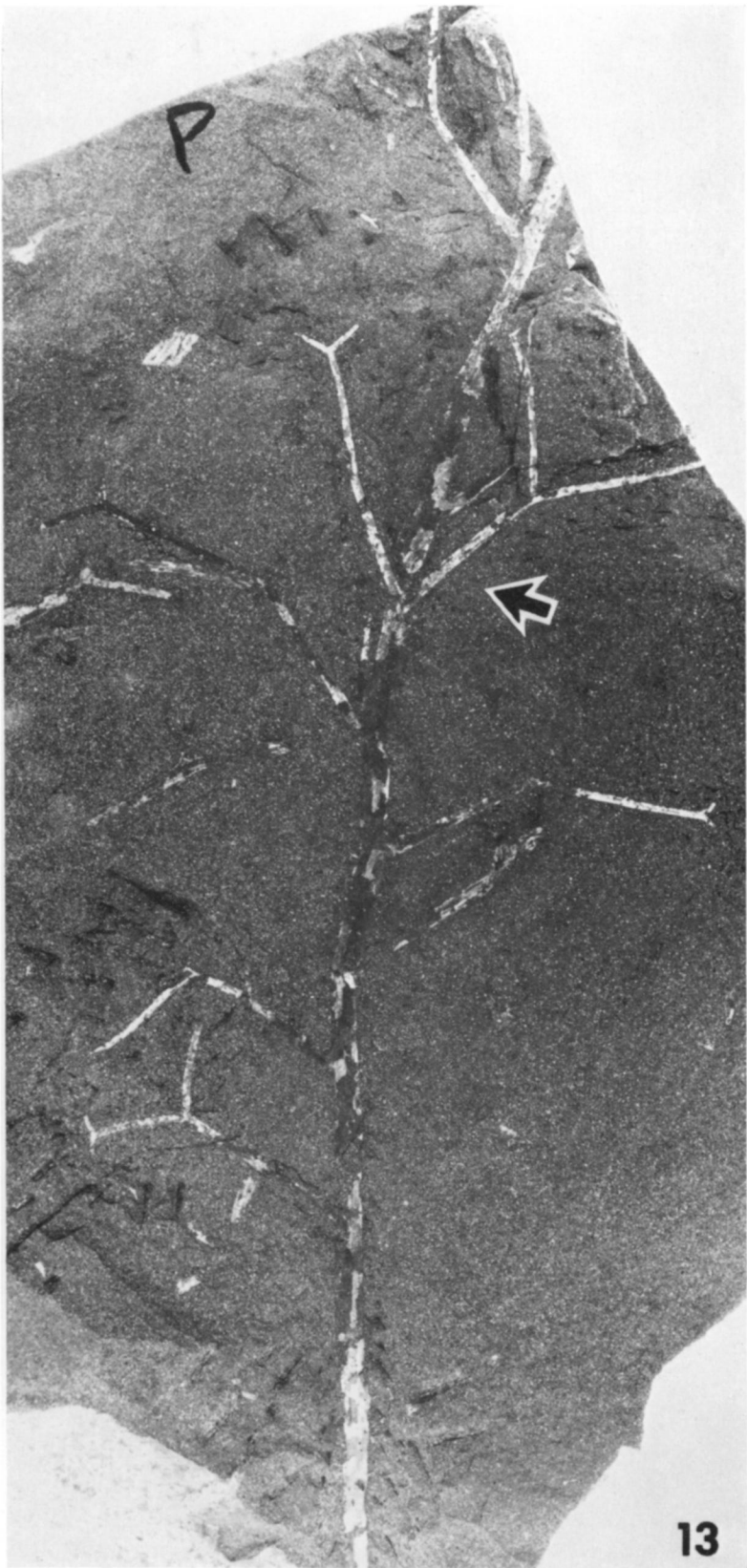
The main axes of most specimens measure 4 mm in diam at the widest point. The longest axes that we have (Fig. 13, 14) are about 20 cm long and show very little tapering through this distance. They are broken at both ends so that the basal and terminal parts are not known. The plants may have attained a height of about 6 decimeters.

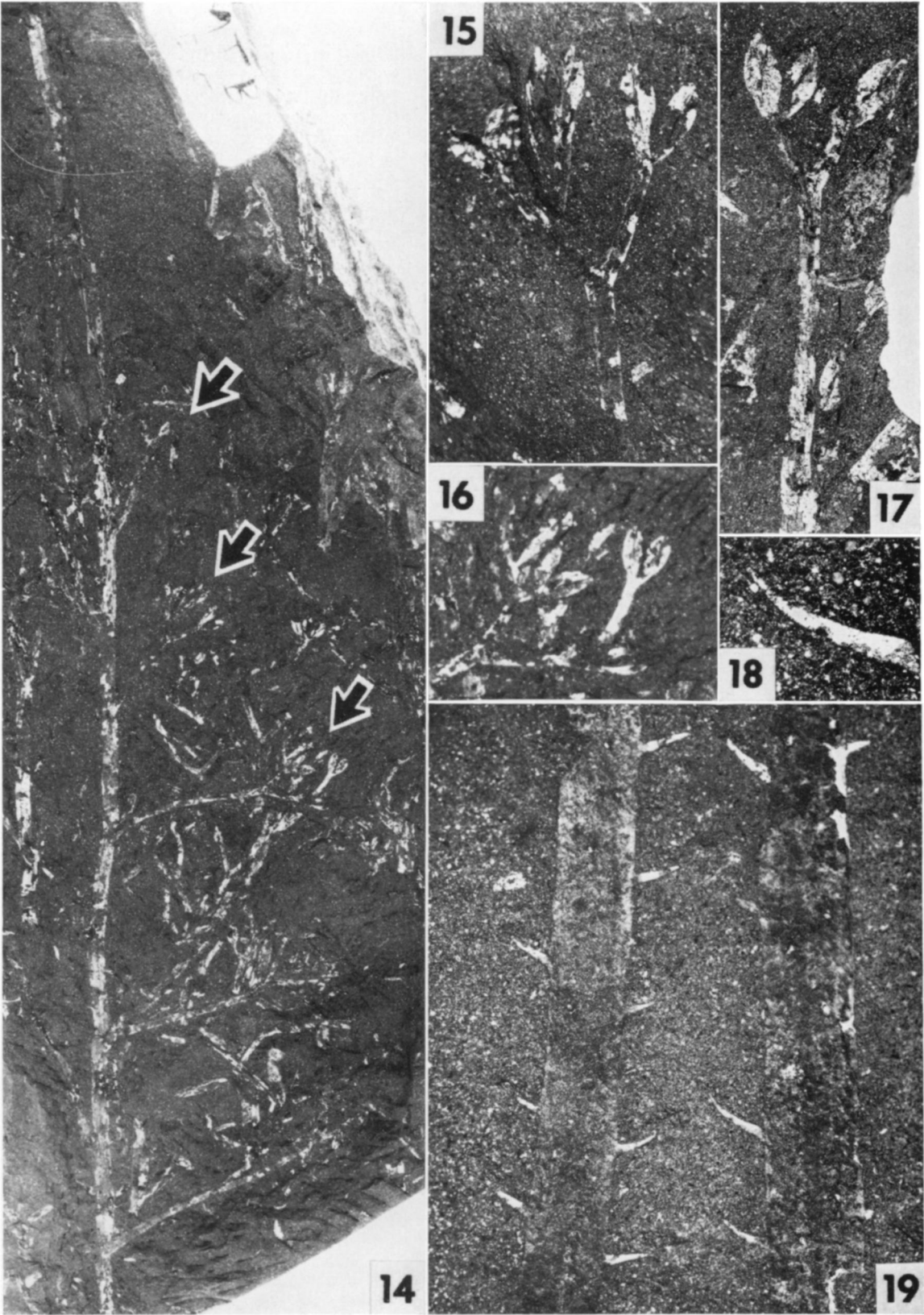
All axes bear spine-like emergences that are quite distinctive (Fig. 19). On main stems, the emergences are about 2 mm long and 0.4 mm broad at the proximal end and taper to a delicate needle-like point (Fig. 18). They are never abundant; the most densely covered axes we have found are shown in Fig. 19. The spines are even less abundant than this on most axes but a careful search reveals their presence. The emergences were arranged all around the stem and in no recognizable pattern. Since they do not leave a conspicuous scar, they are rarely observed in face view on the compressions. Pointing slightly upwards, the spines form an angle of 70°–80° with the axis. By comparison, for example, with *Sawdonia ornata* they are sparse, shorter, and much more delicate. The spines decrease in number and size on some of the sterile side branches until they are no longer present distally. On other sterile and all fertile side branches the enations are absent (Fig. 20).

