Plant Paleontology in the State of Maine — A Review

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ABSTRACT

The history of paleobotany in Maine is presented along with reviews of major Devonian floras and their impact on our understanding of early vascular land-plant evolution. The Late Silurian and Devonian represent a time span in which plants emerged onto the land surface, diversified, and evolved major structural features. Data for these events are preserved in fossil floras present in strata ranging from Lower to Upper Devonian in north-central and easternmost coastal Maine. Some critical floras reviewed are those of the Lower Devonian Trout Valley Formation, Middle Devonian Mapleton Sandstone, and Upper Devonian Perry Formation. An updated assessment of geological age, species composition, and evolutionary significance is given for each plant-bearing formation in Maine.

INTRODUCTION

Continental strata in the state of Maine are relatively sparse, but their significance in the study of early land plant evolution is considerable. Five formations distributed throughout the state and representing a time interval from Late Silurian to Late Devonian have yielded numerous plant megafossils (Fig. 1). These fossils have provided an important database for our understanding of the emergence and subsequent dominance of vegetation on the land surface. The quantity and quality of paleobotanical information obtained from the Maine paleofloras are somewhat out of proportion to the limited number, size, and exposure of these continental formations. Furthermore, the prognosis is excellent. Known fossil localities are expected to be productive for years to come and the discovery of new localities is anticipated with continued field work. Maine’s contribution to paleobotany, in particular the problem of early vascular land plant evolution, has been and will be outstanding.

Late Silurian and Early Devonian events are critical to our understanding of the transition of plants from aquatic to terrestrial environments. The scenario as often painted is that aquatic plants, presumably algal in nature and estuarine in habitat, became adapted to dry land, perhaps as a result of their competition for space (i.e., for light as an energy source and/or for mineral nutrients necessary for growth). The change may have been gradual, involving adaptation first to periodic dessication.
caused by tidal fluctuations and then to permanent dessication in supratidal zones. A host of morphological, anatomical, and physiological adaptations would have to be orchestrated for success. For example, these plants would also have to evolve a means of coping with the greater amounts of UV light present outside of water and a way of acquiring water internally. Knoll et al. (1986) present current theories about such a transition and review the Silurian fossil evidence relating to it.

Early Devonian plant fossils from Maine and other regions continue the story of this transition. The rapid evolution of plants newly adapted to the land surface is shown by the extensive diversification of vascular plant taxa or plant structures during the Early Devonian (Gensel and Andrews, 1984; Edwards and Fanning, 1985; Knoll et al., 1986; Gensel, 1986). The Maine plant fossils, plus others from nearly contemporaneous strata in New Brunswick and the Gaspé Peninsula, provide a detailed view of such evolutionary change for the North American portion of the Old Red Sandstone Continent.

Middle Devonian events continue the theme of morphological diversification in vascular land plants with the appearance of several new plant lineages and innovations in plant structure. Differentiation of the plant stem into various specialized organs (the incipient megaphyllous leaf and the root), the development of secondary stem-thickening tissues, and the arboretous habit are prominent features present during this time. Historically, Middle Devonian strata in Maine have yielded less information than Lower and Upper Devonian strata. Part of this is due to the limited surface exposure of Middle Devonian beds, but some of it may be the result of our emphasis on the highly productive Lower Devonian localities. The brief studies already published on Maine’s Middle Devonian flora indicate potential for further contributions. Recent finds of permineralized (petrified) remains will contribute further information about the structural evolution occurring within this epoch.

Late Devonian time marks the culmination of the rapid diversification of vascular land plants. Leafy arboretous species of great stature are now present. Of extreme importance are the innovations in reproductive biology. Several taxa display heterospory—production of two kinds of spores resulting in unisexual gametophyte plants. This is a major step toward the evolution of the seed. In rare instances seeds have been reported from the Late Devonian in other geographical regions. From a historical point of view, many genera and species of plants were first recognized and named from the Upper Devonian strata of Maine. Even though Upper Devonian localities in Maine are few and surface exposure is minimal, new collections from old sites and restudy of curated specimens will further clarify our understanding of the biology and systematics of these historical taxa.

**LINEAGES OF EARLY LAND PLANTS**

It seems appropriate, here, to briefly introduce some concepts concerning the structure and classification of early vascular land plants. The majority of these fossils represent fragmentary remains of stems, reproductive organs and, in some cases, roots and leaves of the sporophyte phase (spore-producing plant) of the life cycle. The smaller, more delicate gametophyte phase (egg and sperm-producing plant) of the life cycle was either not preserved or was so different in form from modern counterparts that gametophyte plants have not as yet been recognized as such.

Early and even some Middle Devonian plants are comparatively small and simple. For many years they were collectively referred to as "psilophytes." However, as the data accumulated, recent workers have recognized that several evolutionary lineages were included in this catchall group. This recognition culminated in the classification scheme proposed by Banks (1968) in which several new early land plant groups were distinguished. The present review examines many different types of plants so it is appropriate at this point to summarize the characteristics of the major lineages.

(1) The **RHYNIOPHYTES** are small plants (one to several decimeters tall) consisting of leafless, dichotomizing stems, some of which are terminated by a sporangium which has no
special means of dehiscence (splitting open). The vascular strand consists of a few tracheids making up a solid cylinder of xylem with first-formed elements in the middle (a centarch protosteles).

(2) The TRIMEROPHYTES are larger (a decimeter to one or more meters tall) and more complexly branched plants (with main axes and lateral branches) bearing large clusters of sporangia at the tips of some side branches. Their vascular strand is more massive, but still a centarch protosteles. Sporangia dehisc longitudinally. Trimerophytes are regarded as being descendants of the rhytiophytes and precursors to several later-appearing plant groups, such as progymnosperms, ferns, etc.

(3) The ZOSTEROPHYLLOPHYTES are plants several decimeters tall with both equal and unequal branching, an exarch protosteles (first-formed xylem occurs at margins of vascular strand), and large, laterally borne, globose or reniform sporangia. The latter open along their outer margin, often by means of specialized cells.

