



Rotted wood–alga–fungus: the history and life of *Prototaxites* Dawson 1859

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Abstract

The Devonian flora discovered and collected by W.E. Logan in 1843 remained unstudied until 1855 at which time the collections were offered to J.W. Dawson. His attention was immediately drawn to a single large specimen in the collections, which he identified and described as partially rotted wood of a conifer (Dawson, 1857). He proposed the name *Prototaxites* (Dawson, 1859) thereby expressing his concept of the genus. That concept remained unchallenged until Carruthers (1872) heatedly ridiculed both the name and the author and illegitimately substituted the name *Nematophycus*. His subjective opinion was that the fossil represented a fragment of a very large alga, like *Lessonia*. His classification, challenged only once (Church, 1919), persisted in all subsequent reports. Dawson remained adamant in his definition of *Prototaxites* until he illegitimately substituted the name *Nematophyton* for *Prototaxites* (Dawson, 1888) and denied (Dawson, in Penhallow, 1889) that he had ever classed the genus with the conifers. The names *Nematophycus* and *Nematophyton* are later synonyms of *Prototaxites* and, although inappropriate in connotation, *Prototaxites* is nomenclaturally valid. No undoubted original nor associated specimens are available for choice of a lectotype. This report has a triple purpose: (1) to name, as neotype, a recognizable specimen collected by Dawson for which the locality and stratigraphic data are known, (2) to redescribe the genus as structurally composed of three interactive forms of hyphae, i.e. large thin-walled, septate, branching, generative hyphae; large thick-walled, non-septate, skeletal hyphae; and small thin-walled, septate, branching, binding hyphae, which combine to form a gigantic, phototropic, amphigenous, perennial sporophore with saprobic nutrition, and (3) to classify it in the Kingdom Fungi. Generic synonymy with *Prototaxites* is proposed for *Nematophycus* (Carruthers, 1872). © 2001 Elsevier Science B.V. All rights reserved.

Keywords: *Prototaxites*; Fungi; Devonian; Canada; neotype; paleoecology

1. Introduction

Among the fossil plants that were collected by W.E. Logan along the shores of Gaspé Bay (1843), the most enigmatic specimen resembled a fragment of a small tree. That resemblance seemed to have influenced subsequent interpretations of the permineralized anatomy of the specimen (Dawson, 1857) as well as the

anatomy of other specimens collected later by Dawson (1858). Microscopical examinations of ground thin-sections concluded that all of the specimens were silicified, partially rotted wood, as indicated by the very loose organization of the tissues and the presence of an entangled meshwork resembling fungal mycelia. The wood was not so rotted to preclude naming the species *Prototaxites logani* and classifying it with the conifers, particularly among the Taxineae (Dawson, 1859). The etymology of the generic name indicated his interpretation, and for 29 years, Dawson, in his several papers (Dawson,

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1859–1882b and 1888) dogmatically repeated and supported his conclusions.

Carruthers (1872), in the meantime, was the first to change the concept of *Prototaxites* by disclaiming any relationship of the genus with the conifers. He proposed an illegitimate substitution of the name *Nematophycus* for *Prototaxites*; formally classed it with the Codiaceae among the green algae; informally compared it with *Lessonia* among the brown algae; and set into motion the concept that the genus was a marine alga. That concept has not been rejected in any descriptive papers since the date of his publication. New species have proliferated.

The purpose of this report does not include a synonymy of all of the species, even though years of personal research have gone into the study of *Prototaxites* and all of its species based on available, original material. On the subject of original material, I have found that no *undoubted original* specimens studied by Dawson (1857, 1859, 1871) are extant. There is no nomenifer, nor are there specimens from which a lectotype might be named. Locality and stratigraphic data are available for the specimen used by Penhallow (1889) in his emended diagnosis of “*Nematophyton*”–*Prototaxites*. The specimen is in the collections of the Peter Redpath Museum, Montreal, Quebec, Canada and is designated the neotype of *Prototaxites*. A fragment of the specimen in the Paleobotanical Collections of the United States National Museum, Washington, DC is used to emend the genus and to establish its classification with the Fungi.

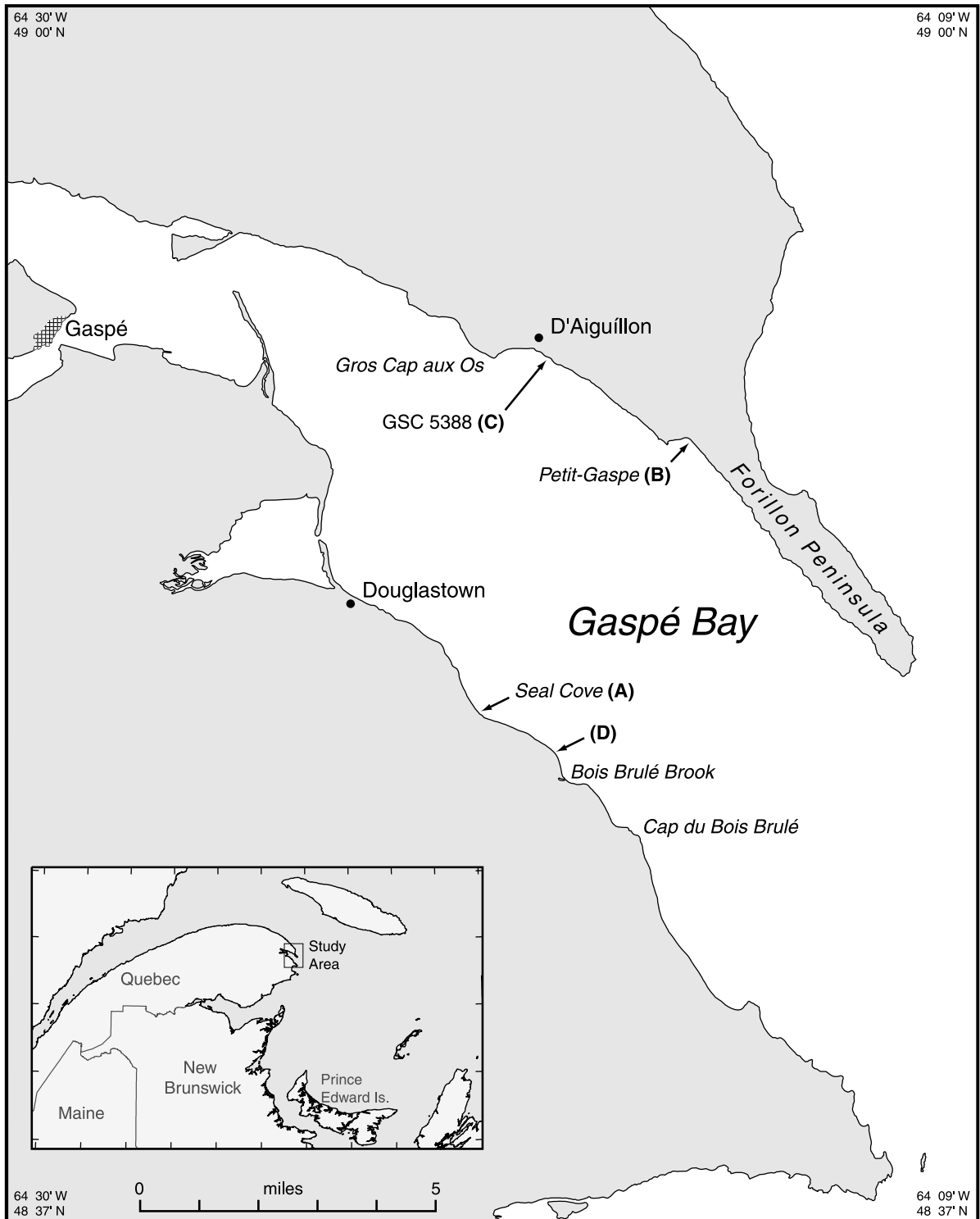
2. Brief history

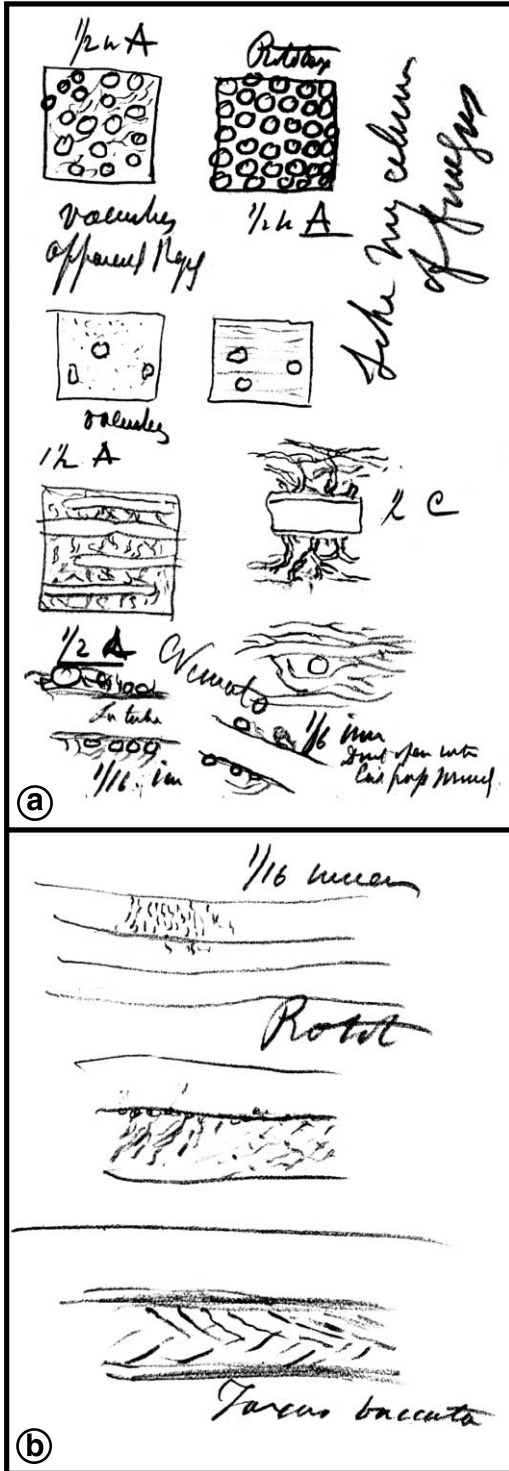
W.E. Logan was the first person to collect and document the occurrences of fossil plants in the well-exposed sections of Devonian strata along the shores of Gaspé Bay, Quebec, Canada. He accomplished this in the summer of 1843 during his mapping and exploration of the Gaspé Peninsula for coal and other mineral resources. In his field note book (1843,

p. 62, August 14–17) he commented on collecting fossil plant remains at a site named earlier by Bayfield (1837) as Cape Bréhaut. At the time of Logan’s visit, the local fishermen referred to the site as Seal Cove, by which name it is known today (Fig. 1). Logan, in apparent deference to Bayfield, labeled his collection site as Cape Bréhaut. That collection and all of the other collections he had made during his survey received no attention until he offered them to J.W. Dawson for study in 1855 (Dawson in Penhallow, 1889). A particular specimen in the collections aroused Dawson’s curiosity as it appeared to be fossilized wood. Thin-sections were prepared and Dawson interpreted and described the specimen as partially rotted wood of a tree closely related to conifers (Dawson, 1857). He did not formally propose a name for the fossil but did cite the source of the specimen as Cape Brachaut (sic). The citation was meant to read Cape Bréhaut, and the spelling was corrected in his subsequent papers. His report established the site from which the first specimen of the unusual fossil was obtained. The site is in the Battery Point Formation, early Emsian of the Devonian section, in Gaspé Bay.

Enthused by the variety and apparent abundance of fossil plant material in Logan’s collections, Dawson journeyed to Gaspé (Dawson, 1858) to observe the occurrences of the fossils as Logan had described them. He collected specimens, including more of the curious wood, and published his first descriptions of some of the elements in the fossil flora (1859). He used Logan’s original specimen and those he had collected himself to formally describe and propose the name *Prototaxites* for the ‘wood’. The etymology of the name clearly indicated his interpretation of the affinities of the genus with the Taxineae and particularly with the Recent genus *Taxus*. He may have had other thoughts about the identity of the fossil as suggested by his sketches of microscopic details of *Prototaxites* and *Taxus baccata* which were found among his collections. In his typically bold hand he wrote “Like mycelium of fungus” alongside the

Fig. 1. Geographical locations of collection sites, Gaspé Bay, Quebec, Canada. (A) Seal Cove, where the first specimen of *Prototaxites* was collected among other fossils by W.E. Logan during his mapping of the sections east and west of Seal Cove, 18–21, August 1843; Field Notebook, pp. 62–64. (B) Petit Gaspé (L. Gaspé), site of collection of “Specimen No. 5” by J.W. Dawson, 16–17 August, 1869; Field Notebook 1, pp. 31–32. (C) Geological Survey of Canada Locality #5388, specimen collected by D.C. McGregor, 15 May, 1959; Field #59-6, Notebook 1, p. 12. (D) Collection site of specimen of *Prototaxites* with vascular plant inclusions W.E. Stein, Jr. Locality #91-13, July, 1991.