The specimen in Fig. 13 shows the sterile branches in an alternate arrangement. The most

Fig. 11–13.—Fig. 11, 12. *Psilophyton dapsile*. Fig. 13. *Psilophyton microspinosum*. 11. Detail of sterile axis, showing dichotomous branching and tips of branchlets. U.S.N.M. 192300. $\times 2.4$. 12. Sterile axis, showing dichotomous branching with a tendency toward overtopping. U.S.N.M. 192301. $\times 2.5$. 13. Specimen of *Psilophyton microspinosum*, showing sterile branches; arrow indicates most complete lateral with three orders of branching. U.S.N.M. 192320. $\times 1.0$. Specimen in Fig. 13 photographed under xylol.

Fig. 14–19. *Psilophyton microspinosum*. 14. Holotype, showing pseudomonopodial habit; arrows indicate side branches bearing sporangia. U.S.N.M. 192303. $\times 0.8$. 15. Detail of branch with sporangia from Fig. 14 (middle arrow); branchlets are not recurved and the sporangia are erect and paired. $\times 2.9$. 16. Sporangia from branch indicated by lowest arrow in Fig. 14. $\times 1.9$. 17. Sporangia showing their paired and erect arrangement; reverse side of holotype. $\times 2.9$. 18. Detail of spine-like enation from right axis in Fig. 19 (second from bottom on left side). $\times 12.6$. 19. Two axes with emergences. U.S.N.M. 192304. $\times 4.4$. All specimens photographed under xylol.





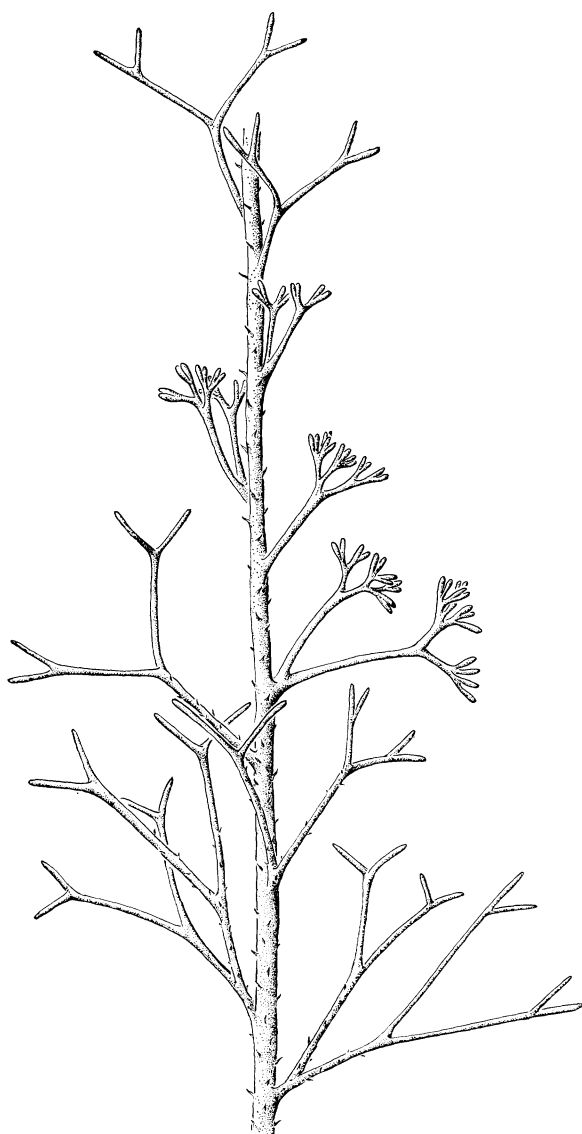


Fig. 20. Reconstruction of a portion of *Psilophyton microspinosum* about natural size; plants may have reached 60 cm high.

complete branch (arrow) overlies the main axis and dichotomizes at three levels. It is about 4.5 cm long and varies from 2 mm wide at its base to 1 mm wide distally. The branch dichotomizes about 1 or 2 mm after departing from the stem. The two limbs produced by this division are 2.2

cm long and form an angle of 65° . The second division gives rise to limbs 1.6 cm long and an angle of 80° . The third and last dichotomy produces limbs 5 mm long and an angle of 105° . Although sterile, this specimen is assigned to *Psilophyton microspinosum* because of the presence of the distinctive enations.

The holotype (Fig. 14) is 19.5 cm long, 3.5 cm wide, and shows the manner in which the sporangia are borne (arrows) especially well. Almost all of this specimen was exposed by degaging. The fertile branches bear the sporangia in a distinctively erect manner which is different from the recurved fashion considered typical for *Psilophyton*. One might tend to dismiss the erect or recurved position of sporangia as an artifact of preservation and of little taxonomic significance. However, in all the specimens that we have studied this characteristic is constant. There are now three plants in the Order Trimerophytales described with erect sporangia: *Trimerophyton robustius* (Hopping, 1956), *Dawsonites roskiliensis* (Chaloner, 1972), and *Psilophyton microspinosum*. This characteristic may eventually prove to be of some significance, but it does not seem important enough at the moment to warrant a generic distinction.

Three fertile branches are present on the holotype (Fig. 14, arrows). The lowermost branch is 4.5 cm long and varies from 2 mm wide basally to 1 mm wide distally. At least three dichotomies are evident on the specimen. There may have been one or two more divisions undetected and most likely the number of dichotomies varied from branch to branch. The sporangia of this axis are enlarged in Fig. 16. The middle branch (Fig. 14) is enlarged in Fig. 15, is 3.0 cm long and 1 mm wide. The uppermost branch (Fig. 14) measures 2.0 cm long. An isolated fertile axis from the reverse side of the specimen is illustrated in Fig. 17; it is 2.7 cm long. The sporangia (Fig. 15–17) are paired, elliptical, 3.5–4.0 mm long and 1.0 mm wide.

The restoration (Fig. 20) is based essentially on two specimens: one fertile (Fig. 14) and one sterile (Fig. 13). Both specimens bear identical spinelike enations and this is the basis of their association.

Psilophyton Dawson emend. Hueber and Banks, 1967; *Psilophyton microspinosum* Kasper et al., sp. nov.

Fig. 21–26. *Psilophyton forbesii*. 21. Ultimate branchlet with three pairs of sporangia. U.S.N.M. 192305 A. $\times 5.0$. 22. Two pairs of sporangia; upper pair twined about each other. U.S.N.M. 192305 A. $\times 5.5$. 23. Three pairs of sporangia. U.S.N.M. 192305 A. $\times 5.2$. 24. Fertile specimen of *P. forbesii*; this specimen and its counterpart (see Fig. 27) demonstrate organic connection between sporangia and axis. U.S.N.M. 192305 B. $\times 1.7$. 25. Detail of sporangia in Fig. 24; arrow indicates a pair of sporangia twisted about each other. $\times 5.0$. 26. Sporangia of plant from new locality assigned to *P. forbesii*. U.S.N.M. 192307. $\times 5.8$. Fig. 21, 23–26 photographed under xylol.