(4) The LYCOPODS are herbaceous or woody plants of predominantly rhizomatous habit, varying greatly in size (from a few decimeters to many meters) and in extent of branching. They possess microphyllous leaves and exarch protosteles. In most species the globose or reniform sporangia are borne on the upper surface or in the axils of the leaves.

(5) The PROGYMNOSPERMS are plants of shrub or tree size with much-divided branch systems, some of which terminate in laminar leaves. The stems have well-developed secondary vascular tissue as is found in modern gymnosperms. Their sporangia are borne on the tips of branches or on the surfaces of leaves. These plants show a more "modern" growth habit and structure and are more advanced in reproduction since some are heterosporous.

(6) The CLADOXYLS and IRIDOPTERIDS are two separate lineages of plants whose affinities are less well understood. They apparently are derived from the trimerophyte line and one or both may represent precursor(s) to the horsetails. Cladoxyls are distinguished anatomically by their much-dissected vascular strand and iridopterids by their deeply lobed vascular strand and distinctive lateral branch trace formation. External morphology of many taxa is still unknown, as most species are based on short lengths of permineralized stems. Where known, branching in some cladoxyls is dichotomous and digitate. Finely divided ultimate appendages are borne on some of the branches in dense spirals or whorls and some terminate in oval-elongate sporangia.

HISTORY OF PALEOBOTANY IN MAINE

Significant paleontological studies in Maine began in the 1860's with the work of the Canadian geologist, Sir John William Dawson (Table 1); these were followed much later by a contribution from David White in 1905, and then little was done until the mid 1960's. From that time on, numerous studies have appeared. In view of the pioneering work of Dawson and White we have included brief, general biographical sketches along with summaries of their paleontological contributions.

The first important reports describing plant fossils from the state are those of Dawson (1861, 1862, 1863; Fig. 2) who studied the flora of the Perry Formation in southeastern Maine. Many of these fossils were described as new species since so little was known about Devonian plants. The Perry plants are not well preserved, being quite fragmentary, but Dawson's reports were a significant beginning.

Dawson's studies also provided the first substantial paleontological evidence for the Devonian age of the Perry Formation, until then a controversial issue in Maine geology. Jackson (1837), the state geologist for both Massachusetts and Maine, at first regarded the Perry Formation as equivalent to the Carboniferous strata of New Brunswick and Nova Scotia. Later he suggested that it was the same age as the red beds in Connecticut and New Jersey and might possibly be Silurian (Jackson, 1851). Using plant fossils from the Perry Formation, Rogers (1859) correlated the formation with the "Kiltorcan" of Ireland which he considered to be Lower Carboniferous—all of which summed up to a rather confused situation! In 1861, C. H. Hitchcock became the State Geologist of Maine and asked Dawson to establish the age of the beds of the Perry Formation. Dawson's study, presented in Hitchcock's (1861) report on the geology of the Perry Basin, assigns a Devonian age to the formation which has held up to this day.

J. W. Dawson (1820-1899) was born in Pictou, Nova Scotia, and started making collections of fossil plants when he was twelve. He studied at Pictou College and then went to Edinburgh where he met such eminent men of the times as Forbes,
Balfour, and Jamieson. Upon returning to Canada in 1842, he met Charles Lyell who was on one of his American tours, and the two spent considerable time together. In days when travel conditions were quite different from today, Dawson explored the coastal areas of the Gaspé Peninsula, New Brunswick and Maine. Of particular interest are his studies of the land plants of the Early Devonian. However, the importance of these studies to understanding early evolution in plants was not appreciated until some decades later. Probably his best known work is his monumental *Acadian Geology* (Dawson, 1891). Dawson’s paleobotanical studies are in part summed up in *The Geological History of Plants* (Dawson, 1888). He was one of Canada’s great educators, serving as Superintendent of Education for Nova Scotia and as Principal of McGill University in its early years. Some interesting aspects of his life as a naturalist in those years are to be found in his autobiography, *Fifty Years of Work in Canada* (Dawson, 1901).

The next work of importance in paleobotany in Maine was a monograph by Smith and White (1905) on *The Geology of the Perry Basin in Southeastern Maine*. The report (the paleobotanical part of which was by David White) seems to have been spurred by persistent rumors and economic expectations that coal in commercial quantities might be available in the Perry Formation. The significance of the monograph lies in its meticulous treatment of the flora. The plants are carefully described and illustrated, and a thorough synonymy and discussion are given. White lists 29 taxa of plants, 16 of these being Dawson’s.

David White’s (1862-1935; Fig. 3) first important work in paleobotany and stratigraphy involved collecting and studying the plants from Gay Head on Martha’s Vineyard and his demonstration that they were of Cretaceous age. He is probably best known for his extensive work with late Paleozoic plants which included monographic treatments of the Coal Measure plants of Missouri and the Permian floras of Brazil and the Grand Canyon. He served as Chief Geologist of the U.S. Geological Survey, as Home Secretary of the National Academy of Sciences, and Chairman of the National Research Council’s Committee on Paleobotany. E. W. Berry (1935, p. 391) wrote of David White: “No geologist of his time had a wider influence on the scientific life of the nation, or took a more active part in that of its capital.”

The only major contribution to Maine paleobotany during the hiatus between Smith and White (1905) and the revival of the 1960’s is the work of two German paleobotanists, Kräusel and Weyland (1941). They present the first photographic illustrations of the Perry flora and, more significantly, their approach is thoroughly modern in aspect. Besides careful specimen description, they are concerned with the biology of whole organisms, i.e., their concept of species allows for some variation in morphology between organisms and, hence, between specimens. This philosophy is reflected in the fact that they reduce Smith and White’s 29 taxa to 9.
It is important to realize that the paleobotanical studies in Maine summarized thus far have all dealt with the Late Devonian flora from the Perry Formation. The paleobotanical revival in the 1960's centered in new areas (northern Maine) and at lower stratigraphic levels (Lower and Middle Devonian). The historical development of these studies will be incorporated into the various discussions of the floras themselves, starting with that of the Trout Valley Formation in Baxter State Park.

EARLY DEVONIAN FLORA IN MAINÉ

Plants of Early Devonian age have been found in northern Maine in two different formations: the Trout Valley Formation and the Fish River Lake Formation. These two floras will be treated sequentially below.