1/2 in A	1/2 in A	(1/2 inch A)
Prototax	Prototax	(Prototaxites)
vacuoles apparent rays	vacuoles apparent rays	vacuoles apparent rays
1/2 in A	1/2 in A	1/2 in A
vacuoles	vacuoles	vacuoles
1 1/2 A	1 1/2 A	1 1/2 A
1/2 C	1/2 C	1/2 C
1/2 A	1/2 A	1/2 A
Wemoto	Nemato	(Nematophyton)
La tube	La tube	(Large tube)
1/16 in	1/16 in	(1/16 immersion)
1/16 in	1/16 in	(1/16 immersion)
Duct open with end poss missig	Duct open with end poss missig	(Duct open with end possibly missing)
Like my celium of fungus	Like my celium of fungus	(Like mycelium of fungus)
1/16 micron	1/16 immer	(1/16 immer)
Prototax	Prototax	(Prototaxites)
Taxus baccata	Taxus baccata	(Taxus baccata)

A = eyepiece lens = ca. 5x
C = eyepiece lens = ca. 8x

1 1/2 inch = objective lens = ca. 8x
1/2 inch = objective lens = ca. 20x
1/16 inch = objective lens = ca. 125x

Ergo: 1 1/2 inch A = 40x
1/2 inch A = 100x
1/2 inch C = 160x
1/16 inch A = 625x
1/16 inch C = 1000x

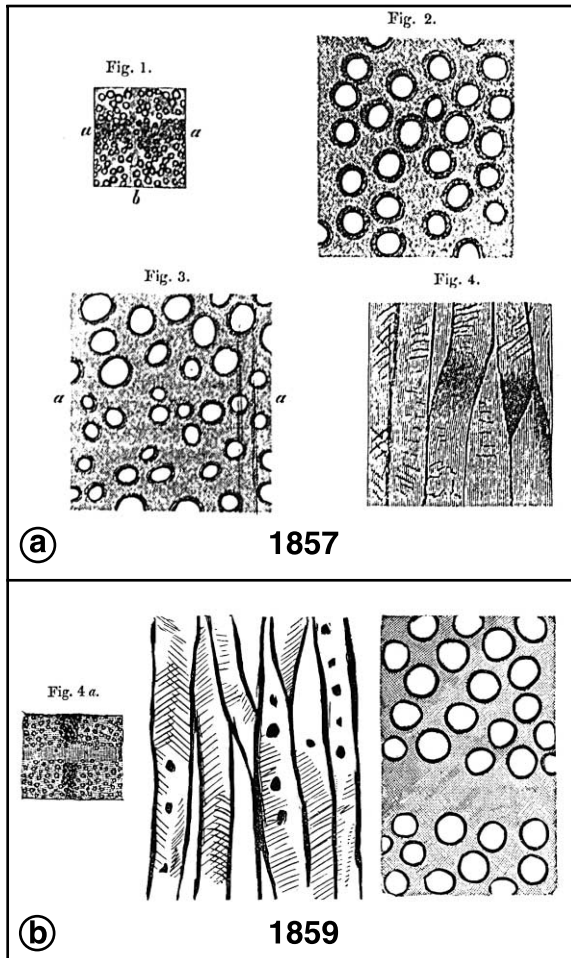


Fig. 3. *Prototaxites loganii* Dawson. Reproduced here are published illustrations derived from Dawson's original pencil sketches. (a) Dawson (1857), p. 175, figs. 1–4. (b) Dawson (1859), p. 484, figs. a–c.

details of *Prototaxites* (Fig. 2). Obviously, he did not consider that observation any further. Those sketches may have been the source for the production of the woodcuts illustrating his descriptions in 1857 and 1859 (Fig. 3a,b). The original specimens of his new

genus have been lost or are inextricably mixed with later collections. These circumstances preclude the selection of a specimen as a lectotype from among the early collections.

Dawson spent time, beginning July 22, 1869 (Dawson, Field Note Books #1 and #2), investigating the Devonian strata along the north and south shores of Gaspé Bay. He found occurrences of *Prototaxites* along both shores in which the 'trunks' were still embedded in sandstone matrices and associated with other plant remains, particularly with *Psilophyton*. Each discovery supported his belief that the genus was terrestrial and indeed a large tree. Sketches and subsequent illustrations (Figs. 4a–c, 5a,b and 6a,b), with commentaries in his field note books (Dawson, 1869a,b; 1881a,b; 1882a,b), reflected the increasing confidence he held in his classification of the genus. His commentaries and notation of dates have helped in establishing precise localities for some of the genera he later described, however, in many cases, the locality data accompanying his collections are given simply as Gaspé without stratigraphic control. At one point in his writings, he commented on collecting fragments of two large logs of *Prototaxites* (Dawson 1869a,b); one was three feet (0.914 m) the other two feet (0.606 m) in diameter. The latter specimen was illustrated (Dawson, 1871, p. 17) from the sketch in his field note book (Dawson, 1869a, p. 11), which is reproduced here (Fig. 4a). Unfortunately, the whereabouts of the two specimens cannot be traced. Their particular value was in the precise locality data as described in Dawson's field note books. Four (4) prepared thin sections of *Prototaxites* remain in his collections in the Peter Redpath Museum, Montreal but can only be assumed to have been prepared from one or the other of those two specimens. The sections are in longitudinal–tangential plane, have no labeling to indicate the source specimen and are of no value in tracing the history of the genus.

During the interval following his formal description of the genus and his additional field work, he

Fig. 2. *Prototaxites loganii* Dawson. Pencil sketches, drawn by J.W. Dawson from observation of microscopic details of *Prototaxites* and *Taxus baccata*. The sketches are in his collections at the Peter Redpath Museum, Montreal, Quebec. (a) Notations are principally of magnifications of the different images. Note in the upper right side "Like mycelium of fungus". (b) The notations on the upper images are magnification and "Protot" Dawson's usual abbreviation of *Prototaxites*. The lower figure is his impression of the spiral thickenings in *Taxus*. (c) Interpretations of the notations made by Dawson on his sketches are given here. (d) The conversions of the references to magnifications have been derived from catalogs from makers of microscopes and lenses published at the turn of the 20th century, e.g. W. Watson and Sons, London, 1923.

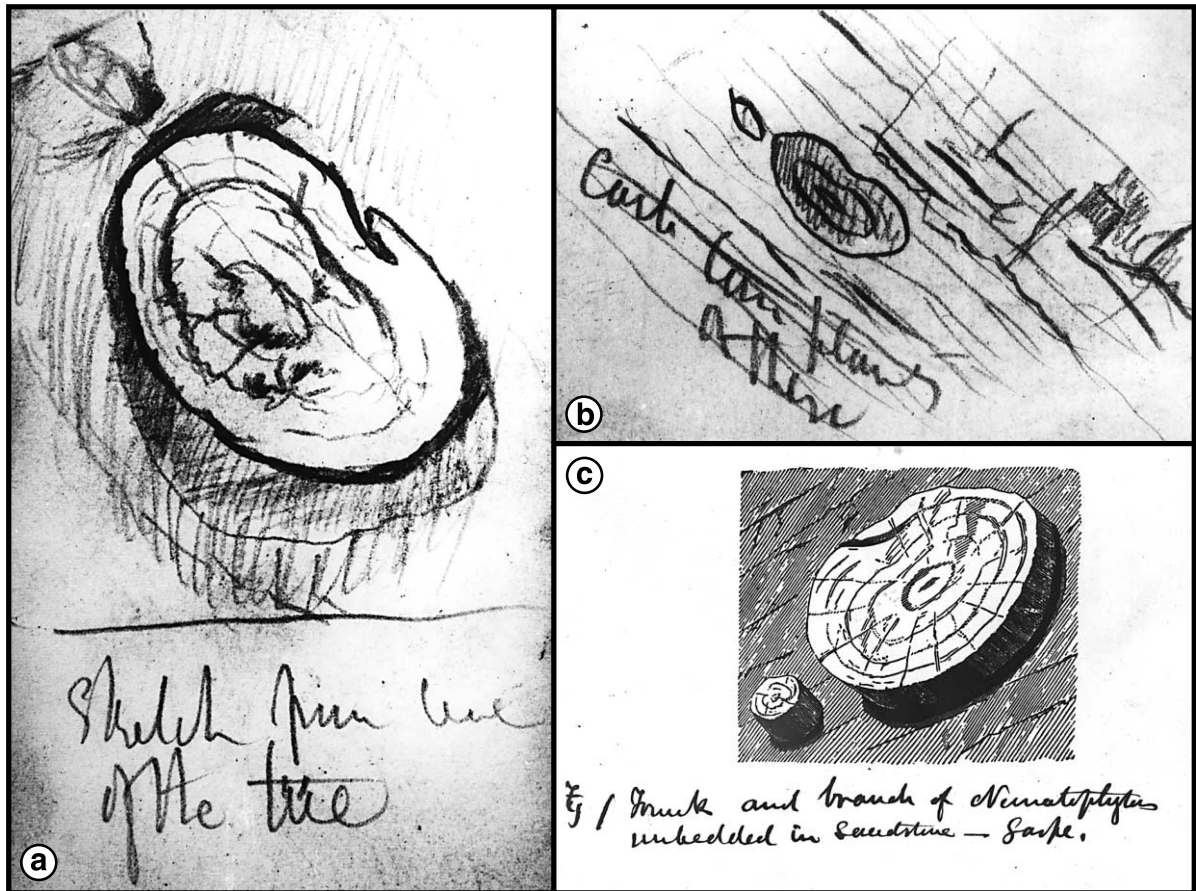
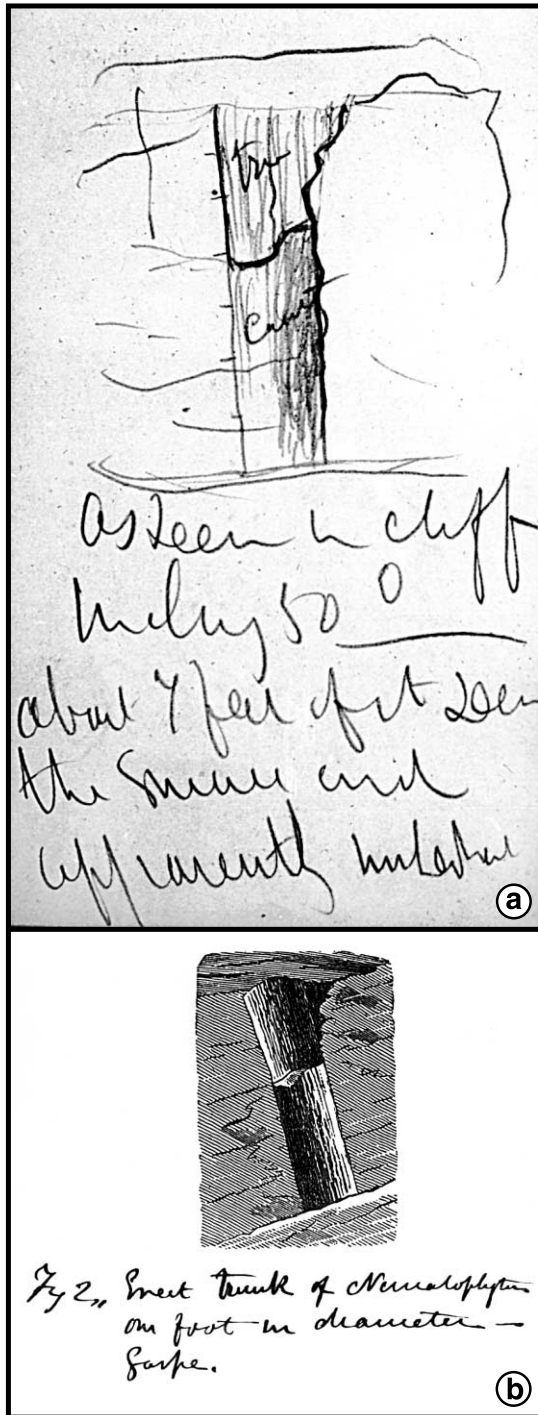


Fig. 4. *Prototaxites loganii* Dawson. Pencil sketches in Field Notebook #2 Dawson (1869b) and subsequent reproduction in publication. (a) "Sketch from life of the tree" is Dawson's notation on p. 11. (b) "Carb (Carbonized) Comm(inuted) plants and these" is the notation on p. 12. The notations have been interpreted from Dawson's usual way of abbreviating terms and from his famously illegible handwriting. (c) An original proof print with Dawson's handwritten caption for the illustration derived from his sketches in 1869. The finished image was rotated 90° from the original, perhaps for some artistic purpose. The caption reads: "Fig. 1. Trunk and branch of Nematophyton embedded in sandstone - Gaspé." And the image was printed in Dawson (1871), p. 17 and Dawson (1888), fig. 1.

published papers in different journals on the Devonian floras of northeastern North America (Dawson, 1859–1870). Most of the papers were repetitive, however, they stimulated interests among scientists in England who were intrigued by the Devonian age of the floras. Their interests resulted in an invitation from the Royal Society of London to deliver the prestigious Bakerian Lecture for the year 1870. He was delighted to accept the invitation as an opportunity to present his observations on the Devonian Flora of Gaspé. He took a suite of specimens with him which he distributed freely among those parties interested in particular species

in the flora. Original specimens and prepared thin-sections of *Prototaxites* were given to W. Carruthers, a respected British botanist, for examination and comment.

Dawson's lecture was well received but at the end he was informed that its content would not be published by the Society. Publication of the lectures had been customary in former years. Disappointed, Dawson returned to Canada where the content and illustrations of his lecture were published through the auspices of the Geological Survey of Canada (1871).



Dawson had not anticipated the scathing and slanderous observations and comments published by Carruthers (1872) who took it upon himself to re-define and rename *Prototaxites*. Carruthers vehemently denied any classification of the genus with conifers and suggested three other possibilities: (1) the lichens; (2) the fungi; or (3) the algae. He commented that no one would venture to consider the first two and that without any doubt, *Prototaxites* belonged with the algae. He continued by illegitimately substituting the name *Nematophycus* for *Prototaxites*. He classified the genus with the Codiaceae of the green algae however he made direct comparison to the very large brown alga *Lessonia fruscenscens* Bory described by Hooker (1847) from the coasts of the Falkland Islands (Fig. 7). Subjectively, *Prototaxites* has been classed principally with the brown algae, particularly with *Laminaria* and related forms, and secondarily with the red algae (Jonker, 1979; Schweitzer, 1983). No one questioned Carruthers' conclusion until A.H. Church (1919) offered the observation that *Prototaxites* could just as well be a fungus considering the sizes attained by some Recent woody fungi. Church's comment was ignored.