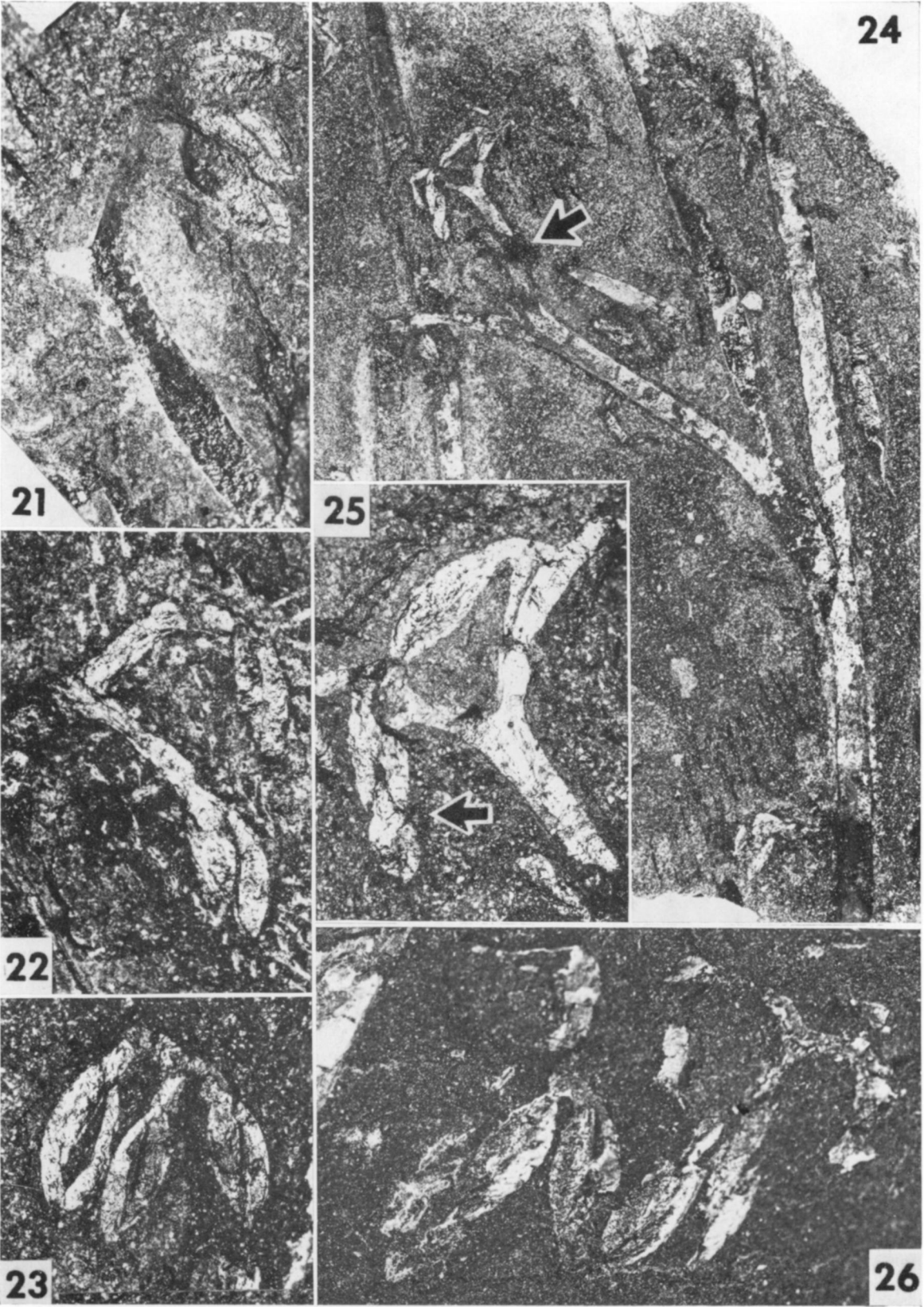




Fig. 27. Composite diagram of fertile axis of *Psilophyton forbesii* based on specimen shown in Fig. 24. Stippling indicates sporangia present on the counterpart (Fig. 21–23). Cluster of sporangia (arrow) is redrawn below to show which sporangia belong to the specimen and its counterpart.

Diagnosis—Plants erect, perhaps 60 cm tall with pseudomonopodial habit; main axes 4 mm wide, bearing sparsely distributed emergences; emergences 0.4 mm broad at base and 2 mm long,

tapered to a delicate needle-like point and re-curved slightly upward; sterile branches alternate, dichotomizing usually three times, angle of forking about 90°; fertile branches alternate, dichotomous with terminal, erect, elliptical paired sporangia 3.5–4.0 mm long and 1 mm wide.

Holotype—Specimen illustrated in Fig. 14–16 (U.S.N.M. 192303).

Paratypes—Specimens in Fig. 13 (U.S.N.M. 192320), Fig. 17 (U.S.N.M. 192303, reverse side), Fig. 18, 19 (U.S.N.M. 192304), unfigured (U.S.N.M. 192302).

Type locality—Locality #6 in this article.

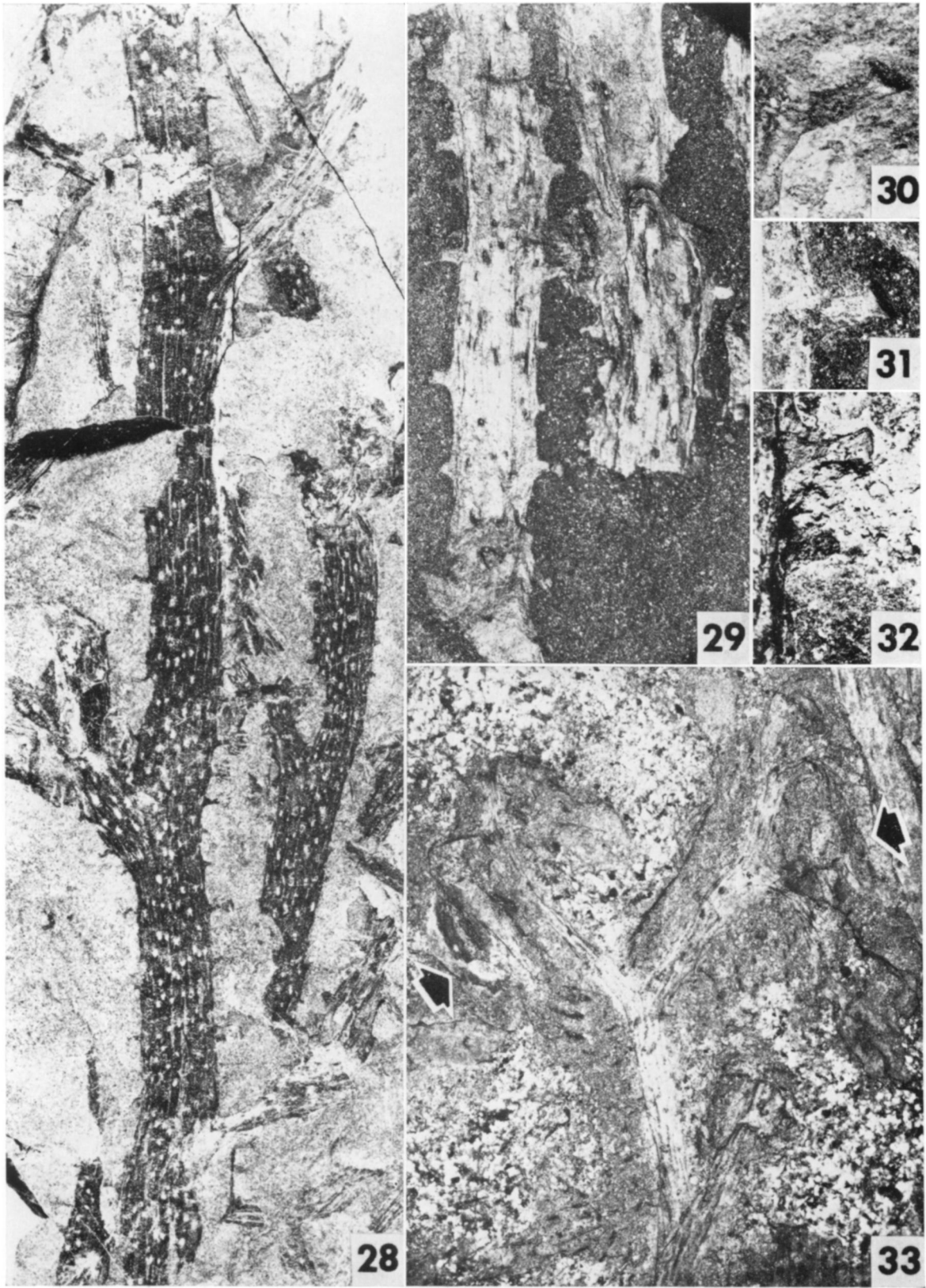
Horizon—Trout Valley Formation; Schoharie (=Emsian of Europe), Lower Devonian.