Flora of the Trout Valley Formation

Of the various localities in Maine where fossil plants have been found, Trout Brook and its tributaries in Baxter State Park have produced the most significant information. Therefore, it is especially appropriate to record in some detail the history of the work that has been undertaken there and the plants that have been discovered. The area, shown in Figure 4, includes the banks of Trout Brook from “The Crossing” upstream for about 6 kilometers and localities along Dry Brook and South Branch Ponds Brook.

The first published report of fossil plants found in this area is that of Erling Dorf and Douglas Rankin (1962) (Table 2). The plants that they described were actually discovered between 1955 and 1957 by Rankin during explorations sponsored by the Maine Geological Survey and Harvard University. Since the discovery of plants in this previously undescribed formation is so important to Maine paleobotany, we quote the following from their account (p. 999):

All the plant fossils occur in a heretofore unnamed formation in the Traveler Mountain and Telos Lake quadrangles, north-central Maine (Rankin, 1958 and 1961). This formation, here named the Trout Valley formation, is composed predominantly of clastic rocks and occupies the valley of Trout Brook between the west shoulder of Trout Brook Mountain and the north shoulder of Burnt Mountain. . . .

With our more recent contributions to the Trout Valley flora, it seems appropriate to record something of the history of the developments that followed the Dorf-Rankin introduction. In the early 1960's Ely Mencher, a professor at M.I.T., was engaged in stratigraphic studies in northern Maine. Mencher was aided by William Forbes of Washburn who had an extensive field knowledge of northern Maine geology. With the hope that the fossil plants they were finding would be helpful with age determinations, Mencher invited James M. Schopf of the U.S. Geological Survey to participate in the field work. Schopf was one of the leading authorities of his time on Paleozoic plants and he, in turn, asked Henry Andrews (University of Connecticut) to join the group in the summer of 1965.

The pathways to success in paleontology are certainly varied and often unpredictable. Much of the plant material that was being found was quite fragmentary and not too encouraging. It was no secret that the forested areas of north-central Maine were not generally regarded as a likely place to look for fossil plants. The “breakthrough” came when Schopf and Andrews were invited to examine some large specimens at Forbes' home. The specimens contained some spectacular fossil plants, described later as Psilophyton forbesii (Andrews et al., 1968). These had been collected by Forbes at the South Branch Ponds
A. E. Kasper and others

TABLE 2. FLORAL COMPOSITION OF SILURIAN/DEVONIAN PLANT-BEARING FORMATIONS IN MAINE

<table>
<thead>
<tr>
<th>Age</th>
<th>Formation</th>
<th>Taxon</th>
<th>Selected references</th>
</tr>
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<tbody>
<tr>
<td>UD</td>
<td>Perry Formation</td>
<td>Archaeopteris jacksonii</td>
<td>Posnick, 1982</td>
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<td></td>
<td></td>
<td>Barinophyton richardsonii</td>
<td>Posnick et al., 1983</td>
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<tr>
<td></td>
<td></td>
<td>Lepidophyton rhombicua</td>
<td>Posnick, 1982</td>
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<td></td>
<td></td>
<td>Phyllophyton brownianum</td>
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<td></td>
<td></td>
<td>cf. Rhacophyton incertum</td>
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<tr>
<td></td>
<td></td>
<td>Barinostrobus spicatus</td>
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<td></td>
<td></td>
<td>cf. Cyclostigma</td>
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<tr>
<td></td>
<td></td>
<td>cf. Tetraxylopterys</td>
<td></td>
</tr>
<tr>
<td>MD</td>
<td>Mapleton Sandstone</td>
<td>cf. Sawdonia ornata</td>
<td>Schopf, 1964</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Barrandeina(?) arostookokensis</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Calamophyton forbesii</td>
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<tr>
<td></td>
<td></td>
<td>Hostinella sp.</td>
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<td></td>
<td></td>
<td>Aphyllopetria sp.</td>
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<tr>
<td></td>
<td></td>
<td>cf. Stolbergia</td>
<td>present report</td>
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<td></td>
<td></td>
<td>cf. Cladaxylon</td>
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<td></td>
<td></td>
<td>cf. Calamophyton</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>cf. Schizopodium</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>cf. Rhacophyton</td>
<td></td>
</tr>
<tr>
<td>MD</td>
<td>Chapman Sandstone</td>
<td>Pachytynea sp.</td>
<td>Schopf, 1964</td>
</tr>
<tr>
<td>LD</td>
<td>Trout Valley Formation</td>
<td>Sawdonia ornata</td>
<td>Dorf and Rankin, 1962</td>
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<td></td>
<td></td>
<td>Psilophyton forbesii</td>
<td>Andrews et al., 1968</td>
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<tr>
<td></td>
<td></td>
<td>Kaulungophyton akmitha</td>
<td>Gensel et al., 1969</td>
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<td></td>
<td></td>
<td>Tenuicruda sp.</td>
<td>Andrews and Kasper, 1970</td>
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<td></td>
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<td>Prototames sp.</td>
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<td>Persica quadrifaria</td>
<td>Kasper and Andrews, 1972</td>
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<td>Psilophyton dapsil 1</td>
<td>Kasper et al., 1974</td>
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<tr>
<td></td>
<td></td>
<td>Psilophyton microspinosum</td>
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<td></td>
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<td>Psilophyton princeps</td>
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<tr>
<td></td>
<td></td>
<td>Drepnophyclus sp.</td>
<td>Andrews et al., 1977</td>
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<tr>
<td></td>
<td></td>
<td>Thrusophyton sp.</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>Leclerecia sp.</td>
<td>Kasper and Forbes, 1979</td>
</tr>
<tr>
<td>S/LD</td>
<td>Fish River Lake Formation</td>
<td>cf. Dawsonites arcuatus</td>
<td>Kasper et al., 1974</td>
</tr>
<tr>
<td></td>
<td></td>
<td>cf. Psilophyton dapsil 1</td>
<td>Kasper and Forbes, 1983</td>
</tr>
<tr>
<td>S</td>
<td>Frenchville Formation</td>
<td>Echostominella heathana</td>
<td>Schopf et al., 1966</td>
</tr>
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Brook locality shown on the map (Fig. 4, # 3). It was immediately evident that here was the kind of lead that paleontologists long for. Indeed, it initiated several summers of extensive field work, chiefly by Forbes, Andrews, Kasper, and Gensel; the latter two were graduate students with Andrews at the time.