Subsequent to the scathing criticism Dawson continued his argument for the classification of *Prototaxites* with the conifers (Dawson, 1873, 1875). He also continued his field work, and in 1881, visited sites along the southern shores of Gaspé on Chaleur Bay and the mouth of the Restigouche River. Quarrying activity at the latter site, known as the Bordeaux Quarries, revealed a large number of 'trunks' of *Prototaxites*. The sizes and occurrence of the 'trunks' convinced Dawson even more of the arborescent habit and terrestrial habitat of the genus, an opinion he had stated from the very beginning of his studies. His field

Fig. 5. *Prototaxites loganii* Dawson. Pencil sketch in Field Notebook #1, p. 15, Dawson (1869a) and its subsequent reproduction for publication. (a) Notation for the sketch is "As seen in cliff reclining 50°... about 7 feet of it seen... the small end apparently embedded". The notations on the drawing of the specimen read "tree" on the upper portion and "cavity" on the lower. (b) An original proof print, derived from the sketch, with Dawson's handwritten caption "Fig. 2. Erect trunk of Nematophyton one foot in diameter... Gaspé". The artist's rendition has produced an optical illusion whereby the "cavity" may be the "tree" or the "tree" may be the "cavity". Illustration was used in Dawson (1871, p. 17) and Penhallow (1889, Text Fig. 2) in support of his interpretation of the arborescent habit of the genus.

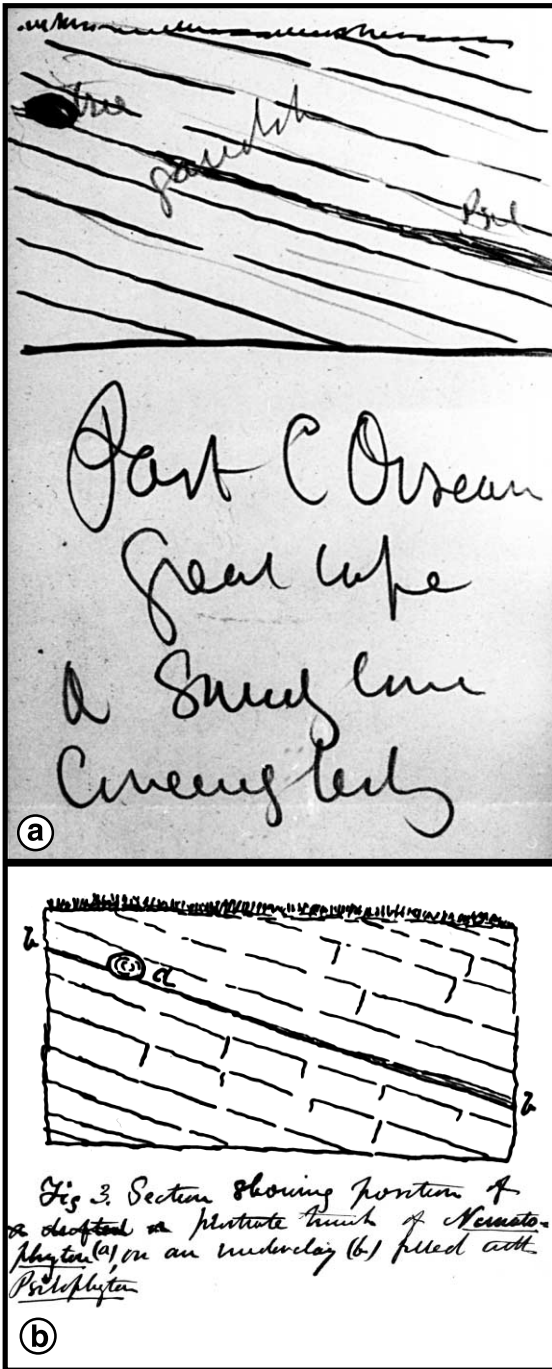


Fig. 3. Section showing portion of a drifted or prostrate trunk of *Nematophyton* (a) on an underlay (b) filled with *Psilophyton*



Fig. 7. Drawing of *Lessonia fruscenscens* Bory reproduced from Vol. 1, Part 2, Plate CLXXI, Hooker (1847). This is the species that influenced Carruthers in his comparisons with *Prototaxites*. Trunks (stipes) are 5–10 ft long, as thick as a human thigh, dichotomously branched, branches pendulous, with leaves 1–3 ft long, growth increments are evidenced by concentric rings. The ordered arrangement of the cells in the stipe are comparable with those of *Limnaria* pictured here in Plate VIII, 5,6, and discussed in the text.

note book (1881a, p. 12) contains a sketch of one of the logs he saw at the quarry and that sketch and the subsequent illustration are reproduced here (Fig. 8a,b).

He left the quarries and crossed the river to the shore of New Brunswick and proceeded from Campbellton to Dalhousie along the section of shales and

Fig. 6. *Prototaxites loganii* Dawson. Pencil sketch in field Notebook #1, p. 28, Dawson (1869) and the proof print derived from the publication. (a) The notation indicates the locality as: “Past C. Oiseau(.), Great Cape(.), a sandy cove (.), arenaceous beds”. Dawson misunderstood the French name for the Cape which was, and still is, Gros Cap Aux Os (bones not birds). The notations on the sketch are: “tree”, sandst(one), Psil(ophyton). (b) Proof print of the artist’s rendition of the sketch. The caption is handwritten by Dawson: “Fig. 3. Section showing portion of (“ a drifted or” crossed out) prostrate trunk of *Nematophyton* (a), on underlay (b) filled with *Psilophyton*”. Illustrated as Text Fig. 3, Penhallow (1889) in support of his interpretation of the terrestrial habitat of the genus.

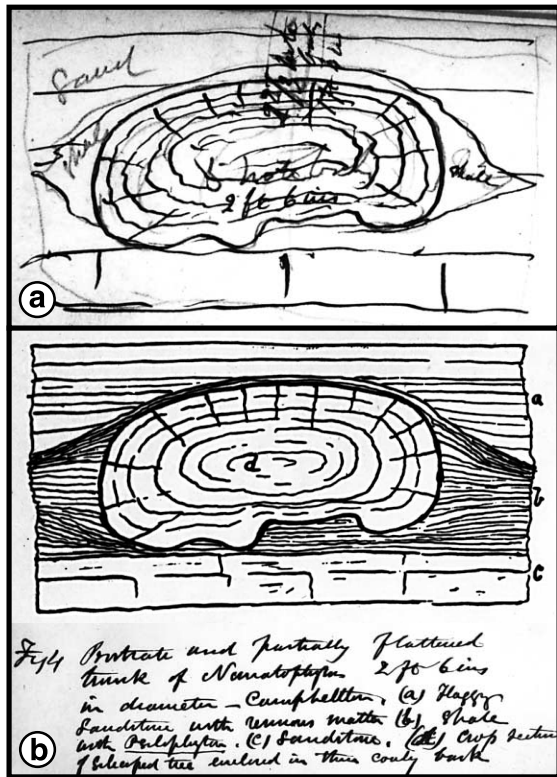


Fig. 8. *Prototaxites loganii* Dawson. Pencil sketch in Field Notebook, July 25, p. 12 (Dawson, 1881) and proof print derived from the sketch. (a) Sketch of the cross-section of a trunk seen by Dawson in the Bordeaux Quarries. Notations on the sketch are: “2 2/3 with bark, 1 ft 4 in, 2 ft 6 in without bark”; “shale” and “shale” at the sides, and “sands(tonc)” above and to the left. His notes about the specimen are on the facing page 13 and they are: “This must have been a prostrate trunk covered in coarse sandstone. Has a distinct crumbling coaly bark about 1/10th of an inch thick. Psilo(phyton) in shale drifted with it”. (b) Proof print of the artist’s rendition of the sketch. The caption for the illustration contains more information about the specimen: “Fig. 4. Prostrate and partially flattened trunk of *Nematophyton* 2 ft 6 in in diameter - Campbellton. (a) Flaggy sandstone with resinous matter, (b) shale with *Psilophyton*, (c) sandstone, (d) Corp section of silicified tree enclosed in thin coaly bark”. Illustration appeared in Penhallow (1889), as Text Fig. 4.

sandstones rich in fossil plant remains comparable in age to those along the shores of Gaspé Bay. He recorded observations of the fossils in his notebook (Dawson, 1881a) but did not collect many specimens. At the end of his field work in the area, he combined the few specimens from New Brunswick with the larger number he obtained from the Bordeaux Quarries in Quebec. The collections were shipped to

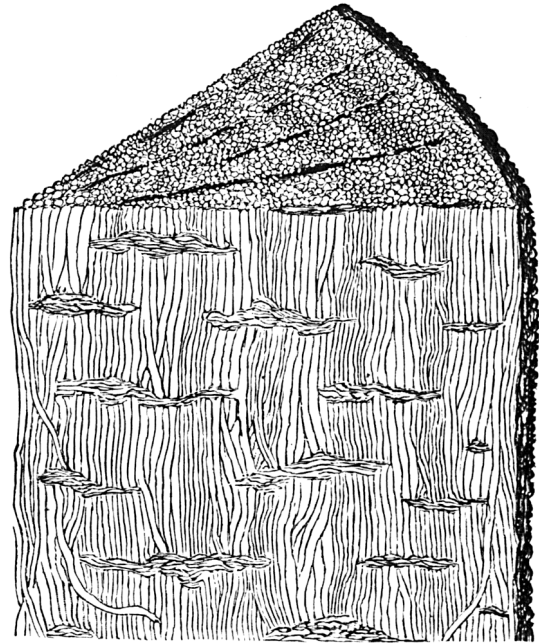


Fig. 9. *Prototaxites loganii* Dawson. Reconstruction of the anatomy of a specimen of *Prototaxites* in transverse and oblique section. The drawing was made by Penhallow for Dawson who used it in 1888, fig. 4, p. 23.

Montreal from Dalhousie. Specimens of *Prototaxites* from the Bordeaux Quarries have confusing labeling in which Dalhousie is indicated as their site of collection.

Between 1883 and 1888, Dawson’s immediate attention turned away from Devonian floras as indicated in the bibliography of Dawson’s works compiled by Ami (1900, 1901). He wrote papers based on his visit to Egypt, studies of Carboniferous reptilian remains, Tertiary and Mesozoic floras, religion, and education. During the same time, he must have been working on the manuscript of his book “The Geological History of Plants” (Dawson, 1888). In that text, he illegitimately substituted the name *Nematophyton* for *Prototaxites* (p. 40) and illustrated a restoration of the anatomy of a ‘log’ as drawn by Penhallow, which is reproduced here (Fig. 9). Dawson repeated his interpretations of the genus under the newly proposed name and presented his first reconstruction of ‘*Nematophyton*’/*Prototaxites* as he envisioned it in a ‘Silurian’ landscape. The reconstruction is extracted from that landscape and redrawn here (Fig. 10). In Dawson’s words: “They are trees of

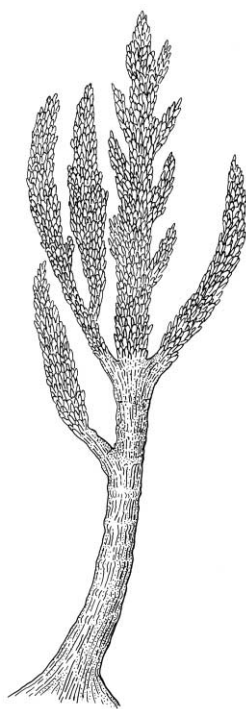


Fig. 10. Dawson's reconstruction of "*Nematophyton*"/*Prototaxites* is extracted and redrawn here from his fig. 14, "Silurian vegetation restored" (Dawson, 1888). The reconstruction embodies all of his interpretations of the genus as a conifer only to have him deny his intent to do so in the following year (Dawson in Penhallow, 1889).

large size, with a coaly bark and large spreading roots, having the surface of the stem smooth or irregularly ribbed, but with a nodose or jointed appearance.", and further: "Of the foliage or fronds of these strange plants we unfortunately know nothing". However, he comments that the superficial eminences on *Nematophyton* might correspond to leaf bases and the spirally arranged punctures, which it shows on its surface, represent leaf traces. Those comments help explain the 'leaves' that ensheath the upper branches in the reconstruction.

The subject of the "spirally arranged punctures" is discussed later in this report.

The publication by Penhallow (1889) contains an "Introductory Geological Note" by Dawson in which he reviews his years of field work and studies of *Nematophyton* (*Prototaxites*). He admits to an unfortunate choice of the generic name. However, at the same time, he denies that it was his intent to suggest a close affinity to coniferous trees, particularly to *Taxus*. He comments that "botanists have persisted in inferring that I regarded this wood as coniferous and allied to *Taxus*". Unfortunately, he had expressed the relationship in all of his previous papers, and we see here a weak defense of the inappropriate name, *Prototaxites*.