Derivation of species name—From the Latin “spinosus” meaning “thorny” and the prefix “micro-” meaning “small” with reference to the small thorn-like enations.

Psilophyton forbesii Andrews et al., 1968—This is the first plant that we encountered in our study of the Trout Valley flora. The original specimens were collected by Forbes and Bradford Hall (Univ. of Maine, Orono) from Locality #3 in 1964. Although abundant material of rather lengthy stems was found, the description of the reproductive organs was based on only one small specimen (Andrews, Kasper, and Mencher, 1968). We now have a more complete fertile specimen from the type locality that confirms our initial report. The original diagnosis is as follows: Plants of monopodial habit with a central axis up to 9 mm in diam. Side branches fork equally or unequally. Most of the larger axes are strongly ridged longitudinally. Apparently naked, there being no evidence of emergences. Sporangia ellipsoidal, 3.5–4 mm long and 1.3–1.8 mm broad, borne in terminal pairs.

The fertile specimen is illustrated in Fig. 24 and a diagram is presented in Fig. 27. Tracings from photographs of the specimen and its counterpart were superimposed on each other to obtain the composite diagram. The stippled areas represent sporangia which are present on the counterpart. Naturally, the stippled areas appear in reverse of what they are on the actual specimen (Fig. 21–23). The uppermost cluster of sporangia (Fig.

Fig. 28–33. *Psilophyton princeps*. **28.** Main axis, showing pseudomonopodial branching and bearing enations along its margin and on its surface, i.e., white spots. U.S.N.M. 192308. $\times 1.4$. **29.** Axes with the distinctive peg-like emergences. U.S.N.M. 192309. $\times 2.9$. **30.** Detail of individual enation. U.S.N.M. 192310. $\times 7.2$. **31.** Enation. U.S.N.M. 192311. $\times 8.0$. **32.** Enations. U.S.N.M. 192312. $\times 8.6$. **33.** Ultimate branchlet with sporangia indicated by arrows; peg-like emergences are clearly visible on the specimens but not in the photograph. U.S.N.M. 192313. $\times 3.6$. All specimens photographed under xylol.



27, arrow) is redrawn as an inset below to show the sporangia present on the specimen and counterpart (Fig. 23, 25).

The major axis (Fig. 24) is 9.3 cm long and 3.0 mm wide with no distal tapering. Three major dichotomies are evident in the photograph. Excavation uncovered a fourth division in a plane at right angles to the rock surface (Fig. 24, arrow). The upper limb produced by this dichotomy bears sporangia (Fig. 25) and the lower limb remains unexcavated because of the overlying sporangia. Three more dichotomies are present distally on the specimen—only two are evident in the photograph (Fig. 25). If the major axis (Fig. 24) is the distal portion of the main stem then there were at least six divisions in a side branch. If the major axis is part of the branch system itself, then there were at least seven divisions in a lateral.

Figures 21–23 show details of the sporangia on the counterpart. The recurved nature of the ultimate branchlets is much more evident than in the original description. The average length of the sporangia, based on this more complete material, is slightly longer, between 4.0 and 5.0 mm. Another feature which is more obvious now is the pairing of the sporangia. Not only are the sporangia paired but in some instances they actually twine about each other (Fig. 25, arrow). In retrospect this feature is noticeable in the original fertile specimen (Andrews et al., 1968, Fig. 5—left lowermost sporangia). We have also observed this characteristic in macerations of the type species, *P. princeps*, from the south shore of the Restigouche River, near Dalhousie, New Brunswick, Canada (see: Hueber, 1967, Fig. 16, 17).

In the summer of 1970 we made a collection of fossil material from a second locality (Locality #5) in the Trout Valley Formation. This collection consists exclusively of a plant that we believe should be assigned to *Psilophyton forbesii*. The largest axes of this plant are 3 mm in width (U.S.N.M. 192306 A, not figured). This is much smaller than the largest axes of *P. forbesii* from the type locality. However, the sporangia of the plant from the new site (Fig. 26) are essentially identical in size and shape to those of *P. forbesii*. The specimens from the new locality could be terminal portions of large plants or they could represent a population of smaller individuals. Since no stems larger than 3 mm in diam were found, the latter possibility seems to be most likely.

Specimens—Fig. 21, 22, 23 (U.S.N.M. 192305 A), Fig. 24, 25 (U.S.N.M. 192305 B), Fig. 26 (U.S.N.M. 192307) and unfigured (U.S.N.M. 192306 A).

Psilophyton princeps Dawson emend. Hueber, 1967—The type species is known only from the shores of Gaspé Bay, Quebec and the north shore

of New Brunswick. This is the first report of *Psilophyton princeps* (sensu Hueber, 1967) outside of Canada. Our specimens of the plant were obtained from Locality #3 about 15 feet north of the point where *P. forbesii* was found. Both of these species occur as pure stands, that is, no other plant was found associated with them. We obtained about 25 or 30 specimens of *P. princeps* from a weathered ledge; further collecting was rendered impossible by an extensive and very hard overlying conglomerate.

The collection gives us a good understanding of the vegetative aspects of the plant. Axes (Fig. 28) show a strong pseudomonopodial habit and range from a maximum of 10 mm in diam down to about 1 mm for the ultimate branch terminations. The distinctive peg-like emergences (Fig. 29–32) are well preserved and occur on all branch orders, even penultimate and ultimate branchlets. Hueber (1967) describes these pegs as being “. . . blunt, 2 to 2.5 mm long, rigid and randomly arranged, tipped by cup-like disc. . . .” We have examined their form and arrangement as carefully as possible in the Maine specimens. Figure 28 gives an accurate idea of the distribution of the pegs along a main axis. Many of the pegs can be seen protruding from the margins of the stem and the white spots on the stem surface indicate points where the pegs were attached. On our specimens these emergences vary from 1.5–2.5 mm long and, for the most part, stand out at right angles to the axis. In the drawing (Fig. 34) the part of the stem between the hatch lines has been copied as accurately as possible from a photograph of the above specimen (Fig. 28). It is evident here, as Hueber (1967) has pointed out, that the pegs are randomly arranged. In some regions there is a faint suggestion of a spiral pattern. However, none of our specimens show a greater degree of organization than is indicated in Fig. 28.

Fertile material was scarce, but several specimens showing recurved branchlets with paired fusiform terminal sporangia were present. Each of these axes bears the peg-like emergences characteristic of *Psilophyton princeps*. Because of the coarse-grained matrix these specimens photographed poorly. However, one such specimen is illustrated in Fig. 33; the sporangia are indicated by arrows.

Specimens—Fig. 28 (U.S.N.M. 192308), Fig. 29 (U.S.N.M. 192309), Fig. 30 (U.S.N.M. 192310), Fig. 31 (U.S.N.M. 192311), Fig. 32 (U.S.N.M. 192312), Fig. 33 (U.S.N.M. 192313).

FOSSIL PLANTS FROM THE EAGLE LAKE AREA: Eagle Lake lies approximately 70 miles due north of the Trout Valley localities (Fig. 1). Two sites in the Eagle Lake area (Fig. 3) have proven productive: the Nadeau Thoroughfare (Locality #9)

and the Red River (Locality #8). At each of these exposures fertile *Psilophyton*-like plants have been found. Because of their fragmentary nature, however, they are presently assigned to the form genus, *Dawsonites*, and in particular to the species, *D. arcuatus*.