Most of our exploration and collecting has been done in the rock exposures along the banks of Trout Brook, and we introduce this with the following background information. Dorf and Rankin (1962, p. 1001) state that:

The maximum exposed thickness of the Trout Valley formation is about 1500 feet, and the formation crops out over an area of about 1.5 by 8 miles.

The Trout Valley Formation unconformably overlies the Traveler Rhyolite which, in turn, rests conformably on the Matagamon Sandstone of Becraft-Oriskany (= Siegenian) age (Rankin, 1965). An absolute date for the Traveler Rhyolite has been determined by Bottino et al. (1966) as 360 ± 10 Ma. This allows a range of 350 to 370 Ma for the rhyolite, which places the oldest possible date for the Trout Valley Formation between earliest Middle Devonian and latest Late Devonian using the geologic time scale of Harland et al. (1964). This is not a very precise determination for the age of the formation. Based on the nature of the flora itself, it was our early opinion that the strata were of late Early Devonian age, but as more information has accrued, it is possible that the formation may be earliest Middle Devonian in age. Further discussion of this will be given following a description of the plants.

The Trout Valley Formation is somewhat enigmatic. In their initial account Dorf and Rankin (1962, p. 1001) note that: "The formation is remarkably undeformed. . . . " How do we account for the fact that this rather small patch of sedimentary rocks has escaped distortion, if not complete destruction, over the
Plants paleontology

hundreds of millions of years since the original deposition?

Whatever the reasons may be for the preservation of the Trout Valley Formation, it has proven to be a rich source of plant remains. Our information comes from only a very small part of the total area. About 200 meters upstream from The Crossing lies the most extensive outcrop yet found (Fig. 4, #1); it has yielded large quantities of fossil plants which will be described below. Other localities along the banks of Trout Brook consist of rather small lenses where, in some cases, fossils may be found one year and are gone the next because of erosion during the spring. At the westernmost (upstream) point, considerable fossiliferous rock has been found in the stream bed and has been traced to an outcrop along the south bank (Fig. 4, #7). Some of the fossil plants are sufficiently well-preserved to provide us with a clear understanding of their appearance in life. Others are known from more fragmentary remains, or else do not reveal the reproductive organs needed for precise identification and classification. It is tantalizing to speculate on what fossils lie hidden in the surrounding heavily wooded areas.

Below will follow brief descriptions of the better known plants of the formation, dealing with The Crossing locality in some detail. As shown in Figure 5, the beds here are slightly tilted; the entire exposure contains fossil plant material in varying amounts. One of the better preserved plants, confined to a narrow band several cm thick, is *Psilophyton dapsile* (Fig. 6). This small, simple plant is characteristic, generally, of the earliest vascular land plants and of more primitive trimerophytes. It is a decimeter or two tall, consisting of a dichotomous (Y-shaped) branch system (Fig. 7a), many of the branchlets being terminated by pairs of sporangia about 2 mm long and 0.5-0.9 mm wide (Fig. 7b). It was found in abundance and in association with no other plant remains, suggesting that it existed in life as a pure stand.

We have found several distinct species referable to *Psilophyton*. Therefore, it is appropriate to explain the importance of this genus and to point out some of the features of a primitive land plant. The genus has a long nomenclatural history that was initiated in 1859 by the Canadian geologist, Sir J. W. Dawson, with his description of material found along the north shore of Gaspé Bay named *Psilophyton princeps*. Specimens assigned to *Psilophyton* reveal considerable information about the characteristics of the earliest vascular land plants and about the stages in the developing complexity of plants in the Early Devonian. Several species of this genus have been found in the Trout Valley Formation. The first plant that we studied in the flora, *Psilophyton forbesii*, was found at the South Branch Ponds Brook locality (Fig. 4, #3). *P. forbesii* was a much larger plant than *P. dapsile*. The strongly developed central stem of the former attained a diameter of nearly 1 cm and bore dichotomous side branches, some of which terminated in pairs of sporangia 3.5 to 5.0 mm long. It is likely that the plant attained a height of a meter or more. Specimens were also found along Trout Brook at locality #5 (Fig. 4).

A third species, *Psilophyton microspinosum* (Fig. 8), is intermediate in size between the other two and is distinguished by the presence of sparsely distributed slender spines (emergences) about 2 mm long. The plants occurred in a small lens about 1 meter above water level, there being perhaps a cubic meter of rock containing well-preserved specimens.

Specimens of a fourth species, *Psilophyton princeps* (Dawson) Hueber, were found in an outcrop about 7-8 meters north of where *P. forbesii* was first discovered. The stems of *P. princeps* are distinguished by their abundant, peg-like emergences which are clearly shown in the photo (Fig. 7c). *P. princeps* was the first Early Devonian species described by Dawson in 1859. This plant has only rarely been reported outside of its original
Figure 7. Some plants typical of the Lower Devonian Trout Valley flora. X 2.7. (a) Sterile branchlets of the trimerophyte *Psilophyton dapsile*. (b) Fertile branchlets of *P. dapsile*. X 2.8. (c) Two axes (stems) of the Early Devonian trimerophyte *Psilophyton princeps*. Note peg-like emergences. X 1.4. (d) Dichotomizing smooth axes occurring abundantly in several localities. No reproductive structures are attached so affinities are unknown. X 0.5.
Plant paleontology

locality in the Gaspé Peninsula. A few specimens with sporangia were recovered at the Maine locality (Kasper et al., 1974). The material from the Trout Valley Formation resembles that from the type locality (Gaspé Bay), differing only slightly in the form and size of the emergences.

It is appropriate to reflect at this point on the significance of the information afforded by these plants. Numerous species of *Psilophyton* have been described from scattered Lower and Middle Devonian localities worldwide. Its significance as a genus may be problematical, but the species assigned to it seem to offer very significant data on the evolution of the more primitive early vascular land plants. We have not found petrified material in the Trout Valley flora, but *Psilophyton* specimens from other localities reveal a slender, cylindrical core of xylem (water-conducting tissue) in the axes. The different species show an increase in size, the development of strong central stems, a diversity in the kinds of emergences, and considerable variation in the abundance and size of the sporangia.