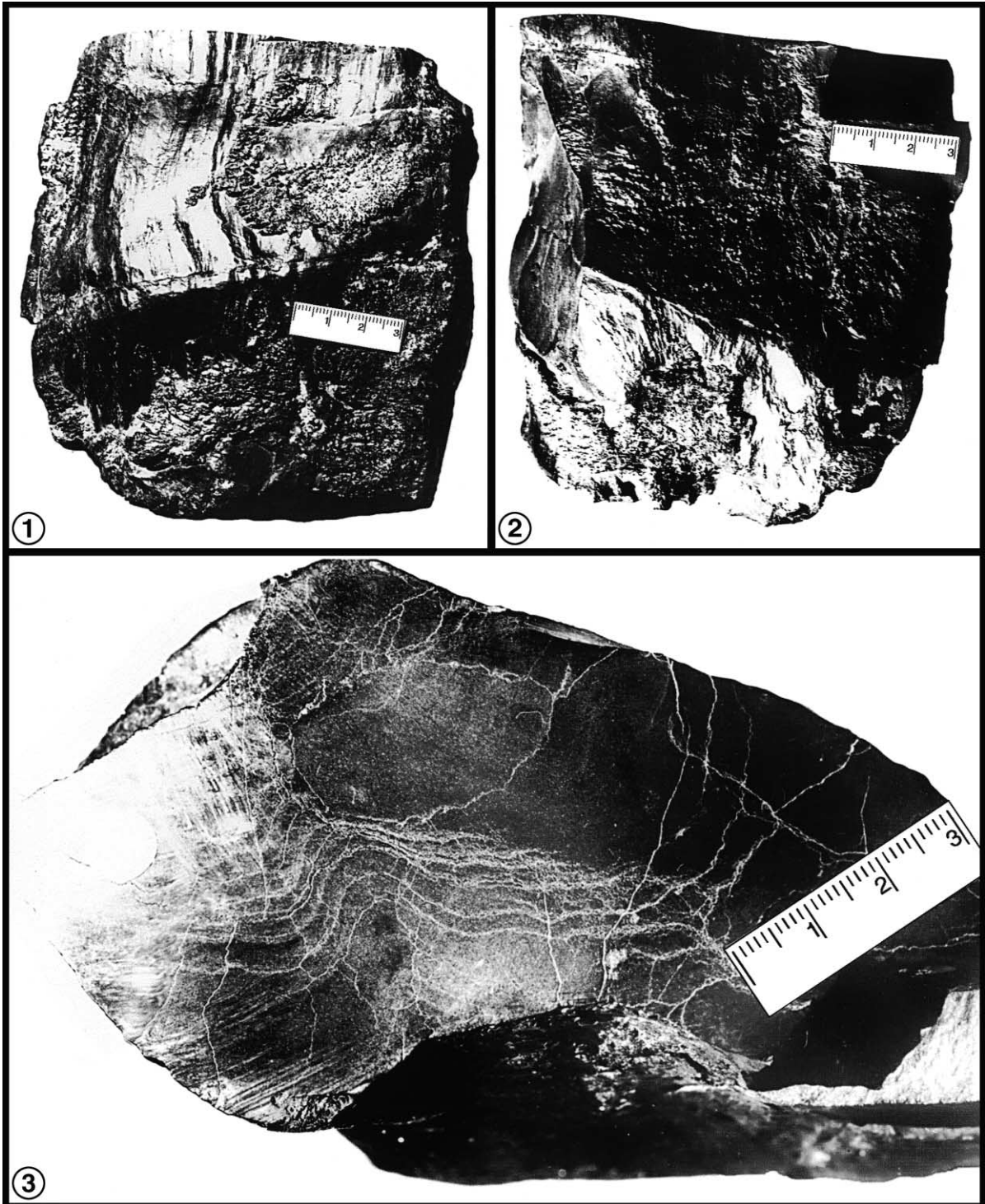
Subsequent to Dawson's 'Introductory' portion of the paper, Penhallow ignored the evidence that *Prototaxites* was a terrestrial plant and perpetuated both the illegitimate name, *Nematophyton*, and the classification of the genus with the large brown algae, the Laminariaceae. At the beginning, he appeared to support the work of Dawson, but at the end, his support turned to Carruthers. He felt justified in doing so by presenting an enlarged, though poorly illustrated description of the anatomy of the genus.

The description he gave was based on "Specimen No. '5' in the Peter Redpath Museum". There are six specimens in the collections of the museum bearing a large number '5' applied with white paint. One of them is the specimen that Penhallow described in detail but illustrated only with photomicrographs. The specimen is illustrated here (Plate I, 1–3). One specimen among the six bears a small label, a form used personally by Dawson and on which he wrote "L. Gaspé". This label indicates, in Dawson's typical abbreviations, that the specimen was collected at Little Gaspé, a site on the north shore of Gaspé Bay (see Fig. 1). Dawson collected *Prototaxites* at that site on July 26th and 27th, 1869, as noted on pages 31–32 in his Field Note Book #1 (Dawson, 1869a), which are

PLATE I

Neotype of *Prototaxites loganii*, Peter Redpath Museum, #12.231.

1. Lateral view as described by Penhallow (1889). Note fine longitudinal ridges and coaly surfaces.
2. Reverse side of specimen, lateral view. Note continuation of raised 'node' with a median furrow and friable coaly surface.
3. Polished transversely cut surface. Note distorted growth increments ending at margins of the specimen. The ridges on the lateral surface are a reflection of the compact tissue (the hymenium) at the margins of the increments.



reproduced here (Fig. 11), and in his review (Dawson in Penhallow, 1889). Although the significance of the number '5' could not be determined in the records of the Peter Redpath Museum, it may be assumed with certain confidence that the six specimens form a suite collected from the same site and subsequently were numbered identically. This determination of the collecting site for "Specimen No. 5" establishes the specimen as one collected by Dawson at a specific time and most importantly at a specific horizon in the stratigraphic section in Gaspé Bay. The specimen is designated as the neotype for *Prototaxites* later in this report.

3. Materials and methods

3.1. Specimen No. 5

(A) A fragment from "Specimen No. 5" (Penhallow, 1889), 6.5 cm high, 6 cm wide and up to 5.2 cm thick, is in the Paleobotanical Collections of the United States National Museum (USNM #510098). The specimen is in a very large collection acquired as a gift from R.D. Lacoë (USNM Accession #70216, 6/25–7/5, 1923). Mr Lacoë was a private collector who concentrated on acquiring fossil plant specimens from the great Carboniferous coal fields in the State of Pennsylvania. He used his surpluses of representative species for exchange with other collectors, or museums. He did not restrict his collecting to Carboniferous species but attempted to broaden the representation of fossil floras in his collection. He corresponded with Dawson and proposed an exchange of species from the Carboniferous of the United States for Devonian as well as Carboniferous species from Canadian sources. Dawson agreed to an exchange and sent Lacoë a small suite of specimens, in July, 1885, from the Devonian of Gaspé and from the Carboniferous of Nova Scotia. The fragment of *Prototaxites* was in the suite of specimens from Gaspé, and its color, surficial characteristics and preservation match those of the original specimen described by Penhallow. It also bears an identical number '5' in white paint. One end of the original specimen (Plate I, 1) had been sectioned transversely at the time of Penhallow's description. The fragment in the Lacoë Collection may have been removed from the

smaller of the two sections. That fragment is used in the redescription of the species.

(B) Additional specimens. Fossil and Recent specimens have been prepared or studied in support of the description and analysis of the genus.

1. Sources and locality data for the additional fossils are as follows:

(A) Geological Survey of Canada, Ottawa, Ontario, Canada.

(a) G.S.C. Locality # 5388. From loose boulder of conglomerate on beach about 400 yards east of old dock at D'Aigillon, (Gaspé, Quebec). Coll. D.C. McGregor, Field # MK 59-6, Notebook 1, page 12, May 15, 1959. Battery Point Formation, Emsian (Lower Devonian).

(b) G.S.C. Locality # 6272. North side of Restigouche River. Shore opposite Bordeaux Quarry. Coll. D.C. McGregor, Field # MK-62-5, May 31, 1962. La Garde Formation, Emsian (Lower Devonian).

(B) Paleobotanical Collections, United States National Museum, Smithsonian Institution, Washington, D.C.

(a) USNM Paleobotany Locality # 14256; specimen USNM # 510099. Field notes: Outcrop of black shales highly altered by igneous intrusion overlying the shales. Fossil plants abundant, highly altered, but may be compared with spinous plants such as *Psilophyton* spp. or *Sawdonia* spp. Fragment about 20 cm in diameter and 28 cm long of *Prototaxites* collected from the top of the section. South shore of Chaleur Bay, immediately west of Pin Sec Point, New Brunswick. La Garde Formation, (Dineley and Williams, 1968), Emsian, Lower Devonian. Coll. F.M. Hueber and J.P. Ferrigno, June 19, 1966.

(b) USNM Paleobotany Locality #14255, USNM #510100. Caesar's Bore, Queensland, Australia. Dotswood Formation, Frasnian, Upper Devonian. Coll.: F.M. Hueber and D.H. Wyatt, 1975.

(c) USNM Paleobotany Locality #14259, Specimen photographed, no collection. Outcrop 18 miles south of Jabal Qiyal al Kabir, northern Saudi Arabia. Al Jauf Formation,

in black shale
 below is probably
 P. of this is sub-
 aquatic stems
 of the present
 plant

Little Gaspe
 Cove / at point
 coarse grey &

reddish sandstone
 at middle of
 grey sandstone &
 rust rusty
 shales &
 grit beds &
 Protaxites
 bottom of cave
 where limestones
 come in view
 lying

Middle Devonian. Discovered by Dr Charles R. Meissner, Jr., United States Geological Survey Mission in Saudi Arabia. 1987 (retired). Photograph by Dr Meissner.

(d) Fragment of *P. southworthii* (Arnold, 1952). Paleobotanical Collections USNM #168964 (Accession # 291655). Kettle Point Shale, Fammenian, Upper Devonian, Kettle Point, Lambton County, Ontario, Canada.

(C) Binghamton University (State University of New York at Binghamton, New York) Specimen # SUNY-B 7022-114, sections 114B-1 and 114C-1.1. Locality 91-13, cliff outcrop along shore north from mouth of Bois Brulé Brook, South shore. Gaspé Bay. Battery Point Formation, Emsian (Lower Devonian). Loaned to F.M.H. for study, registry MNHH OR 413933.

2. Sources and locality data for Recent plant specimens.

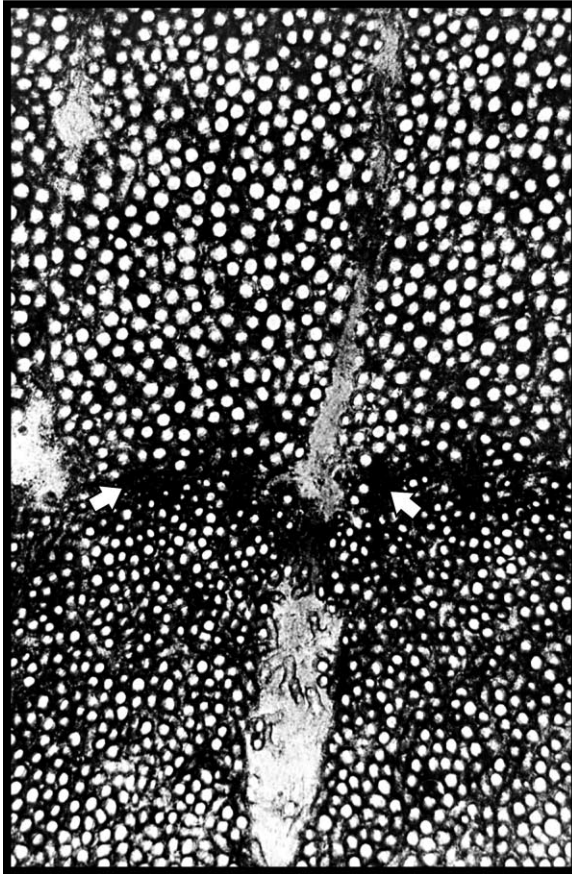
(A) A specimen of *Lactarius* sp. was collected locally in the State of Maryland and donated to this study by E. Farr, Department of Botany, National Museum of Natural History, Smithsonian Institution (specimen was not vouchered).

(B) Segments of the stipe of *Laminaria* were collected by the writer from tidal wash on the north shore of Gaspé. The segments were preserved in FAA (formalin-acetic acid-ethyl alcohol) until sections were prepared. Specimens were not vouchered.

(C) A large specimen of *Ganoderma* sp. was collected from the base of a diseased oak

Fig. 11. *Prototaxites loganii* Dawson. Pages 31 and 32 of Dawson's Field Notebook #1 (1869a) are reproduced here as a point of reference in the search for a specimen that had been collected by Dawson and for which there was stratigraphic control. Although Dawson's script is not readily decipherable, many of its characteristics can be learned and interpretations can be made with some confidence. The notes are a part of his observations as he followed the section of strata from Gros Cap aux Os to Little Gaspé, and on July 26 and 27, 1869 he made observations and collected at Little Gaspé. The entries are: "in black shale below is Psilophy(ton) ? (question) if this is the subaquatic stem of the present plant. _____ Little Gaspe Cove. At point coarse grey and reddish sandsto(nes)[.] At midway grey sandy and rusty with grey shales and grit beds and Protaxites to bottom of cave where limestones come in view (?flat) _____ lying" _____.

PLATE II



Neotype of *prototaxites loganii*.

Transverse section at growth increment. Note change in density and size difference in the skeletal hyphae and coltricioid cluster (medullary ray) passing through the increment; $\times 75$.

tree (aff. *Quercus rubra*). The specimen had been observed for 5 years before it was lifted from the base of the tree. The site was at the southwest corner of the intersection of Dorset Avenue and Little River Turn Pike, Montgomery County, Maryland. The tree has been removed. Slides and specimen are in the Paleobotanical Collections, USNM.

3.2. Methods

Standard techniques were used in preparing transverse, radial, and tangential ground thin-sections of the fossils. The sections were examined using a

Leitz research microscope with standard, variable, incandescent light source. A camera with automatic exposure capabilities was attached to the microscope. Photographs were taken using Kodak Tech-Pan film at an ASA index of 125.

All specimens studied with the scanning electron microscope (SEM) were carbon-coated and sputter-coated with gold/palladium. The SEMs used were a Cambridge 220 and an Hitachi Model 570 with a Polaroid camera attachment for photographic prints and negatives.