Plant from Nadeau Thoroughfare—At a point about 50 yards north of the railroad bridge over the Fish River, various fragmentary remains have been found but the preservation in general is not very encouraging. We did, however, uncover reasonably good specimens of a plant from the east side of the railroad cut.

The material from this locality occurs in dense mats of smooth, longitudinally striated axes that range from 1.5–2.0 mm in diam. One of the largest rock specimens collected is about 50 cm long and the surface shows dozens of axes that are aligned more or less parallel to each other. Due to minor fracturing of the rock it is not possible to follow an individual axis the entire length but it seems safe to estimate that the plants were a minimum of 30 cm tall in life. Specimens in which the material is somewhat less matted show the pseudomonopodial branching pattern of individual plants to better advantage (Fig. 40). The side branches for the most part seem to dichotomize only once or twice. A sterile, recurved tip of a branchlet is shown in Fig. 37. Other branches terminate in clusters of sporangia (Fig. 35, 36). The sporangia are elliptical, paired and measure 3.0–4.0 mm long and about 1.0 mm wide.

Specimens—Fig. 35 (U.S.N.M. 192314 A), Fig. 36 (U.S.N.M. 192315), Fig. 37 (U.S.N.M. 192316 A), Fig. 40 (U.S.N.M. 192317).

Plant from Red River—Fossil plants have been found at several localities along the banks of Red River for a distance of about $\frac{3}{4}$ mile above and below Red Ledge. The specimens described here came from Locality #8 (Fig. 3). This may be reached by a road that departs west from Route 11 immediately after crossing the fish River. The road circles south and approaches Red River about one-third mile east (downstream) of Red Ledge.

The outcrop contains vertical beds that extend 4–5 feet in length from the river's edge up the bank. The innermost unweathered rock cannot be split. The rock matrix itself is a hard, fine-grained sandstone that fractures into small pieces that rarely exceed 15 cm long. Only a small quantity of material was obtained.

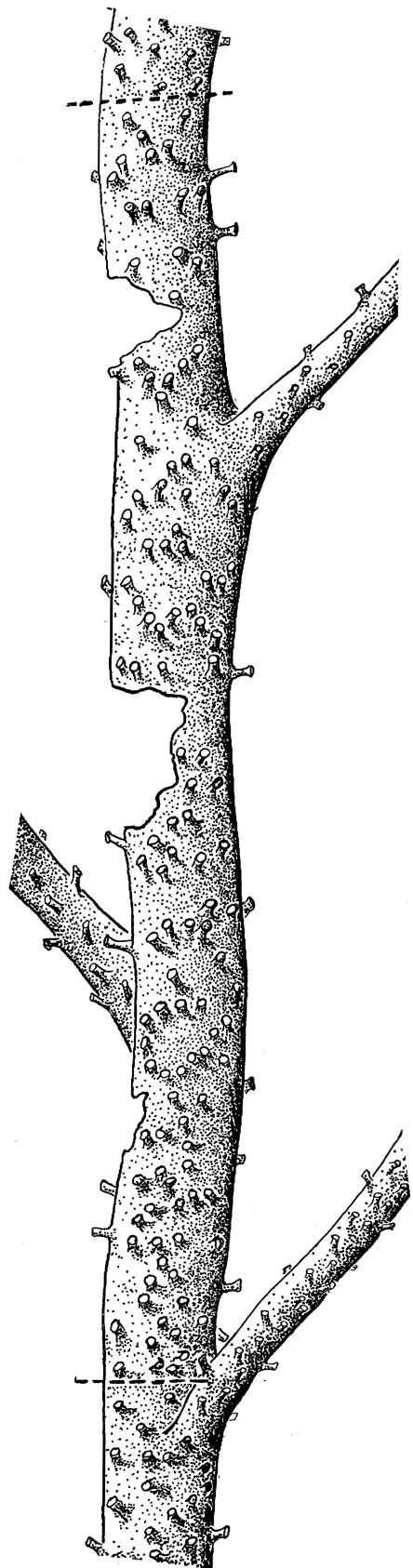
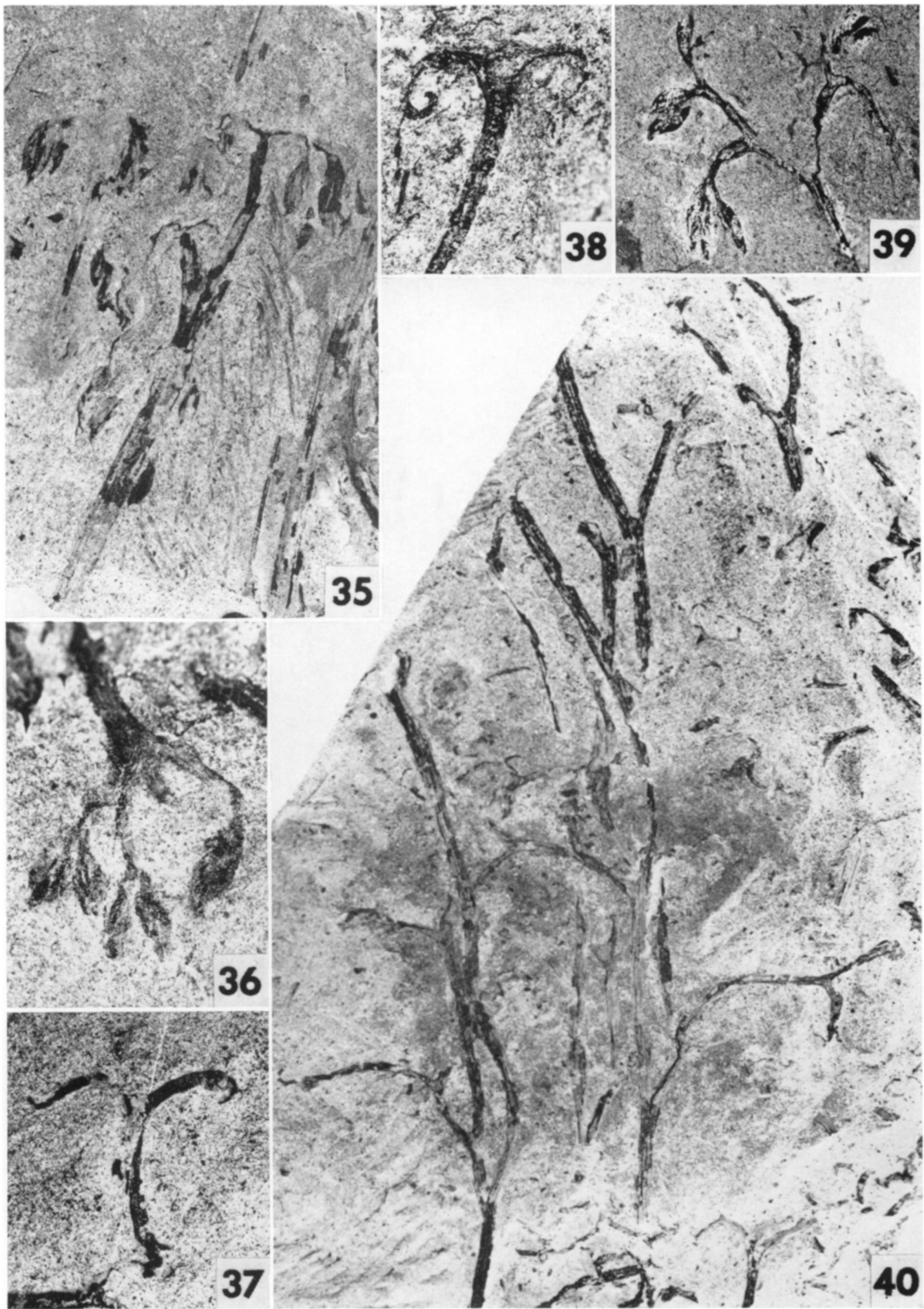


Fig. 34. Drawing of main axis of *Psilophyton princeps* based on specimen in Fig. 28, showing the form and distribution of the peg-like enations.