Several other plants have been found at The Crossing locality which supply varying amounts of information. Representative specimens of what is the most abundant component of the flora are shown in Figure 7d. The main axes of the plant are 3 mm in diameter and these bear dichotomously forking branches. The plants probably attained a meter in height and are found as a "pure stand" in great abundance through several decimeters of the cliff. It is clear that it was a dominant element of the flora, probably for a considerable period of time. The material is thought to represent a *Psilophyton* species, but we have never encountered the fertile parts, the sporangia, which are critical for identification.

In contrast to large quantities of material, one of the most interesting plants that we have found is known from only a few specimens, but it affords a great deal of information. *Kaulangiophyton akantha* (Fig. 9) is probably closely related to the lycopsids. It is known from axes that branch to form H- or K-type patterns, and these bear sparsely distributed, stout spines up to 2 mm long which do not seem to be oriented in any regular pattern. Interspersed among these spines, on some of the branches, are large sporangia (6-8 mm in their greatest diameter) borne terminally on short stalks (Fig. 10a). Spores have not been isolated from these structures, but comparisons with similar organs in other fossil plants leave no reasonable doubt as to their identity. The sporangia probably contained very large numbers of spores—a characteristic of many of the early vascular land plants. At several places along Trout Brook we have found spiny stems up to 2 cm in diameter which suggest either larger plants of *Kaulangiophyton* or a completely different plant.

A particularly vexing plant that we have found at The Crossing is shown in Figure 10b. Numerous specimens were recovered from a band of rock about 10 cm thick; the axes are 5-6 mm in diameter and are densely covered with delicate, needle-like emergences 2 mm long. It is very different from anything else that we have found but, so far, we have not encountered fertile specimens. Fossil plants of this general nature have been reported from several other Early Devonian horizons and are assigned to the "form genus" (the affinities of which are unknown), *Thursophyton*. This generic name means the "Thurso plant" and refers to specimens found many years ago in Middle Devonian rocks at Thurso in northern Scotland.

A kilometer upstream from The Crossing, we (Kasper and Andrews) encountered plant remains in a low, nearly flat ledge

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**Figure 8.** Restoration of the Early Devonian trimerophyte *Psilophyton microspinum*. Axes are covered with tiny spines.

**Figure 9.** Restoration of the pre-lycopod *Kaulangiophyton akantha*.
Figure 10. Plants of the Trout Valley flora. (a) Distal region of fertile stem of *Kaulangiophyton akantha*; note large, stalked sporangia. X 1.3. (b) Spiny axes similar to the genus *Thursophyton*; arrow indicates spine. X 1. (c) Large central axis of the trimerophyte *Pertiqa quadriifaria* with several lateral branches terminated in sporangia. X 0.2. (d) Detail of a fertile lateral branch of *P. quadriifaria*; arrow indicates sporangia. X 0.8.
Plant paleontology

along the north side of the brook (Fig. 4, #2)—an outcrop quite different from the vertical cliff at The Crossing locality. Both the plant fossils and the lithology of the sedimentary rocks were quite different from anything that we had found previously.

The plant was given the name *Pertica quadrifaria* (Figs. 10c, 10d, 11). The generic name is from the Latin meaning a “long pole or rod” and refers to the stout upright stems. The specific name refers to the four-rowed arrangement of the primary branches. The latter were three-dimensional in their branching pattern, some being sterile and presumably photosynthetic, while others terminated in very dense clusters of sporangia from which spores were isolated (Figs. 10c, 10d). *Pertica* represents a more complex and advanced trimerophyte than *Psilophyton*, showing some early stages in the differentiation of branch systems leading to the origin of megaphyllous (broad-leaf type) leaves. *Pertica* also presents a good example of the mode of preservation of many Devonian plants. When the rock is first split open, only a small part of the plant may be revealed. It is evident that at the time of deposition the plant or plant parts were buried in the enclosing sediment without significant distortion and thus were preserved in three dimensions.

In 1985 the Maine Legislature selected *Pertica quadrifaria* as the state fossil. One of the more recently discovered plants in the Trout Valley Formation is *Leclercqia complexa* found in small quantities about 6 kilometers upstream from The Crossing (Fig. 4, #7). It is of special interest relative to the age of the formation. *Leclercqia*, named for the distinguished Belgian paleobotanist, Suzanne Leclercq, has been reported previously from several widely separated Middle Devonian localities including New York State, Belgium, and Queensland (Australia). It also occurs in late Lower Devonian strata in northern New Brunswick. The Trout Valley specimens are not especially well preserved, but are sufficiently so as to leave no doubt as to their generic identity. The stems range in size up to 1.5 cm in diameter and are densely clothed with leaves that are 5-parted and about 5 mm long. Some of the leaves bear a single sporangium on the upper surface. The internal anatomy of the stems is known from the New York specimens where they reveal a well preserved, slightly fluted cylinder of xylem.

Numerous specimens of the curious fossil plant *Protopaxites* have been found in the conglomerate that is exposed along the upper reaches of South Branch Ponds Brook. This is a widely distributed Devonian plant, both geographically and stratigraphically. Its silicified trunks attain a maximum diameter of nearly a meter. These trunks consist of large and small tubes closely intertwined; the former are aligned longitudinally while the latter are randomly oriented. Although problematical as to its taxonomic affinities, *Protopaxites* is generally regarded as the stem of a giant alga or fungus. The Maine specimens found thus far are poorly preserved and do little more than reveal the presence of this plant in the flora.

Future field work may be expected to reveal still more new plants and to add to our knowledge of some presently known only from fragmentary remains. As one final example, we have
found distinctively spiny stems along Dry Brook about 200 meters upstream from where the road crosses the brook (Fig. 4, # 4). We tentatively attribute them to the lycopod genus *Drepanophycus*. The stems differ from any others known in the flora, but thus far no fertile specimens have been found. The area is heavily forested, but it is evident that significant and abundant fossils are present.