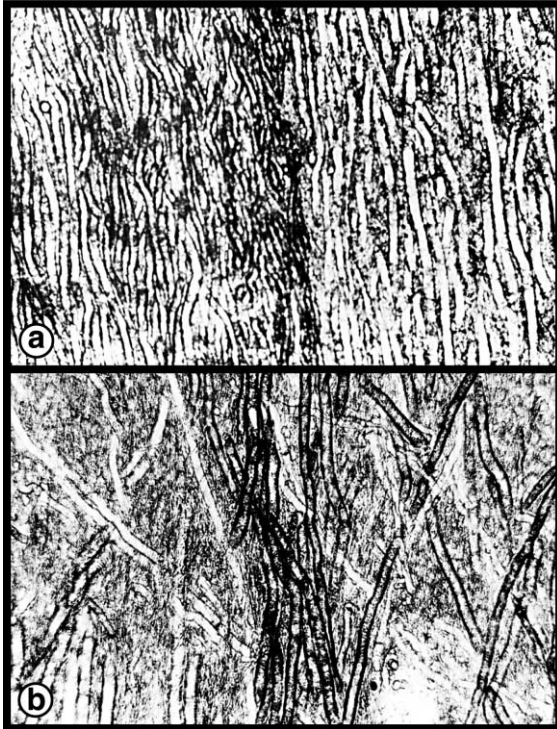
Transverse, radial, and tangential, sections, approximately 1 mm thick, were cut with an ultra-thin diamond blade. One surface of each of the sections was smoothed on wet, 600 grit Carborundum paper. The sections were cleaned by immersion in an ultra-sonic bath. After thorough drying in a dust free area, the sections were mounted on plastic disks using Epoxy 220 resin, with the semi-polished surfaces exposed. The specimen mounts were then immersed in concentrated (52%) hydrofluoric acid from 1 to 1.5 min, carefully lifted out and placed in a running tap-water bath for 1–2 h, or until a reading of pH6 was constant, which is the pH of the locally supplied city water. The sections were removed from the water bath, rinsed lightly, without agitation, in glass-distilled water and then carefully drained of excess water by tipping the section and touching the lower edge with absorbent tissue. The sections were allowed to air dry in a dust free area. Once dry, the individual sections were mounted on aluminum stubs with carbon based adhesive, and coated for SEM study.

The specimen from GSC. Loc. #5388 is a fragment that was not permineralized, but instead, has the appearance of original, though carbonized tissues. Small pieces were split from the specimen, glued to aluminum stubs with white glue (Elmer's) and coated for SEM study.

A portion of the holotype of *Prototaxites southworthii* (Arnold, 1952) was prepared as ground thin-sections and for SEM studies by the same methods as described above.

Thick (2 mm), free-hand sections were cut from fresh specimens of *Lactarius* sp. and *Ganoderma lucidum* using single-edge razor blades. The sections of the stipe of *Lactarius* were freeze-dried then mounted on aluminum stubs with 'sticky-tab' adhesive (non-water based adhesive). The specimen of *Ganoderma*,

PLATE III



Neotype of *Prototaxites loganii*.

- a. Radial longitudinal section across growth increment with obvious change in density and thickenings in the skeletal hyphae at the margin; $\times 65$.
- b. Tangential longitudinal section at surface of a growth increment and skeletal (thick-walled hyphae) randomly change course laterally at the growth increment. The dark area in the center is a small papilla at the surface of the hymenium; $\times 65$.

as a 'woody' fungus, was dry and relatively hard and requiring frequent replacement of razor blades to obtain free-hand sections which were without tears or disruptions of the tissue. The sections were mounted directly on aluminum stubs and coated for SEM study.

A segment from a stipe of *Laminaria* was rinsed free of preservative (formalin–acetic acid–ethyl alcohol) with distilled water. Thick (2 mm), free-hand sections were cut and freeze-dried in order to reduce distortions in the tissues. The sections were mounted on aluminum stubs with non-water based adhesive and stored in a dessiccation jar until time for examination in the SEM. The mounts were sputter-coated with gold/palladium.

4. Systematics

This classification above the rank of Order is based on the discussions in C.J. Alexopoulos et al. (1996) and definitions in Hawksworth et al. (1995).

Super Kingdom **Eukaryonta**
 Kingdom **Fungi**
 Division **Amastogomycota**
 Subdivision **Basidiomycotina**
 Class **Basidiomycetes**
 Subclass **Holobasidiomycetidae**
 Order **Prototaxales**
 Suborder **Prototaxineae**
 Family **Prototaxaceae**
 Genus **Prototaxites** Dawson, 1859, emend

Neotype: *Prototaxites loganii* ("logani") Dawson, 1859: Plate I, 1–3; Plate II, 1; Plate III, 1a,b; Plate IV, 1a,b; Plate V, 1a–c; Plate VI, 1a–c; Plate VII, 1a–d. Fig. 14b.

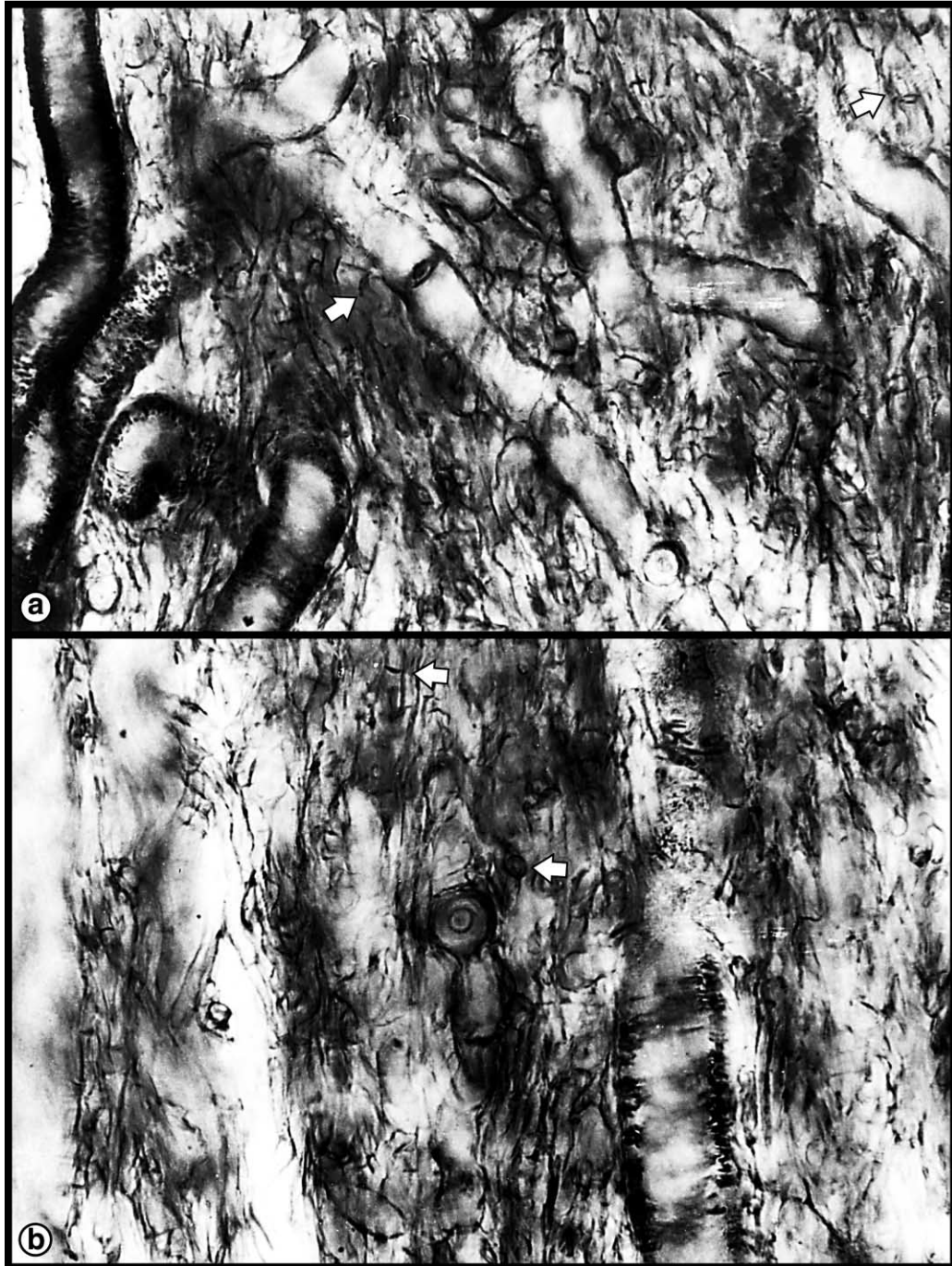
Syn. *Nematophyton logani* (Dawson) Penhallow, 1889, Trans. Roy. Soc. Canada. VI(IV), 27–47. *Nematophycus logani* (Dawson) Carruthers, 1872, Monthly Microscopical Journal. 8, 160–172, pl. 30–31.

Diagnosis: Terrestrial, astipitate sporophore, very large, up to 1.25 m in diameter, 8.8 m tall, with an amphigenous, thickening euhymenium; perennial growth, borders of growth increments marked by increased density of tissue. Tissue consists of three hyphal elements: (1) skeletal hyphae, thick-walled, large, long, straight or flexuous, aseptate, unbranched; (2) generative hyphae, thin-walled, large, septate with open or occluded pore, profusely branched, without clamp connections; and (3) binding hyphae, thin-walled, small, septate with pore, profusely branched, without clamp connections. Coltricioid hyphae, originating from generative hyphae, form isolated longitudinal, spindle-form clusters and radially elongate clusters that may pass through one to several growth increments. Radial width of growth increment highly variable. Hymenium narrow, marginal at growth increment, with densely crowded hyphae, dendrophyses and protobasidia. Spores unknown.

Prototaxites loganii Dawson, 1859 ("logani") emend.

Diagnosis: Characters as for the genus. Skeletal

PLATE IV

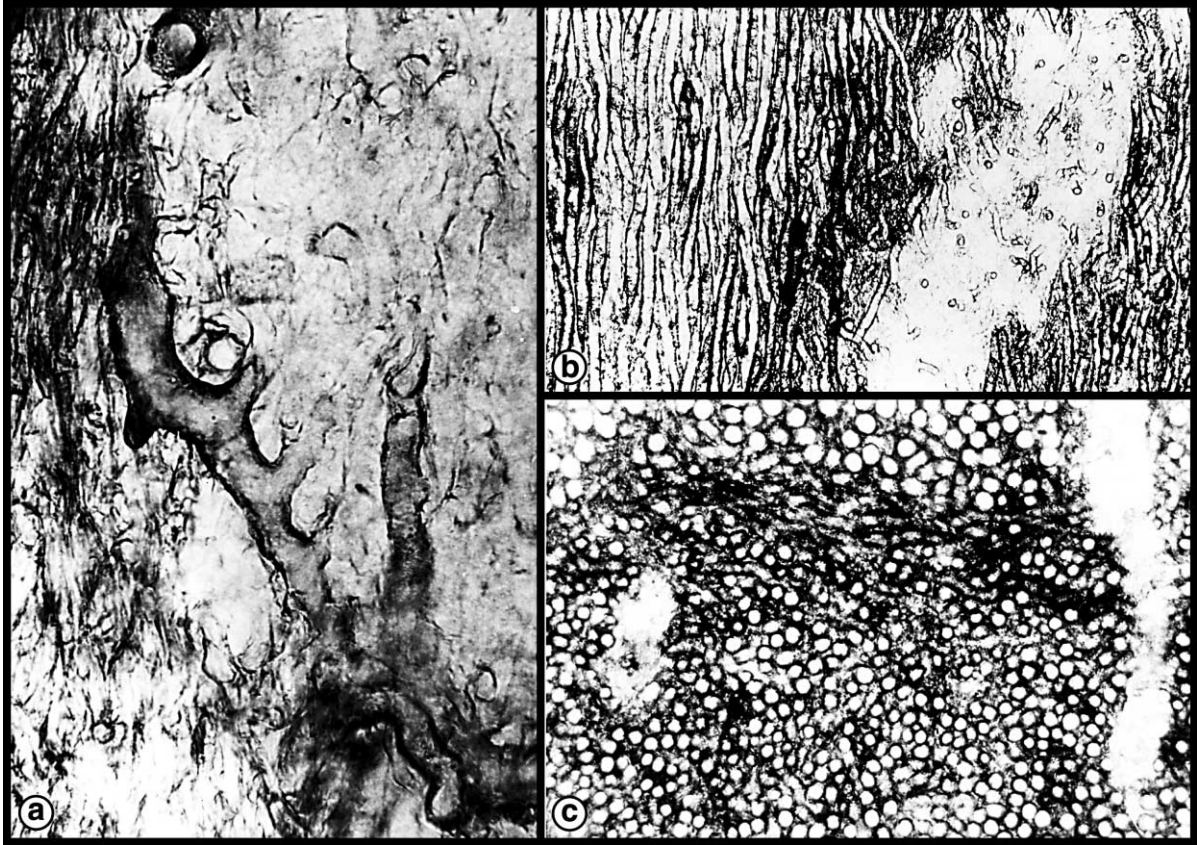


Neotype of *Prototaxites loganii*.

a. Lateral view of generative hypha with occluded porate septum, septate binding hyphae at arrows; $\times 300$.

b. Face view of septum with a very small perforation in the pore cover (?doliopore) in a generative hypha. Examples of septate binding hyphae are at arrows; $\times 300$.

PLATE V

Neotype of *Prototaxites loganii*.