PLANT	BRANCHING PATTERN	MAXIMUM WIDTH COMPRESSED AXES	LENGTH OF SPORANGIA	ORNAMENTATION OF AXIS SURFACE	
1. <u>P. princeps</u>	pseudomonopodial & dichotomous	10.0 mm	7.5-8.0 mm	peg-like emer- gences 1.5-2.5 mm long & ribbing	
2. <u>P. kräuselii</u>	dichotomous	5.0 mm	2.0-2.2 mm	hair-like emer- gences, ? mm	
3. <u>P. forbesii</u>	pseudomonopodial & dichotomous	9.0 mm	4.0-5.0 mm	ribbing	
4. <u>P. dapsile</u>	dichotomous (pseudomonopodial)	2.0 mm	1.7-2.1 mm	none	
5. <u>P. microspinosum</u>	pseudomonopodial & dichotomous	4.0 mm	3.5-4.0 mm	needle-like emer- gences 1.5-2.0 mm	
6. {	Plant from Nadeau Thoroughfare	pseudomonopodial & dichotomous	2.0 mm	3.0-4.0 mm	ribbing
	Plant from Red River	pseudomonopodial & dichotomous	2.5 mm	3.0 mm	ribbing
	<u>Dawsonites arcuatus</u> (in part)	pseudomonopodial & dichotomous	3.0 mm	3.0-5.0 mm	ribbing

Fig. 41. Chart listing the major characteristics of the five fertile species of *Psilophyton*, the Red River and Nadeau Thoroughfare plant, and *Dawsonites arcuatus*.

The plants consist of pseudomonopodial axes with a maximum diameter of 2.5 mm (U.S.N.M. 192321, not figured). The side branches dichotomize several times and the sterile ultimate branchlets are strongly recurved (Fig. 38). Most of the presumed main axes are longitudinally ribbed but in some specimens the ribbing ceases in the side branches. Some of the axes consist of a relatively thick carbonized compression. Where this has been removed the carbon remains present within furrows. It thus seems that the longitudinal ridges and furrows represent some kind of differentiation of the outer cortex—probably discrete bundles of longitudinally oriented fibers.

A few fertile specimens have been uncovered. One of the better ones is illustrated in Fig. 39. The sporangia are fusiform, paired, about 3.0 mm long and 1.0 mm wide. The plant from the Nadeau Thoroughfare site is probably identical to the one from Red River. Both are tentatively assigned to *Dawsonites arcuatus*.

Specimens—Fig. 38 (U.S.N.M. 192318), Fig. 39 (U.S.N.M. 192319 A), not figured (U.S.N.M. 192321).

COMPARISONS—Since Dawson’s original account of the genus *Psilophyton* over a century ago, numerous species have been assigned to it. Unfortunately, most of these are very fragmentary and lack reproductive structures. The most recent and comprehensive treatment of the many species of *Psilophyton* is that of Høeg (1967). Høeg summarizes the data on seven of them which he considers reliably assigned and lists fifteen others as *species excludendae*. Høeg’s treatment was presented before the emendation of the genus (Hueber and Banks, 1967) and prior to the typification and description of the type species (Hueber, 1967) and its “varietal form” (Ananiev and Stepanov, 1968; Hueber, 1971). However, Høeg’s list of *species excludendae* clears the air as regards the great number of indefinable taxa based on very fragmentary information.

Our approach, based on the above information unavailable to Høeg seven years ago, is even more critical. A major criterion for the classification of early vascular land plants has been the orientation and characteristics of their reproductive structures (Banks, 1968). Accordingly, we now consider only those plants for which sporangia are known as being reliably assigned to the genus

←
Fig. 35-40.—Fig. 35-37, 40. Plant from Nadeau Thoroughfare. Fig. 38, 39. Plant from Red River. 35. Ultimate branchlet with pendent paired sporangia. U.S.N.M. 192314 A. × 2.0. 36. Sporangia. U.S.N.M. 192315. × 4.2. 37. Sterile termination. U.S.N.M. 192316 A. × 3.0. 38. Circinate tip of sterile branchlet. U.S.N.M. 192318. × 4.0. 39. Sporangia. U.S.N.M. 192319 A. × 5.3. 40. Longitudinally ribbed pseudomonopodially branched axes. U.S.N.M. 192317. × 1.4. All specimens photographed under xylol.

Psilophyton. Before *Psilophyton* was defined and its type species described in detail, any spiny axis was assigned to the genus; in a sense *Psilophyton* was a form genus. This can no longer be true.

In the following comparisons of the species of *Psilophyton* only those with sporangia known are considered. These are:

Psilophyton princeps Dawson emend. Hueber, 1967

Psilophyton kräuselii Obrhel, 1959

Psilophyton forbesii Andrews et al., 1968

Psilophyton dapsile Kasper et al., sp. nov.

Psilophyton microspinosum Kasper et al., sp. nov.

Høeg (1967) suggests that *P. pubescens* (Kräusel and Weyland, 1938), because of its general morphology and secondary xylem, may belong to the genus *Aneurophyton*. It is probably not correctly assigned to *Psilophyton*. Figure 41 lists the known fertile species and outlines their characteristics; the plants from Nadeau Thoroughfare and Red River, and *Dawsonites arcuatus* are also included.

Psilophyton princeps was an erect plant perhaps 1 meter high. Its main axis, which was close to 10 mm in diam, branched pseudomonopodially, i.e., one limb of the apical dichotomy dominated becoming the main axis and the other became the side branch. The lateral branches were dichotomous three-dimensional structures and bore clusters of sporangia on the recurved ultimate branchlets (Hueber, 1967). The sporangia were paired and fusiform in shape. The stem and side branches—even up to the ultimate branchlets—were covered with peg-like emergences (1.5–2.5 mm long) which stood out at right angles from the axes. In addition, compressed stems show a longitudinal ribbing which is probably due to cortical bundles of supporting tissue. The distinctive features of the species are its large axes with longitudinal ribbing, its peg-like emergences and its long (7.5–8.0 mm) fusiform sporangia.

Psilophyton kräuselii is based on fragmentary material and so the overall size of the plant is uncertain. Only one minute (1 cm²) fertile specimen is known. However, because of the presence of distinctive hair-like emergences this specimen can be reasonably associated with somewhat larger sterile axes. The largest axes are 5 mm wide and bear dichotomous three-dimensional side branches (Obrhel, 1959, 1961). The recurved ultimate branchlets bear small (2.0–2.2 mm long) fusiform sporangia. The distinctive features of this species are its small sporangia and fine hair-like emergences.

Psilophyton forbesii is similar to *P. princeps* in its overall size, in its pseudomonopodial and dichotomous branching, and in its longitudinal ribbing of compressed specimens. It differs from

the latter in that it lacks the distinctive peg-like emergences and its sporangia are much smaller (4.0–5.0 mm long). *P. forbesii* differs from the other fertile species of *Psilophyton* by its large axes, by its lack of emergences and by its intermediate-size sporangia.

Psilophyton dapsile (Fig. 10) was probably a small erect plant, about 30 cm tall. Branching was predominantly dichotomous but sometimes overtopping is evident showing a tendency toward the pseudomonopodial habit. Compressed stems are smooth, without enations of any sort. The minute striae, as mentioned previously, may be an artifact of preservation. *Psilophyton dapsile* most resembles *P. kräuselii* in overall habit but differs from the latter in that it lacks the hair-like enations. It differs from the other fertile species by its minute sporangia (1.7–2.1 mm long), lack of enations, and dichotomous habit.

Psilophyton microspinosum was an erect plant intermediate in size between the taller species (*P. princeps*, *P. forbesii*) and the smaller species (*P. dapsile*, and perhaps *P. kräuselii*). It stood perhaps 60 cm high, with a distinct main stem and dichotomous side branches (pseudomonopodial). The features which distinguish it from the other fertile species of *Psilophyton* are its delicate spine-like enations, its nonribbed axes and its erect sporangia.