We are indebted to William G. Chaloner of Royal Holloway and Bedford Colleges, Surrey, England, for undertaking a study of the spores present in the flora. For the most part they are not well preserved, but the diversity of types suggests the presence of plants that have not thus far been found as macrofossils. Descriptions and illustrations of the spores are given in Andrews et al. (1977).

**Fossils of the Frenchville Formation**

Schopf et al. (1966) described carbonized dichotomizing axes from the Silurian Frenchville Formation in northern Maine (Table 2). The small axes were vertically oriented and perpendicular to the bedding plane. The specimens were proposed, at that time, to be the oldest remains of early land plants yet discovered. Recent reexamination of the material by Strother and Lenk (1983) has called into question the plant affinity of these controversial fossils.

**MIDDLE DEVONIAN FLORA IN MAINE**

**The Mapleton Sandstone Flora**

The presence of plant fossils in the Mapleton Sandstone was noted as early as 1900 by Williams who identified axis fragments as *Psilophyton princeps*. No serious study of them was made at that time, although specimens were sent to David White at the U.S. Geological Survey. Interest centered more on determining the age of the Mapleton Sandstone because of its lithological similarity to the Chapman Sandstone and because it had originally been considered as part of, or included within, the Chapman Sandstone. However, the Mapleton Sandstone unconformably overlies the Chapman Sandstone; further, the Chapman Sandstone is more deformed and indurated, and contains marine fauna and some plant remains that differ from and are stratigraphically older than those present in the Mapleton Sandstone. Boucot et al. (1964) also point out that apparently the Mapleton Sandstone, dated as Middle Devonian in age, is the oldest formation not affected by Acadian folding in that area.

Serious study of the plant fossils of the Mapleton Sandstone began when James M. Schopf received some specimens from Richard Naylor in 1961 for age determination and paleobotanical study. Schopf later obtained additional specimens from Forbes and collected more himself in 1963. He published a report on the plant megafossils from the Mapleton Sandstone in 1964. Schopf identified spiny axes as *Psilophyton princeps var. ornatum* (= *Sawdonia ornata*), fragmentary smooth axes of differing sizes and branching pattern as *Hostinella* and *Aphylopteris* (form genera for smooth axes), stems with "petiolate" lateral appendages as *Barrandeina*, and stems and sporangia as a new species of *Calamophyton, C. forbesii* (Table 2). In an appendix to a report on the geology of the area by Boucot et al. (1964), Schopf provided an assessment of the age of the Mapleton Sandstone based on spores obtained by macerating...
Figure 12.
some specimens of the plant-bearing rock. Both spores and plants suggested a Middle Devonian, perhaps early Givetian, age for the sediment although none of the microfossil or megafossil taxa are fully diagnostic of that age; it is possible that the strata may be somewhat older. Schopf clarified the differences in the types of plants present in the Chapman Sandstone relative to those of the Mapleton Sandstone.

Forbes was instrumental in drawing the attention of one of us (Gensel) to the potential for further study of the Mapleton Sandstone. We collected at two sites, the Winslow Farm locality and a roadside outcrop, starting in 1976. The plant fossils are preserved as fragmentary compression/impression remains and also as permineralized (pyrite and/or limonite) axes. Initial observations suggest that about six different kinds of plants are present. One or possibly two zosterophylls occur—their stems having a solid core of xylem in which the first-formed elements are located to the periphery (an exarch protostele; Figs. 12a,b). One of these (Fig. 12a) compares very closely in overall histology to *Stolber gia* described from Middle Devonian sediments in Belgium by Faire (1967). *Stolber gia* is based on smooth axes identical to those considered to represent the distal sterile segments of a plant called *Asteroxylon elberfeldense* by earlier workers, but regarded as a separate taxon by Faire (1967). Fertile structures of *Stolber gia* are unknown.

Other permineralized axes represent the stems of plants included in the cladoxylates, with one type appearing most similar to *Cladoxylon* or *Calamophyton* (Fig. 12c) and another apparently representing a new taxon (Fig. 13a). Other axes show anatomy consisting of a lobed, spread-apart, vascular strand (Fig. 12d) which is reminiscent of members of the Iridopteridales or *Schizopodium*. Also present are one or possibly two types of stems and perhaps one type of root with secondary xylem which may represent members of the aneurophtylaceous progymnosperms (Figs. 12e,f). Another appears to represent a rachis of the pre-fern *Rhacophyton*. These will be the subject of more detailed study and description in the near future.

Correlation of the permineralized axes with the morphologically preserved plant remains is possible only to a limited extent because little overlap in preservational type occurs. Schopf (1964) reported the occurrence of *Calamophyton* based on compressions/impressions from the Mapleton Sandstone, and observations by Gensel confirm his identification (see our Fig. 13b). One of the cladoxylatean stems may represent that taxon; however, none of the permineralized axes of that type conclusively demonstrate morphology typical of *Calamophyton*. Small axes covered with spines, possibly the basis for the identification of *Psilophyton princeps* var. *ornatum* by early workers and Schopf, are common in our current collections (Fig. 13c). This species has since been renamed *Sawdonia ornata* by Hueber (1971) based on other collections of spiny axes and has been assigned to the zosterophylls. Other Mapleton spiny axes produce slender, dichotomizing lateral branches which differ in morphology from those of *S. ornata* or any other zosterophyll and are more similar to specimens of possible triermerophyte or aneurophtylaceous affinity. Schopf (Boucot et al., 1964) also mentioned a similarity in spine morphology to the poorly understood genus *Thuropityon*, but the spines seem too slender.

Fragments of fertile remains occur, including two kinds of sporangial clusters attached to short lengths of axes (Figs. 13d,e). These tend to resemble trimerophyte sporangia, but might as readily represent the fertile parts of an aneurophtylaceous. Isolated fusiform sporangia are also present. The plants described briefly above support a Middle Devonian age for the Mapleton Sandstone. Most particularly, plants with secondary xylem such as those present in this flora are not known to occur prior to the Eifelian anywhere in the world (Banks, 1980). Cladoxyls and iridopterids are common in Middle Devonian sediments, although the former may first appear in latest Early Devonian (Lessuise and Faire-Demaret, 1980). Zosterophylls range from Early to Late Devonian in age. Study of the microfossil assemblages is currently underway and thus far confirms Schopf's age assessment as well.