- a. Radial longitudinal section of a coltricioid cluster with an actively branching generative hypha forming the cluster; $\times 525$.
 b. Radial longitudinal section of coltricioid cluster included in the margin of the growth increment, small irregularly branching hyphae nearly fill the space, which, in ground thin-section, is light brown suggesting organic residues as the colorant; $\times 75$.
 c. Transverse section at hymenium with generative hyphae active at, and paralleling the margin of, the hymenium; $\times 150$.

hyphae 18–50 μm wide, length undetermined but exceeding 2.5 mm, walls uniformly thickened 2–6 μm , aseptate, unbranched, spaced openly in growth increments, crowded, reduced in size, at outer margins of increments, lumens may be occluded. Generative hyphae 12–42 μm wide, septate, septum with open or occluded pore, clamp connections lacking or incomplete, lengths of component cells highly variable, walls thin; branching profuse, irregular, giving rise to coltricioid clusters of hyphae with open tips in flesh and radially through growth increments, conjugation rare. Binding hyphae 5–7 μm wide, septate, septum with open or occluded pore, without clamp connections, cells 15–54 μm long; branching profuse, irregular

forming mesh between and encircling larger hyphae. Hymenium marked by increased thickening of skeletal hyphae, increased branching of generative hyphae parallel and through surface of growth increment, appearance of dendrophyses and primitive basidia interpreted from remains of individually inflated sterigmata each with prominent spiculum. Spores unknown.

Orthographic change in the specific epithet as noted in Index Nominum Genericorum, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Neotype: Designated specimen, Peter Redpath Museum No. 12.231.

Repository: Type Collection; Peter Redpath Museum, McGill University, Montreal, Quebec, Canada.

Horizon: Base of the Battery Point Formation, *caperatus-emsianensis* spore assemblage of McGregor (1977).

Age: Earliest Emsian, Lower Devonian.

Locality: Section exposed at Petit Gaspé, north shore of Gaspé Bay, Gaspé, Quebec, Canada described by Dawson (1869a, pp. 32–33, illustrated here in Fig. 11). The section was visited by W.E. Logan in 1843 as noted in his field note book, Friday, July, 21; pages 30–31. The section was studied by McGregor (1973) and samples analysed from GSC Loc # 7161 and # 7162.

5. Descriptions

5.1. Neotype: morphology

Penhallow's description (1889) of the surface of "Specimen No. 5" included such details as numerous, fine longitudinal ridges, a very friable, thin coaly layer and to quote: "At about its central portion, the specimen shows a node-like swelling, which is traversed by a narrow furrow passing quite around the stem, thereby imparting an appearance closely resembling the node of a grass, and conveying the impression that it must represent the insertion of a broad-based, sheathing leaf". The lack of remnants of vascular or other structure failed to support his view that it was a leaf base. His description, however, suggests that he considered the specimen a complete segment of a round stem. The surface he described is illustrated here (Plate I, 1), and the reverse side of the specimen is also illustrated (Plate I, 2). The outline of the specimen is nearly square: $12 \times 11 \text{ cm}^2$ and is up to 6.3 cm thick.

The specimen had been cut transversely and the surface of the larger section had been polished for better observation of structural details (Plate I, 3). Penhallow's initial interpretations of the anatomy were based on the polished surface. He did not observe a pith in the section which confirmed his conclusion from other specimens, that the tissue was never present. Radial lines suggested medullary rays, which were later shown to be a misinterpretation of the anatomy. Other lines were interpreted as false layers resulting from alteration of the tissues by pressure. Layers interpreted as 'growth rings', as in

Dawson's original description of the genus, were not concentric but ended abruptly at the margins of the section. The fine longitudinal ridges on the lateral surface of the specimen reflected the differing densities of the tissues in the 'growth rings'.

The original "Specimen No. 5" is a fragment of a large sporophore, not a section of a small stem. The description of the specimen relies principally on the character of its very well preserved anatomy and secondarily on its morphology. Details supportive of the reconstruction of the morphology of the genus are described below from other specimens.

5.2. Neotype: anatomy

(A) The original, ground thin-sections on which Penhallow based his anatomical descriptions are missing.

Penhallow began his description of the 'internal structure' of specimen no. 5 with reference to the layered appearance one could observe in the polished surface of the cross-section (Plate I, 3). He attributed this character to variations in density of the structure wherein large thick-walled cells, 13.6–34.6 μ are at the inner margin of the layer and relatively smaller cells, 13.8–27.6 μ , are at the outer margin. He did not see this as an abrupt change as one might expect to see in the exogenous growth of a tree. He observed that the principal cells of the structure, the large tubular cells, do not follow a parallel course and are of indeterminate length. Further he notes the presence of mycelioid filaments, 5.3 μ in diameter, that cross the larger elements in all directions and produce the illusion of the "double series of spiral fibres" as originally described by Dawson (1859). He saw no structure in the cells that would suggest the presence of a primary cell wall nor of the sharing of cell walls. The ray-like openings in the structure were interpreted as the centers of branching of the large tubular cells. The products of the branchings were assumed to be the mycelioid filaments, which earlier had been considered "fungoid mycelia incident to decay". Subsequent to additional study, the filaments proved to be a normal part of the structure and decay was not the explanation for the loose structure of the tissues.

Penhallow's final conclusions were: the plant was not vascular; did not possess a true bark; the branching of the large cells took place in open areas which

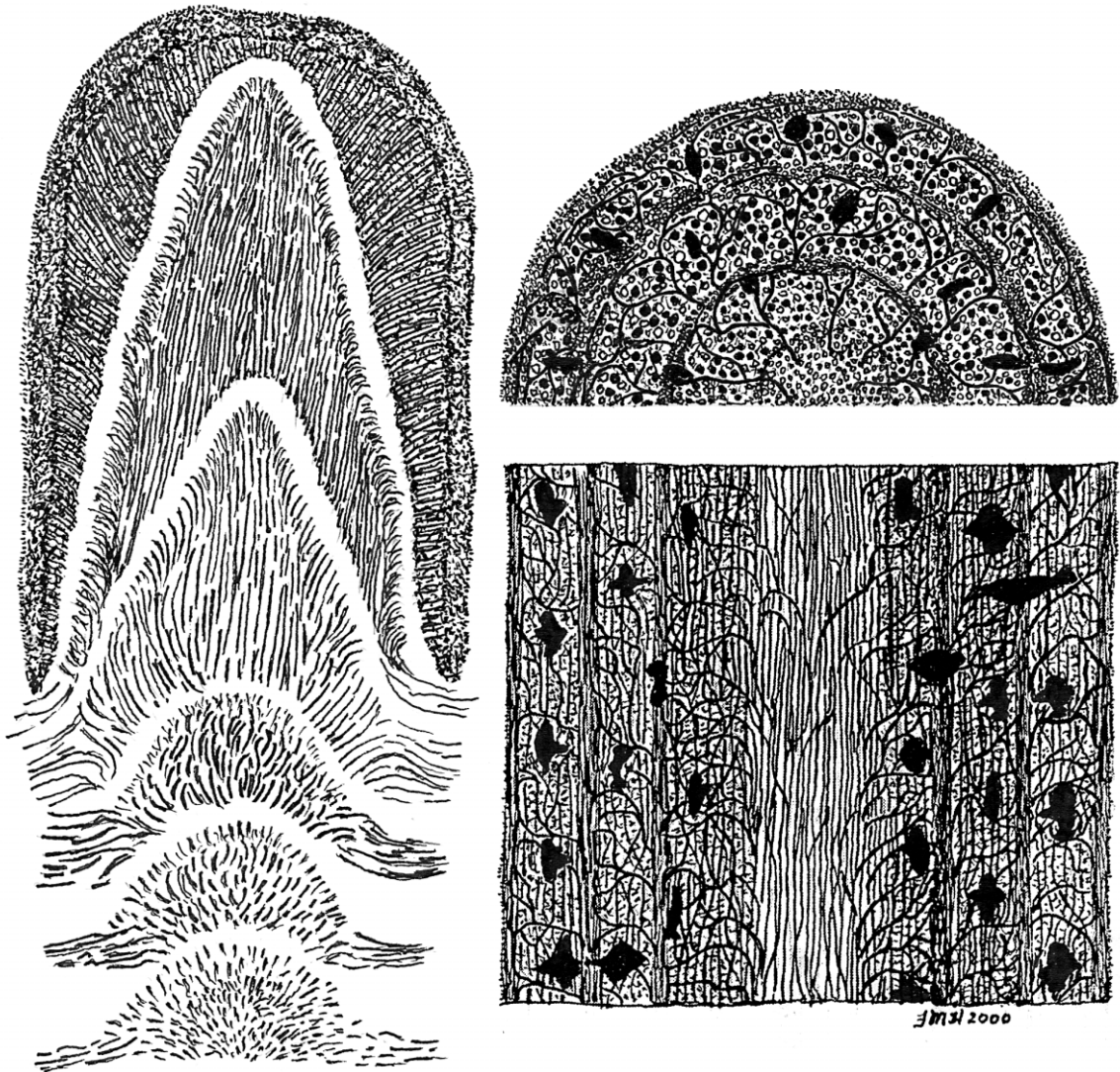


Fig. 12. *Prototaxites*. The hypothetical ontogeny of the sporophore. The initiation and progression in the development of the conical and subsequent dome-shape of the young sporophore is indicated by sequential gaps in the sketch. The models are taken from the development of the stipe in *Clavariadelphus pistillaris* and the addition of growth increments from an examples of *Lachnocladium zonatum*, as shown in Corner (1950). The reconstruction of the longitudinal and transverse views of a young sporophore of *Prototaxites* shows large bodies which are the “medullary spots or rays” as described in the early literature. The generative hyphae are purposefully darker and more sinuous in their pathways through the tissues. The thick-walled skeletal hyphae are indicated, in the transverse section, as black dots only for the purpose of differentiating them from the thin-walled generative hyphae. The binding hyphae could not be represented by any more than small irregular lines between the larger hyphae.

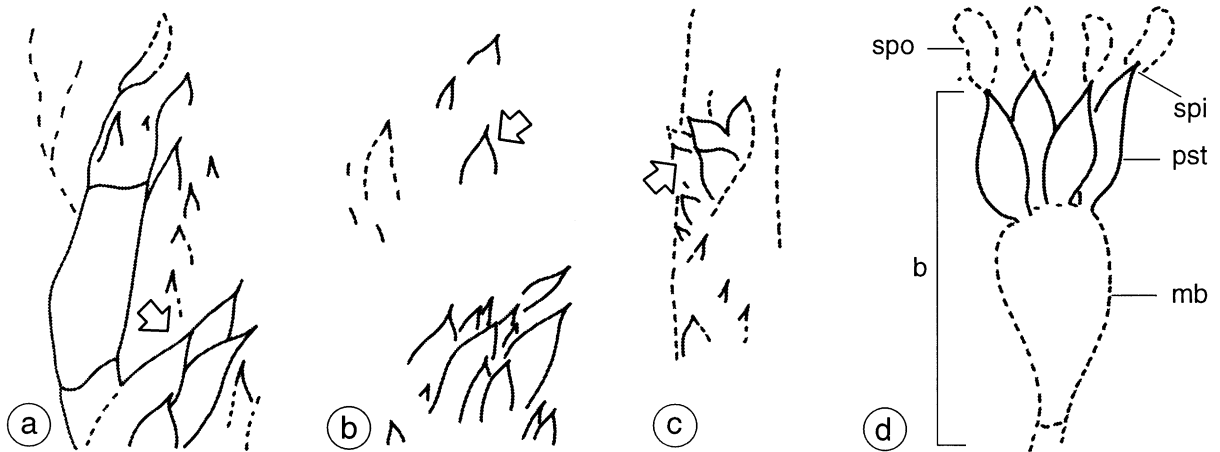


Fig. 13. *Prototaxites loganii* Dawson. Drawings. 1a–c Based on the details of the structures interpreted as inflated sterigmata, each bearing a spiculum, as shown in the photographs, Plate VII, 1a–c. Individual, fully intact, basidia were not observed. 1d Hypothetical reconstruction of a basidium in *Prototaxites* as based on the only remnants repeatedly observed in radial and transverse, ground thin-section of the hymenial growth increments. Hypothetical structures are indicated by dotted lines. Key to lettering: b., basidium; mb., metabsidium; pst., protosterigma; sp., spiculum; spo., spore.

simulated medullary rays; the anatomical characters were normal; there was no doubt that the plant was an alga with affinity to the Laminariaceae, the name *Prototaxites* was totally inappropriate, and the name *Nematophyton* (Dawson, 1888) was to be retained.

(B) There are few specimens of *Prototaxites* like the “Specimen No. 5” of Penhallow. It is exceptionally well preserved and its anatomy is totally representative of the genus. Redescription of the anatomy involves comparison and contrast of the structure of *Prototaxites* with the ontogeny, anatomy and subsequent morphology of a sporophore of a modern fungus possessing an amphigenous hymenium with the addition of perennial growth. The descriptions require substitution of mycological terms for those used earlier in describing the genus as a vascular or algal plant.

The anatomy consists of three forms of hyphae: skeletal, generative, and binding, *sensu* Corner (1932). The definition was based on the ability to tease apart the constituent hyphae of a modern fungus. That technique cannot be duplicated with the silicified tissue of “Specimen No. 5” but nearly all, if not more, of the structural detail of the different hyphae can be clearly demonstrated in ground thin-sections.

All three hyphal forms are clearly visible (Fig.