The specimens from Nadeau Thoroughfare and Red River are believed to be the same species and are assigned to *Dawsonites arcuatus*. Incomplete stem fragments from the former site suggest a plant that was erect, about 40–50 cm tall with a distinct main axis and dichotomously branched laterals (pseudomonopodial branching). The plant is without enations and compressed axes show a distinct longitudinal ribbing. The sporangia are elliptical, paired, 3–4 mm long. These specimens differ from the recognized species of *Psilophyton* either by their axis size, ribbing, lack of enations, or by sporangia length (Fig. 41).

As mentioned above, Halle established *Dawsonites arcuatus* for the unconnected fertile fragments included by Dawson in *Psilophyton princeps*. In addition, Halle included under *D. arcuatus* specimens which he collected from Røragen, Norway. It is these Røragen specimens (Halle, 1916) which are similar to ours from Nadeau Thoroughfare and Red River both in width and ribbing of axes and in sporangium size and shape. The specimens from Røragen and from the two above-mentioned Maine localities may represent a sixth fertile species of *Psilophyton* if and when more complete material is found.

In regard to the above, Hueber (1964) has presented a preliminary reconstruction of the fertile branches of *Dawsonites arcuatus* but no specimens were figure. A detailed study of this plant is underway by Banks, Hueber and Leclercq (Hueber and Banks, 1967).

DISCUSSION—The long and complex history of the genus *Psilophyton* is readily apparent from the literature review. In solving this puzzle, which has taken over a century and involved numerous workers, many decisions had to be made along the way. It must be kept in mind by present-day investigators that these decisions were made based on the information available at that time. Some of the decisions have proved unsatisfactory. The case in point being Halle's selection of the sterile spiny axes (the variety *ornatum*) as the typical form and making the fertile axes another genus and species (*Dawsonites arcuatus*). However, the sterile spiny axes were eventually shown to bear lateral sporangia (= *Sawdonia ornata*) which made them far removed from Dawson's concept of *Psilophyton princeps* as shown by his restoration. Ananiev and Stepanov (1968) prefer to follow the precedent established by Halle, that the spiny axes with lateral sporangia (= *Sawdonia ornata*) continue to be considered *Psilophyton princeps* and that the terminal sporangiate axes of Dawson be called *Dawsonites arcuatus*. We disagree and have accepted Hueber and Banks' (1967) emendation of the genus *Psilophyton* and their selection of a type specimen for the species, *P. princeps*. They have conformed to the guidelines of the International Code of Botanical Nomenclature, had access to Dawson's original collections, and have gathered and studied abundant new material from the original localities. Their choice most closely follows the concept of the original author.

The next logical step would be to clarify the status of the numerous species of *Psilophyton*. Høeg (1967) has attempted this in fine fashion and without benefit of the above definition and typification. His treatment eliminated many species based on unidentifiable fragments.

The present paper is an attempt at further "weeding out." The criterion used by us has been that only plants for which the sporangia are known are retained within the genus. The others, we suggest, be relegated to one of the form genera: *Dawsonites* for fragmentary sporangia (Banks, 1968), *Thursophyton* for sterile spiny axes, and *Hostinella* for smooth pseudomonopodially or dichotomously branched axes. This reduces the number of reliably assigned *Psilophyton* species to five (Fig. 41). A possible sixth species has been described in part under *Dawsonites arcuatus* by Halle (1916), has been partially reconstructed by Hueber (1964), and has been compared with similar material from the Nadeau Thoroughfare and Red River sites in Maine (Fig. 35–40).

At this point we would like to consider the systematic position of *Psilophyton* and present our views on the classification of early vascular plants. Any classification system must be thought of as temporary and reflecting, somewhat, the bias of the investigator. However, the recent contribu-

tion by Banks (1968) was a major breakthrough in the classification of early land plants as it clearly pointed out the existence of three major groups or levels of evolution. These are the "rhyniophytes" with terminal sporangia, the "zosterophylls" with lateral sporangia, and the "trimerophytes" with their differentiation into main stem and side branches bearing clusters of sporangia. These are recognized in a slightly different arrangement below:

Division Rhyniophyta

Class Rhyniopsida

Order Rhyniales

Family Rhyniaceae

Family Cooksoniaceae

Order Trimerophytales

Family Trimerophytaceae

Genus *Trimerophyton* Hopping, 1956

Genus *Psilophyton* Dawson emend. Hueber and Banks, 1967

Genus *Pertica* Kasper and Andrews, 1972

Class Zosterophyllopsida

Order Zosterophyllales

Family Zosterophyllaceae

Family Gosslingiaceae

We prefer giving the major groups of vascular plants Divisional status as do Bold (1973), Scagel et al. (1965), and Cronquist, Takhtajan, and Zimmermann (1966), thus eliminating the all-inclusive Division Tracheophyta. In addition we use the name Rhyniophyta instead of Psilophyta for the reasons mentioned by Cronquist et al. (1966). Our definition of the Division Rhyniophyta would include only extinct (late Silurian and Devonian) leafless vascular plants—*Psilotum* and its allies are treated as in Bierhorst (1971). Two Classes of the Division are recognized to indicate the early separation of two distinct evolutionary lines: the terminal and lateral sporangiate forms (Banks, 1968). Their compatibility within the same Division—Bold (1973) makes them each a new Division—is based on the speculation that the Rhyniopsida (specifically the Rhyniales) gave rise to the Zosterophyllopsida by the processes of overtopping and subsequent reduction of the resultant lateral sporangium-bearing telomes. The fact that the Rhyniales (i.e., *Cooksonia*; Obrhel, 1962) are geologically the oldest vascular plants, that the two distinct lines are evident chronologically soon thereafter, and that the "zosterophylls" have their lateral sporangia on short "stalks"—possibly a remnant of the reduced telome—is the basis of this speculation. The "zosterophylls" are not placed with the lycopods because they are leafless and have not reached that level of advancement. Hueber (1972) suggests only one family, the Zosterophyllaceae, thus eliminating the Gosslingiaceae of Banks (1968).

The Class Rhyniopsida is treated as consisting

of two orders, the Rhyniales and Trimerophytales—again reflecting a second major and chronologically later separation. The Rhyniales probably gave rise to the Trimerophytales by severe overtopping, producing a main axis with side branches, and by a proliferation of dichotomies distally on the laterals, resulting in clusters or masses of sporangia. Bierhorst (1971) treats these two groups on the familial level. Greater significance of the phylogenetic divergence is implied here by placing the respective units at the ordinal level. Bold (1973) and Banks (1968) treat them at the Divisional and Subdivisional levels, respectively.

Psilophyton is placed in the above system in the Order Trimerophytales which is comparable to Banks' Subdivision Trimerophytina. *Psilophyton* had not yet been defined when Banks' system was published so he omitted it. *Dawsonites* is not included in the Trimerophytales because in its expanded use as a form genus it also contains lateral sporangiate axes of the "zosterophyll" type. Finally, the recently described genus *Pertica* is added to the Trimerophytales (Kasper and Andrews, 1972).

With the addition of two fertile species of *Psilophyton* to the three existing ones (Fig. 41), we now offer the following tentative suggestions on the evolutionary trends within the genus. The primitive species, as we envision it, would be relatively small plants (shorter and thinner axes) of strictly dichotomous habit (or just a slight tendency toward overtopping), with no enations or very simple ones (delicate hair-like), and with small sporangia. The advanced species would consist of much taller plants with more robust axes having a distinct main stem with dichotomous side branches. Along with the increased height is the addition of fiber bundles within the cortex (the ribbing in compressed axes). Enations, if present, would be more complex (multicellular, e.g., peg-like) and the sporangia would be much larger. With any speculation on evolutionary trends of elements which are contemporaneous, as these species are, it is difficult to prove which characteristics are primitive (evolved earlier in time) and which are advanced (evolved later in time). Such a series can be read in the opposite direction, i.e., toward reduction. We prefer the simpler explanation—toward increase in size and complexity. Surely at this stage of geologic time the general evolutionary trend was toward proliferation and diversification rather than condensation and reduction.