Further study of the flora of the Mapleton Sandstone will not only contribute significant information about plant evolution in that period of time, but also will allow for floristic comparison with Middle Devonian plants from other parts of eastern North America, namely New York State and Virginia, as well as with well-known Middle Devonian floras of Germany, Belgium and Czechoslovakia. The plants identified in the Mapleton Sandstone thus far are very similar to those occurring in some Givetian localities (Cairo) in New York State (Marten, 1973, 1975) and to some European Middle Devonian floras—differing mainly in paucity of aneurophtylaceous.

**LATE DEVONIAN FLORA IN MAINE**

**Perry Formation Flora**

As mentioned earlier, the history of paleobotany in Maine begins with the reports of plant fossils from Upper Devonian strata in the vicinity of the town of Perry along Maine's easternmost coast. In three papers in the 1860's, Dawson describes and illustrates plant megafossils from strata which are eventually to be named the Perry Formation. Dawson's immediate contribution to the geology of Maine was his accurate assignment of a Devonian age to the Perry Formation. More significant, however, is the fact that these three initial papers (1861, 1862,

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**Figure 13.** Plants from the Middle Devonian Mapleton Sandstone, Maine. (a) Permineralized axis with cladoxylatean anatomy, probably different from axis in Fig. 12c. X 28. (b) Axis showing digitate branching characteristic of *Calamophyton*, a genus considered by some in the line leading to horsetails. X 1.1. (c) Branched, spiny axes; possibly similar to specimens called *Psilophyton princeps* by earlier workers; arrow indicates spines. X 1.6. (d) Axis with short lateral branches terminating in clusters of fusiform sporangia. X 2.4. (e) Distal axis segments, probably of another plant, terminating in fusiform sporangia. X 5.
Figure 13.
1863) and his summary paper of 1871 laid the foundations for Devonian paleobotany in North America.

It is critical to point out that fossil plant specimens from the Perry Formation are rare. Dawson candidly admits that much of his material from the Perry Formation comes from other individuals. The specimens he describes in 1861 are those collected by Richardson for the Geological Survey of Canada and those deposited in the Natural History Society of Portland. Dawson did, however, have an opportunity to collect plant material from the Perry Formation himself with the help of Jethro Brown (Dawson, 1863, p. 460). The locality, as can best be pinpointed from Dawson's rambling narrative, is on the “south side of Little River” which is near Perry, Maine. Smith and White (1905), in their comprehensive treatise of the geology of the Perry Basin, provide two localities for plant fossils in the Perry Formation. One of them, from which they themselves collected material, is believed by them to be the same locality which Dawson himself worked. This is the outcrop on the “right bank of Little River, about one-half mile below the wagon-road bridge at Perry” (Smith and White, 1905, p. 35). Descriptions thereafter of fossil plant specimens from the Perry Formation have been based on museum specimens only (Kräusel and Weyland, 1941; Pettitt, 1965). In 1968 Forbes relocated the original outcrop and subsequent collections have been made by two of us (Forbes and Kasper) over several years. The site is on the south bank of Little River about 300 yards east of the bridge where U.S. Route 1 crosses the river near Perry, Maine. Because only a small peripheral portion of the fossiliferous lens is exposed, only a few specimens can be collected in any one field season. Apparently, each year’s winter ice erodes the outcrop and exposes again a small peripheral segment of the lens.

The two most important species of fossil plants in the Perry Formation are Barinophyton richardsonii and Archaeopteris jacksonii (Posnack, 1982) (Table 2). Both of these were established by Dawson in his first publication on the Perry flora in 1861. The first species Dawson (1861) initially called Lepidostrobus richardsonii thinking that it was a lycopod strobilus (cone) and naming it after Richardson of the Canadian Geological Survey who had found the specimen. Two years later Dawson (1863) placed this species in the genus Lycodites as Lycodites richardsonii. White (Smith and White, 1905) in his revision of the Perry flora recognized that the specimens described by Dawson were not lycopod remains at all but completely new. As a result White established a new genus Barinophyton for Dawson’s material, hence, Barinophyton richardsonii.

Prior to our recent collections, less than a dozen specimens of B. richardsonii had been obtained by Dawson and his colleagues or Smith and White. The species is currently being redescribed based on new fertile specimens. The complete plant is unknown, but the largest specimen (Fig. 14a) is 9.6 cm long and shows a main axis bearing two rows of strobili on either side: alternate and distichous (Posnick et al., 1983). The strobili number 12 in all. The main axis is 5 mm wide and has three of the strobili directly connected. Each strobilus consists of an adaxially curved axis bearing what are interpreted as appendages and sporangia on the adaxial surface. The strobili are broken distally, but are at least 4 cm long and 0.8-1.2 cm wide. Width depends on their orientation during preservation. In 1965 Pettitt macerated a specimen of B. richardsonii in the British Museum collected from the Perry Formation. He obtained megaspores 220-250 µm in diameter and microspores 48-62 µm in diameter. We have been unsuccessful, as yet, in obtaining spores from sporangia.

One unique and startling feature of Barinophyton is the fact that Brauer (1980) has demonstrated conclusively that B. citruliforme from Upper Devonian strata in Pennsylvania has both megaspores and microspores within the same sporangium. This is an important discovery of what may be a major step in the transition from homospory (one size spore with bisexual gametophyte) to heterospory (two sizes of spores with male and female gametophytes). Hopefully, further work on B. richardsonii will shed light on this major question of reproductive biology in early vascular plants.

The second important species of the Perry flora was originally described by Dawson as two species: Cyclopteris jack­sonii and Cyclopteris rogersii. Dawson established C. jacksonii in 1861 naming the material after Charles T. Jackson, the first state geologist. Two years later Dawson (1863) erected the other species and named it for Professor W. B. Rogers. White (Smith and White, 1905) in his floral revision placed these two species in the genus, Archaeopteris, as A. jacksonii and A. rogersii. For reasons to be discussed shortly, all the specimens of Archaeopteris have been treated by us as one species: Archaeopteris jacksonii.