14b). The most obvious are the large thick-walled hyphae, *skeletal hyphae*, which vary from 18 to 50 μm in diameter depending on location in the tissue. Their walls are uniformly thickened from 2 to 6 μm in large individuals (Plate II) and may become so thickened, in small individuals, that the lumen is nearly filled (Plate II; at arrow). The length of the skeletal hyphae, in longitudinal sections, has not been determined because of their flexuous course through the tissue (Plate III, a,b). Segments up to 2.5 mm long have been seen, however, ends are missing due to loss in preparation of the section. The skeletal hyphae are not septate and do not branch. Other large cells are obvious in transverse section (Fig. 14b) and they are described here as *generative hyphae*. The generative hyphae vary in diameter from 12 to 45 μm , thus parallel in size with the skeletal hyphae, their walls are thin (Fig. 13b), they are septate, the septum with an occluded or open pore (Plate IV, a,b), they branch profusely within the tissue and particularly give rise to coltricioid clusters (*sensu* Corner, 1991) within the areas referred to as ‘medullary spaces’ (Penhallow, 1889) (Plate V, a–c), and they are very significant elements within the narrow region of the hymenium (Plate V, c). Incomplete clamp connections (Plate VI, a) as well as conjugative ‘H’ connections (Plate VI, b) are very rare in the generative hyphae. *Binding hyphae*

PLATE VI



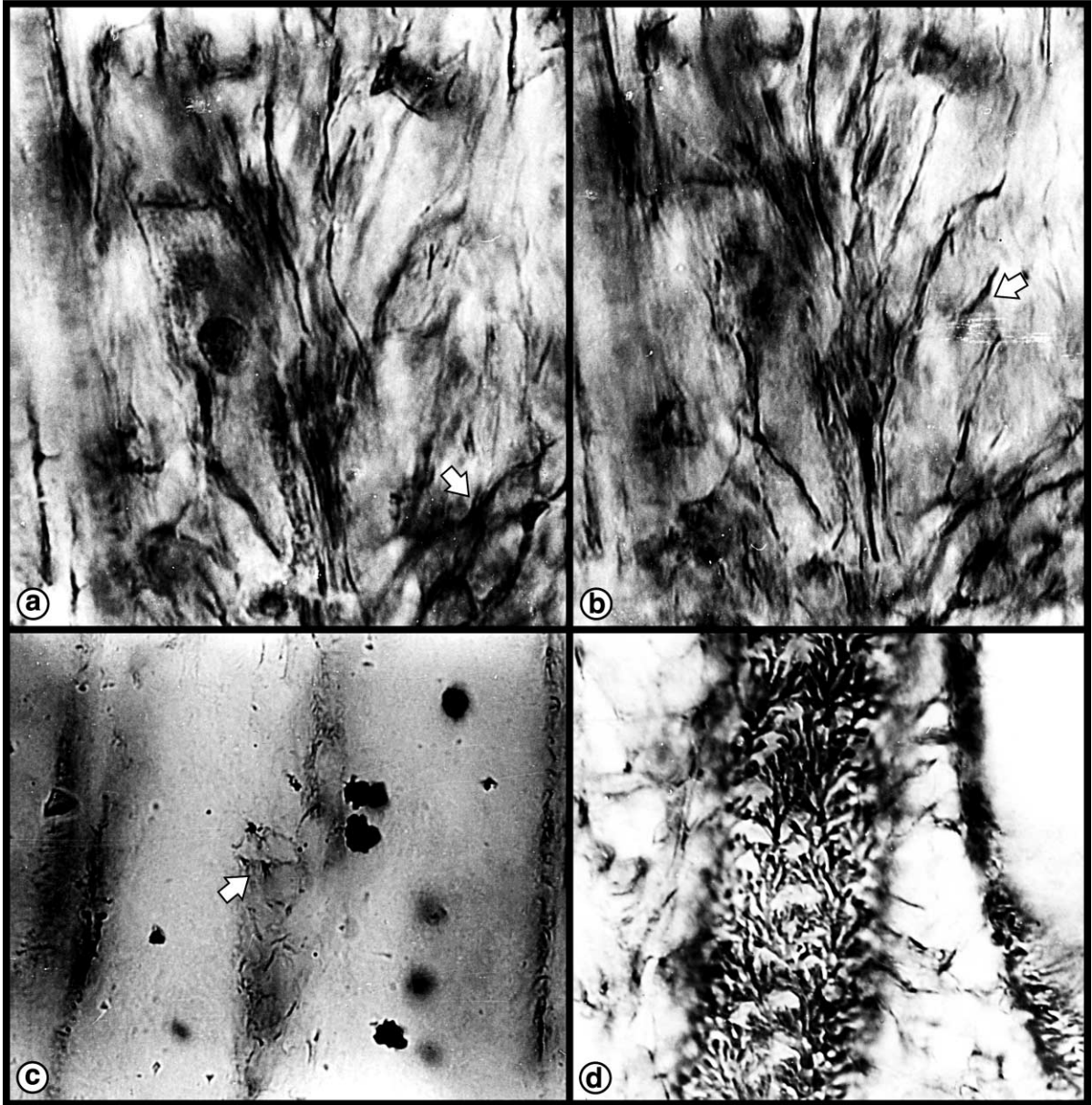
Neotype of *Prototaxites loganii*.

- a. Radial longitudinal section. Generative hypha with apparent incomplete clamp connection at side of perforate septal pore; $\times 300$.
 b. Radial longitudinal section. Generative hypha with conjugative connection, 'H'-form; $\times 375$.
 c. Radial longitudinal section. Binding hyphae forming meshwork around the larger hyphal elements; $\times 300$.

are the third of the hyphal forms present in the tissue. These hyphae, as their name implies, form complex meshworks between and around the large hyphae (Plate VI, c). They are the smallest of the hyphae, varying from 5 to 7 μm wide, cells 15–54 μ long. Branch-

ing is profuse, multi-directional and septate (Plate IV, b; at arrows). No clamp or conjugative connections were seen. The anatomy of these small hyphae, as described here, does not coincide with the definition proposed by Corner (1932) in which binding hyphae

PLATE VII



Neotype of *Prototaxites loganii*.

- a,b. Tangential longitudinal section of hymenial surface. Two different focal planes of the field of view in which the structures are interpreted here as inflated sterigmata with elongate spicula (at arrows). The ovoid body in (1a) is in a generative hypha and unidentified, the hyphal septum is visible above the body; $\times 875$.
- c. Tangential longitudinal section of hymenial surface. Cluster and remnants of structures interpreted as sterigmata with dark spicula; $\times 875$.
- d. Tangential longitudinal section of hymenial surface. Structures interpreted as dendrophyses, here lining the walls of thin-walled generative hypha and found in no other area of the tissues; $\times 600$.

are thick-walled and nonseptate. I prefer to emphasize function in the definition of the small binding hyphae in *Prototaxites* as opposed to the restrictive definition based on anatomy.

5.3. Neotype: hymenium

The hymenium is interpreted here as the original outer margin of a growth increment in which reproductive structures were formed. The zone of the increment as a whole is the site of rapid growth and branching of the generative hyphae (Plate V, c). The hyphae enter the inner surface of the increment, branch, follow along the contour of the increment while producing additional branches that pass outwardly, beyond the hymenium, and into the next zone of incremental growth of the sporophore (Plate II; Plate V, c). Skeletal hyphae are reduced in size, more closely spaced, and more heavily thickened in the region of the hymenium (Plate II; arrows). Space for binding hyphae is greatly reduced. Reproductive elements are interpreted from apparent remnants of primitive basidia in the form of closely linear or clustered, individually inflated sterigmata, each with a prominent spiculum (Fig. 13, Plate VII, a–c). No basal metabasidia were observed. There are no spores remaining in the tissue at the growth increment as is so often encountered in modern fungi. Dendrophyses (Donk, 1964; Smith, 1966) (Plate VII, d) are found only within the region of the hymenium. They are not freely dispersed in the hymenium as in a modern fungus, but appear to line the inner walls of large thin-walled generative hyphae.

5.4. Additional specimens

5.4.1. Fossils: morphology

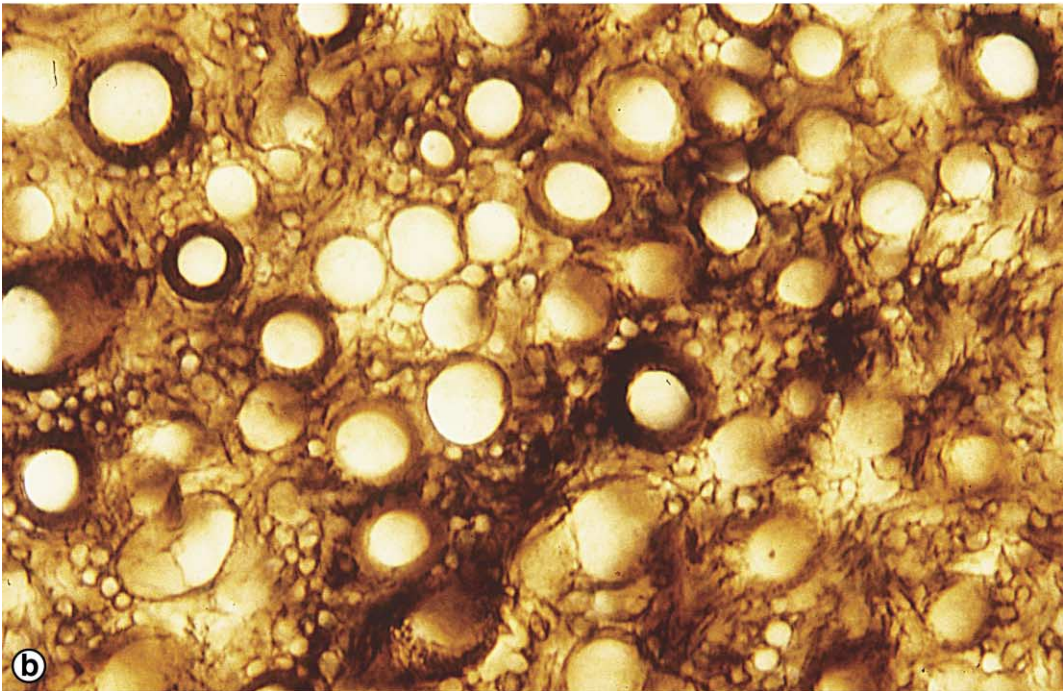
Any descriptions proposed for the morphology of a sporophore such as that represented by *Prototaxites* are confronted with the problem of its size. A specimen observed in Saudi Arabia was 1.37 m in diameter at the base, 5.3 m long, and 1.02 m in diameter at the upper end; the apex was missing (Fig. 14a). The dimensions of another large specimen found in a quarry on Skunnemunk Mountain, New York State, according to varying reports (Ries, 1897; Nevius, 1900; Prosser, 1902), was only 34 cm at the base, 8.83 m long, and 21 cm at the upper end. Clearly it was a very narrow specimen. Its maximum length was

recorded before a section was given to Professor Hollick of Columbia University, New York and before souvenirs were taken by local collectors. A section about 2.13 m long was recovered and that specimen is in the collections of the New York State Museum, Albany New York Catalog No. 160/1, Serial No. 14000090.

Specimens 91 cm (Fig. 4) in diameter and in one instance 2.13 m long (Fig. 5) were described by Dawson (1869a, 1871). Bahafzallah et al. (1981) reported ‘logs’ of *Prototaxites* 0.5 m in diameter and about 2 m in length in the Devonian of northwestern Saudi Arabia. The writer had the opportunity to visit the occurrences in Saudi Arabia and observe the specimen illustrated here in Fig. 14a, which, at this time, is the largest individual on record. If the prejudice toward the remarkable size attained by the genus is put aside, hypotheses may be presented in additional descriptions.

Hypothetically, the mycelium of *Prototaxites* was very large and permeated the soils over extensive areas of the land surface. Fossil evidence has not been found of such an extensive mycelium for *Prototaxites*. However, a small specimen was discovered in which fragments of vascular plants are embedded in the tissue and are invaded by the hyphae (Plate VIII, 1,2). That specimen is interpreted as a fragment of the mycelium as opposed to a fragment of the sporophore.

Portions of the sporophores occur as drift, either as single ‘logs’ or as fragments associated with remains of vascular plant debris. Hypothetically, with the evidence at hand, the morphology, the habit, of the genus was that of an unbranched columnar shaft on a spreading base supported by large rhizomorphs. There is no evidence of branches or appendages even though Dawson envisaged broad, flat leaf-like structures on the upper parts of his reconstructed tree (Fig. 10). He mentioned the possibility that small protuberances or punctations seen on surfaces of some specimens represented leaf traces. Such a surface is shown in Plate VIII, 3, which is a weathered surface tangential to the outer margin of a growth increment. The protuberances or punctations are tangential views of the ‘medullary spots’ or ‘rays’ described by Penhallow (1889, 1893). The spaces are partially filled with clusters of coltricioid hyphae and possibly with mucilaginous substances all of which are preserved by finely crystallized chalcedonic quartz differentially



weathered from the surrounding tissues. Their structure is shown in Plate V, 1a,b and Plate VIII, 13,14.

Prominent growth increments in transverse sections (Plate VIII, 4,5) (the ‘growth rings’, ‘annual rings’ in earlier interpretations) generally, are uniformly concentric in complete, round sections of the sporophore but may also develop eccentrically. The eccentric growth appears, in part, to be reactions to healing of external wounds (Plate VIII, 5,6).

5.4.2. Fossils: anatomy

Sections of the specimen from GSC Loc. 5388, as observed in SEM, exhibit the same morphology and anatomy of the tissue as seen in “Specimen No. 5”. Skeletal hyphae, in longitudinal view, are very long and show no branching, and, in transverse section, are quite well strengthened by thickening of the cell walls (Plate VIII, 7,8). Generative hyphae, in transverse section, are as large in diameter as the skeletal but are thin-walled (Fig. 14b, Plate VII, 8). Binding hyphae form a dense meshwork between the skeletal and generative hyphae (Plate VIII, 7,8) and in longitudinal view are shown on a surface of a skeletal hypha (Plate VIII, 9) paralleling the appearance in the neotype (Plate VI, c) where the same morphology is evident.