If one accepts the above reasoning, then the more primitive species would be *Psilophyton dapsile* and *P. kräuselii* and the more advanced species, *P. forbesii* and *P. princeps*. The others would be intermediate.

The region of northern Maine and in particular the Trout Valley Formation in Baxter State Park

has yielded abundant materials of early Devonian plant fossils. As a result it has added significantly to our knowledge and understanding of the early stages in the evolution of vascular plants. During the eight years of our collecting in the area, the following genera have been recovered: *Psilophyton*, *Kaulangiophyton*, *Taeniocrada*, *Sciadophyton*, *Pertica*, *Drepanophycus*, cf. *Sawdonia*, and *Prototaxites*. There are areas in northern Maine and in the Trout Valley which still remain unexplored and our work is continuing. It seems clear now that the Trout Valley Formation contains, to date, the most diverse early Devonian vascular land flora in the United States.

LITERATURE CITED

- ANANIEV, A. R., AND S. A. STEPANOV. 1968. Findings of the sporebearing organ on *Psilophyton princeps* Dawson emend. Halle in the Lower Devonian of southern Minusinski Trough (western Siberia). In New materials on the stratigraphy and paleontology of the Lower and Middle Paleozoic of western Siberia. Tomsk. Universitet. Trudy 202: 30-46.
- ANDREWS, H. N., A. E. KASPER, AND E. MENCHER. 1968. *Psilophyton forbesii*, a new Devonian plant from northern Maine. Bull. Torrey Bot. Club 95: 1-11.
- , W. G. CHALONER, AND K. L. SEGROVES. 1972. Early Devonian spores from Maine, U.S.A. In 24th International Geological Congress—Montreal Abstracts 1972: 213-214.
- BANKS, H. P. 1968. The early history of land plants, p. 73-107. In Evolution and environment, E. T. Drake [ed.]. Yale University Press, New Haven.
- BIERHORST, D. W. 1971. Morphology of vascular plants. Macmillan, New York.
- BOLD, H. C. 1973. Morphology of plants. Harper and Row, New York.
- BOONE, G. M. 1970. The Fish River Lake Formation and its environments of deposition. Maine Geol. Survey Bull. 23: 27-41.
- BOTTINO, M. L., C. C. SCHNETZLER, AND P. D. FULLAGAR. 1966. Rb-Sr whole-rock age of the Traveler and Kineo Rhyolites, Maine, and its bearing on the duration of the Early Devonian. Geol. Soc. America Spec. Paper 87: 15.
- CHALONER, W. G. 1972. Devonian plants from Fair Isle, Scotland. Rev. Palaeobot. Palynol. 14: 49-61.
- CROFT, W. N., AND W. H. LANG. 1942. The Lower Devonian flora of the Senni beds of Monmouthshire and Breconshire. Phil. Trans. Roy. Soc. London 231B: 131-163.
- CRONQUIST, A., A. TAKHTAJAN, AND W. ZIMMERMANN. 1966. On the higher taxa of Embryobionta. Taxon 15: 129-134.
- DAWSON, J. W. 1859. On fossil plants from the Devonian rocks of Canada. Quart. J. Geol. Soc. London 15: 477-488.
- . 1870. On the primitive vegetation of the earth. Proc. Roy. Inst. 6: 165-172.
- . 1871. The fossil plants of the Devonian and Upper Silurian Formations of Canada. Geol. Surv. Canada 1871: 1-92.

- DORF, E., AND D. W. RANKIN. 1962. Early Devonian plants from the Traveler Mountain area, Maine. *J. Paleontol.* 36: 999–1004.
- EDWARDS, W. N. 1924. On the cuticular structure of the Devonian plant *Psilophyton*. *J. Linn. Soc. Bot.* London 46: 377–385.
- HALLE, T. G. 1916. Lower Devonian plants from Røragen in Norway. *K. Sven. Vetenskapsakad. Handl.* 57: 1–46.
- HARLAND, W. B., A. G. SMITH, AND B. WILCOCK (ed.). 1964. The Phanerozoic Time-Scale. *Quart. J. Geol. Soc. London* 120(supplement): 1–458.
- HØEG, O. A. 1967. *Psilophyta*, p. 191–352. In *Traité de Paléobotanique*, II, E. Boureau [ed.]. Masson, Paris.
- HOPPING, C. S. 1956. On a specimen of *Psilophyton robustius* Dawson from the Lower Devonian of Canada. *Proc. Roy. Soc. Edinb.* 66B Pt. 1, No. 1: 10–28.
- HUEBER, F. M. 1964. The psilophytes and their relationship to the origin of ferns. *Mem. Torrey Bot. Club* 21: 5–9.
- . 1967. *Psilophyton*: the genus and the concept. In *International symposium on the Devonian System*, D. H. Oswald [ed.]. Alberta Soc. Petrol. Geol. Calgary 2: 815–822.
- . 1971. *Sawdonia ornata*: a new name for *Psilophyton princeps* var. *ornatum*. *Taxon* 20: 641–642.
- . 1972. *Rebuchia ovata*, its vegetative morphology and classification with the *Zosterophyllophytina*. *Rev. Palaeobot. Palynol.* 14: 113–127.
- , AND H. P. BANKS. 1967. *Psilophyton princeps*: the search for organic connection. *Taxon* 16: 81–85.
- KASPER, A. E., AND H. N. ANDREWS. 1972. *Pertica*, a new genus of Devonian plants from northern Maine. *Amer. J. Bot.* 59: 897–911.
- KRÄUSEL, R., AND H. WEYLAND. 1938. Neue Pflanzenfunde im Mitteldevon von Elberfeld. *Palaeontographica* 83B: 172–195.
- LANG, W. H. 1931. On the spines, sporangia and spores of *Psilophyton princeps* Dawson, shown in specimens from the Gaspé. *Phil. Trans. Roy. Soc. London* 219B: 421–442.
- . 1932. Contributions to the study of the Old Red Sandstone flora of Scotland, VIII. On *Arthrostroma*, *Psilophyton*, and some associated plant-remains from the Strathmore beds of the Caledonian Lower Old Red Sandstone. *Trans. Roy. Soc. Edinb.* 57: 491–521.
- OBRHEL, J. 1959. Neue Pflanzenfunde in den Srbsko-Schichten (Mitteldevon). *Věstník Ústředního Ústavu Geol.* 34: 384–388.
- . 1961. Die Flora der Srbsko-Schichten (Givet) des mittelböhmisches Devons. *Sborník Ústředního Ústavu Geol.* 26: 7–46.
- . 1962. Die Flora der Pridolí-Schichten (Budňany-Stufe) des mittelböhmisches Silurs. *Geologie* 11: 83–97.
- PAVLIDES, L., E. MENCHER, R. S. NAYLOR, AND A. J. BOUTCOT. 1964. Outline of the stratigraphic and tectonic features of northeastern Maine. *U.S. Geol. Survey Prof. Paper* 501-C: C28–C38.
- RANKIN, D. W. 1961. Bedrock geology of the Katahdin Traveler area, Maine. Ph.D. Thesis, Harvard Univ., Cambridge, Mass.
- . 1965. The Matagamon Sandstone—a new Devonian formation in north-central Maine. *U.S. Geol. Survey Bull.* 1194-F: F1–F9.
- SCAGEL, R. F. ET AL. 1965. An Evolutionary survey of the plant kingdom. Wadsworth Publ., California.
- SMITH, G. O., AND D. WHITE. 1905. The geology of the Perry Basin in southeastern Maine. *U.S. Geol. Survey Prof. Paper* No. 35: 1–107.
- SOLMS-LAUBACH, H. 1891. Fossil botany being an introduction to palaeophytology from the standpoint of the botanist. H. E. Garnsey, trans. Clarendon Press, Oxford.