Archaeopteris is an arborescent progynnosperm (Fig. 15) with a large trunk displaying features of gymnosperm wood anatomy. Its branch systems consist of helically arranged laminal leaves and non-laminar leaves. The latter bear numerous elliptical sporangia on their upper surface.

The Archaeopteris specimens from the Perry Formation are small branch fragments of sterile and fertile foliage (Figs. 14b-d). Several specimens of branches with sterile leaves have been collected. Sterile leaves (Fig. 14c) are generally obovate in outline, tapered proximally to the point of attachment, dichotomously veined, entire margined, and average about 16 mm long and

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Figure 14. Plants from the Upper Devonian Perry Formation, Maine. (a) Specimen of Barinophyton richardsonii showing a portion of axis (bottom) and two rows of strobili; arrow indicates sporangia. X 0.8. (b) Penultimate branch and ultimate branchlets bearing sterile foliage of Archaeopteris jacksonii; the specimen (USNM 422472) is figured in Smith and White, 1905 (Pl. 3, Fig. 1) and is the counterpart to Dawson’s specimen (1871, Pl. 15, Fig. 167). X 0.7. (c) Ultimate branchlet of A. jacksonii showing obovate sterile leaves; the specimen USNM 36460 is figured in Smith and White, 1905 (Pl. 3, Fig. 2). X 1.9. (d) A segment of a fertile branchlet presumably of A. jacksonii; each filiform leaf bears several sporangia on its upper surface. X 2.7.
Figure 14.
of Late Devonian plants morphologically, anatomically, and geographical distribution. Third, it is the basis on which an en­
tire new plant class, the Progymnospermopsida, was estab­lished by Beck in 1960. Archaeopteris is perhaps the best known of Late Devonian plants morphologically, anatomically, and reproductively. However, it presents one of the major enigmas in paleobotany: the many species of Archaeopteris which are based on sterile foliage all have reproductive foliage which is virtually indistinguishable from each other. This difficulty was addressed by Beck in 1969. The problem concerning Archaeopteris is whether we are dealing with one highly variable spe­cies, with many species or, perhaps, with different genera. Since there is often morphological variability in vegetative features and since reproductive structures in all species are indistinguishable, it is not known what actually constitutes a biological spe­cies for Archaeopteris (Beck, 1969). For these reasons and for the fact that Dawson’s taxa are indistinguishable based on his illustrations and descriptions, the Archaeopteris material in the Perry Formation is treated as one species—that first described by him as A. jacksonii (Posnick, 1982).

PALYNIOLOGY

Determining the exact age of terrestrial sediments is often problematical, and this is true of some of the plant-bearing deposits in Maine. The kinds of plants found in the Mapleton flora, for example, are not in themselves diagnostic of a particular time interval, although a general designation such as Early, Middle, or Late Devonian can be made. Other types of evidence, e.g. faunal, are not available or are also inconclusive.

The study of dispersed spores in Devonian sediments has greatly expanded in recent years. As a result, the correlation and dating of sediments are much improved and are on a much broader scale than before. The accumulated data have been summarized in the recent publication by Richardson and McGregor (1986) on spore zones for the Silurian and Devonian of the Old Red Sandstone Continent and adjacent regions. This should aid in regional and worldwide correlation.

Palynological study of rocks of both the Trout Valley For­mation and Mapleton Sandstone has been carried out. In regard to the former, spores are very highly coalified and black, thus limiting identification and analyses. However, the taxa described by Chaloner in Andrews et al. (1977) include Apiculiretusispora, Grandispora douglastownense, Emphanisporites, and some other genera which mostly support a late Early Devonian (Em­sian) age for the formation. Richardson and McGregor (1986) cite the Trout Valley Formation assemblage as representative of their late Emsian, possibly earliest Eifelian, “douglastownense-eurypterota” zone. Therefore, this flora is generally com­parable in age or perhaps slightly younger than the floras of northern New Brunswick and the Gaspé Peninsula which are part of the same tectonic framework. Many plant taxa described from the Trout Valley Formation also occur at the Canadian localities which range from early to latest Emsian in age based on dispersed spore correlations (Gensel and Andrews, 1984; McGregor, pers. commun., 1979, 1981).

Schopf, in Boucot et al. (1964), recorded the occurrence of the dispersed spore genera Cyclogranisperosporites, Tholisperosporites, Auroraspora, and large spiny spores similar to ones called “Type H” by Lang (1925) (= Coryostosporites or Acinotisporites mac­rospinosus) from the Mapleton Sandstone. The two genera, Auroraspora and Coryostosporites, are typical of Middle Devo­
nian spores and that, combined with the absence of spores with bifurcate spines and some distinctive Upper Devonian forms, led Schopf to suggest a Middle Devonian (probably early Givetian) age for the sediments. One of us (Gensel) is conducting further study of the dispersed spores from these sediments.

Andrews et al. (1977) noted that dispersed spores have been obtained from the Perry Formation sediments, but have not yet been studied. The only palynological report from the Perry Formation is that of spores obtained from sporangia of *Barinophyton* by Pettitt (1965). Two of us (Kasper and Forbes) are currently working on a redescription of *Barinophyton* from the Perry Formation and hope to add further information regarding the spores. No precise age, other than Upper Devonian, has been assigned to the Perry Formation. Analysis of the dispersed spores might allow better correlation with other Upper Devonian deposits worldwide.

In summary, then, even though plant fossils have been known from the state for better than a century, the intensive work of the past two decades has vastly increased our knowledge of plant life in the Devonian of Maine and northeastern North America. The interest and cooperation of local residents, professionals working in the region, and the Maine Geological Survey have played a major role in providing impetus, information, and encouragement for the initial discoveries and for our ongoing work in the state. It must be remembered that the results obtained over the last two decades have taken place in an area long believed to be barren of any useful plant fossils. Also evident is the fact that repeated collecting at known outcrops and continued exploration for new plant-bearing strata are likely to yield even more data. Plant fossils from the state of Maine have been a major factor in understanding the remarkable diversity of early land vascular plants of the Devonian Period.

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