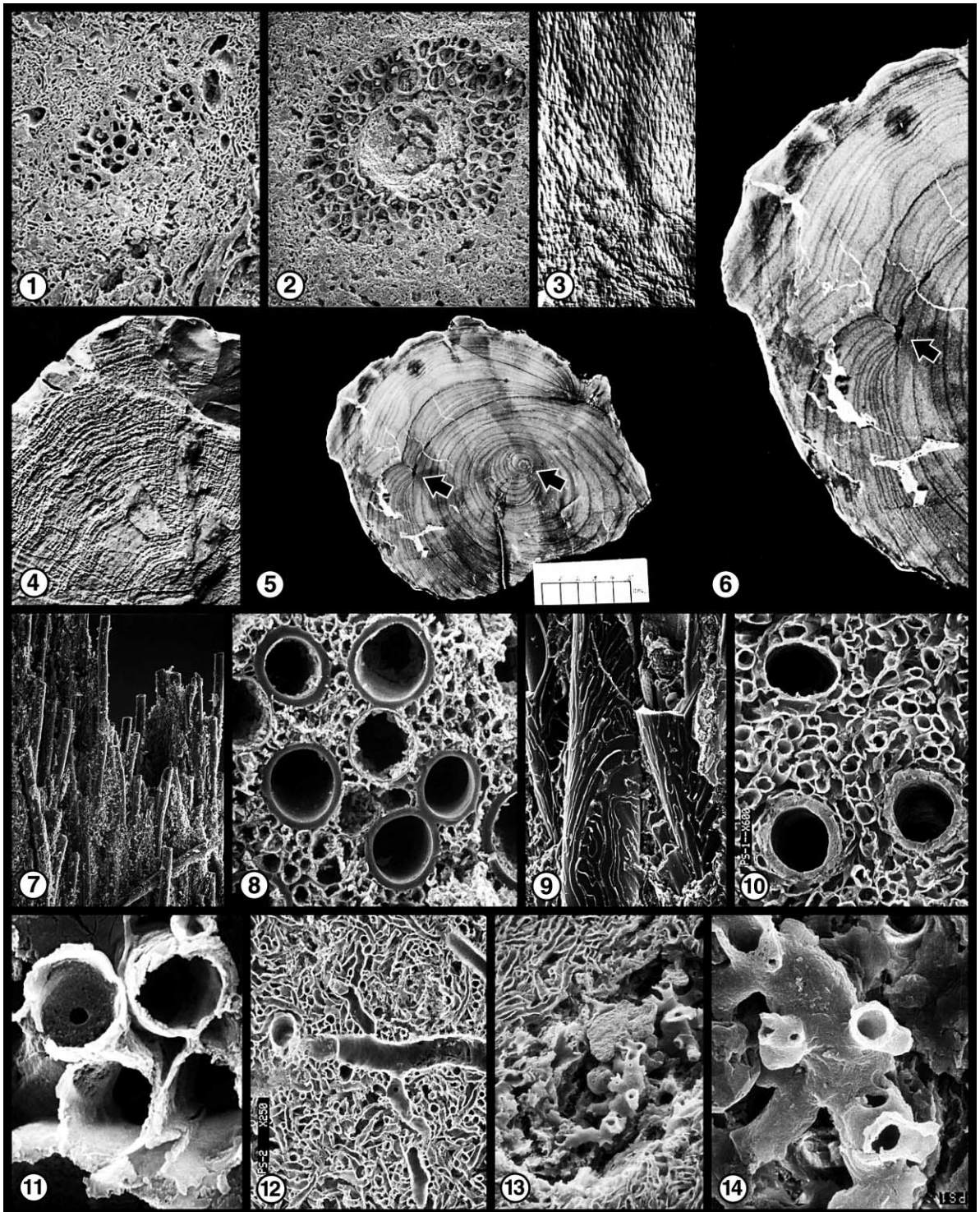
The preservation of the anatomy of *Prototaxites southworthii* (Arnold, 1952), is exceptional. Demineralized sections of the species are especially valuable in comparative studies with the tissues of *Prototaxites loganii*. Although specific differences are not substantial, synonymy is not considered at this time. The sections of *P. southworthii* are illustrated here in SEM photomicrographs as support for the definition of the genus. A transverse section (Plate VIII, 10) illustrates all three of the hyphal forms, the large thick-walled skeletal hyphae, a large thin-walled generative hypha, and the meshwork of small thin-walled binding hyphae. It compares well with Fig. 14b of *P. loganii*. The presence of septae with pores

in binding hyphae is illustrated by a single hypha (Plate VIII, 11). In longitudinal section the morphology and branching of a generative hypha (Plate VIII, 12) is well defined, and compares well with that seen in the neotype (Plate V, 1a). In transverse section, at different magnifications, the form of the coltricioid branching of a generative hypha in a ‘medullary space’ is clearly demonstrated, along with the small pores at the tips of the hyphal branches (Plate VIII, 13,14). With light photomicrography, such details of ‘medullary spaces’ are not so easily illustrated for *P. loganii* in the neotype. However, generative hyphae branch profusely on entering a space (Plate V, 1a) and small hyphal branches crowd to nearly filling the space (Plate V, 1b).

Anatomy is very well preserved in the specimen of *P. loganii* from New Brunswick (Plate VIII, 5). The anatomy at the center of a sporophore is rarely so well preserved as it is in this specimen (Plate IX, 1). Generative hyphae radiate in all directions from the dense central core of skeletal hyphae. Spaces with coltricioid clusters of hyphae are more abundant in the first growth increment than in the subsequent growth increments. Details of the anatomy of the neotype are repeated in this specimen. However, only the illustration of an incomplete clamp connection in a generative hypha (Plate IX, 2) is chosen as a better image of an incomplete clamp connection than that observed in the neotype (Plate VI, 1a). Incomplete clamp connections and conjugative hyphae are rare in the neotype as well as this specimen.

The specimen of *Prototaxites* with fragments of plant remains embedded in its surface (Plate IX, 3,4) is presented to support the interpretation that *Prototaxites* was a terrestrial fungus. The specimen is from the Upper Devonian of Australia and anatomically identified with the genus. It is a round portion of a sporophore approximately 19 cm in diameter and 23 cm long. Plant fragments are embedded in the surface of the specimen (Plate IX, 3), one of which

Fig. 14. (a) *Prototaxites*. The largest specimen known at this time. It was discovered by Charles Meissner of the United States Geological Survey Mission in Saudi Arabia and brought to the writer’s attention who was privileged to visit the site and corroborate the identification of the genus. The log was 17 ft long, with the top missing, and 4 ft in diameter at the base. It had been compressed slightly and was silicified throughout. The specimen was thoroughly documented with photographs. The photograph here was taken by Dr Meissner to whom I am indebted for the gift. (b) *Prototaxites loganii* Dawson. Transverse section of the well preserved tissue in “Specimen No. 5”. All three hyphal forms are clearly illustrated; large thick-walled skeletal hyphae, large thin-walled generative hyphae, and small thin-walled binding hyphae. The image is fully diagnostic for the identification of the species in transverse section $\times 600$.



is identified as a lycopsid (Plate IX, 4). The anatomy of the fragments was completely replaced by limonite without preservation of definable vascular structures. The identification of one of the fragments as a lycopsid is based on the remnants of acicular leaves preserved along the margins of the stem.

5.4.3. Non-fossil: anatomy

The orderly radial files of contiguous thin-walled cells in the transverse section of a stipe of *Laminaria* (Plate IX, 5) are wholly different from the openly spaced and varied anatomy of the cells in the tissues of *Prototaxites* (Plate II, 1). In longitudinal section of the stipe (Plate IX, 6) the cells are of wholly different morphology with thin, contiguous walls and each generally the same length vertically. The section was taken close to the base of the stipe and includes a tissue of agglutinated cells which may give added strength to the stipe. There is no close similarity between the anatomy of *Laminaria* and *Prototaxites*.

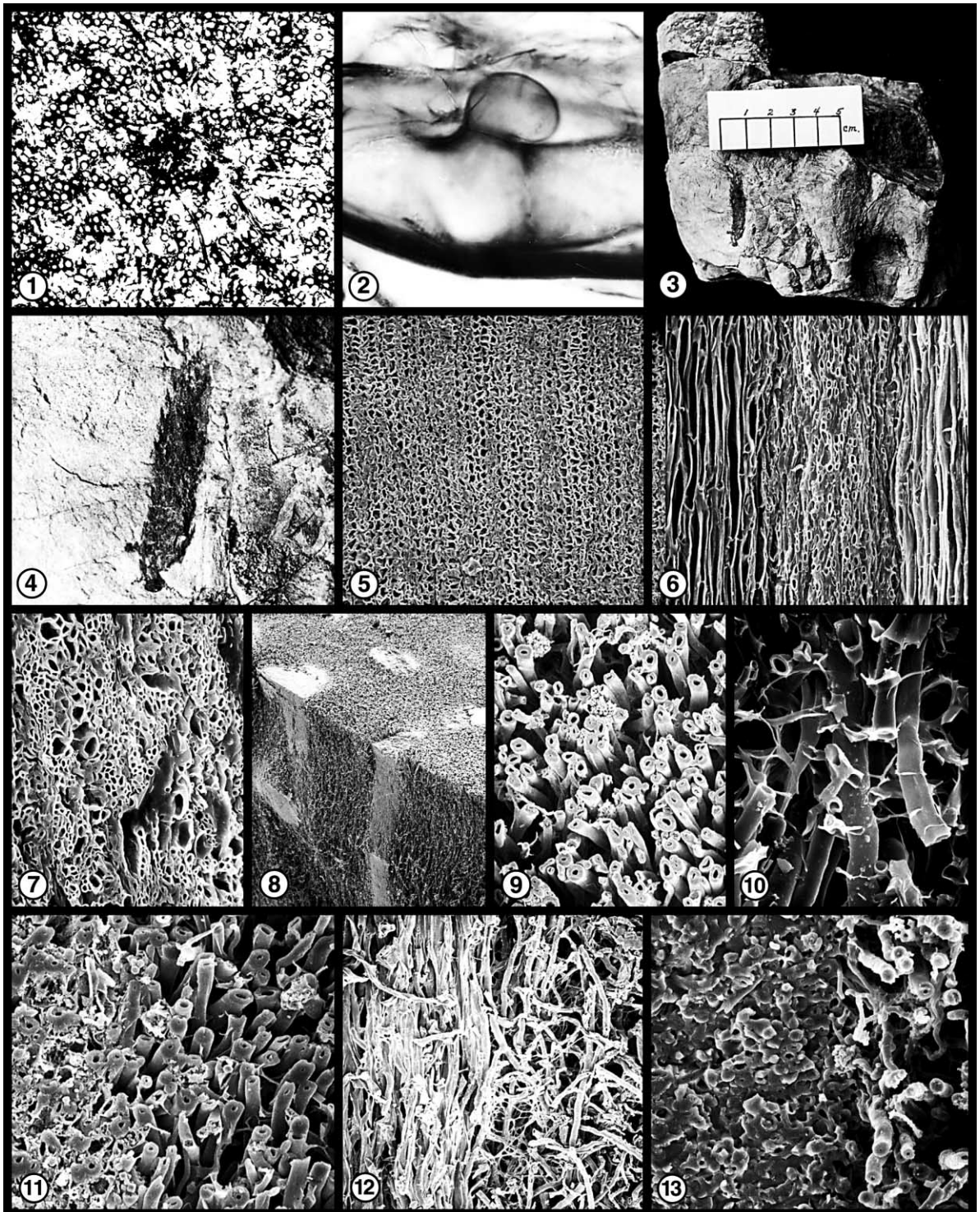
Tissue from the stipe of *Lactarius* sp., in cross-section (Plate IX, 7), is similar in appearance to the tissue of *Prototaxites*, however no thick-walled skeletal hyphae are evident while generative and binding hyphae form the main body of the tissue. There are very large hyphae which are laticifers and when freshly cut, under internal pressures, exude a milky juice which can flood the surface of the section. The

tissue of the stipe of *Lactarius* is soft in texture, lacking the heavily thickened skeletal hyphae so prominent in the structure of *Prototaxites*.

The texture of *Ganoderma lucidum*, when dry, is woody. Sections cut through the massive tissues of the sporophore (Plate IX, 8) reveal heavily thickened skeletal hyphae (Plate IX, 9) loosely held together by highly branched generative hyphae and very small binding hyphae (Plate IX, 10). The tissue is much less densely filled with binding hyphae than one sees in *Prototaxites*. Areas in the tissues of *Ganoderma* (Plate IX, 8), resembling the ‘medullary spots’ in *Prototaxites*, comprise masses of hyphae embedded in hard resinous substances (Plate IX, 13), which may strengthen the sporophore and may represent deposition of metabolic wastes. Growth increments in the body of *Ganoderma* are subtly marked by color differences on the exposed upper surface of the sporophore and are more subtle in transverse sections, particularly when sought for viewing in the SEM. The margin of an increment in *Ganoderma* (Plate IX, 11) is very narrow and similar to that in *Prototaxites*. The diameters of the skeletal hyphae decrease, their walls are more heavily thickened, and they are more closely packed. A radial longitudinal section through a growth increment (Plate IX, 12) reveals the change from loosely organized tissue to compact tissue at the margin. The same

PLATE VIII

- 1,2. Etched transverse sections of *Prototaxites* with vascular plant fragments as inclusions. Specimen from Locality ‘D’. SEM photomicrograph; $\times 150$. (3,4) Specimen from the Bordeaux Quarries, Gaspé.
3. Weathered surface tangential to growth increment. These are the punctuations that Dawson thought were possibly leaf traces. They are the spaces (“medullary spots or rays”) differentially filled with a form of quartz which is more resistant to weathering than the surrounding tissues. The surface pattern is useful in recognizing specimens in the field.
4. Weathered transverse section with differential weathering of the growth increments and radiating spaces which strongly suggests the appearance of similarly weathered wood; $\times 0.5$.
- 5,6. Etched transverse surface of specimen from New Brunswick. The central core is well preserved (arrow), eccentric growth of the increments is quite obvious, and the healing of a wound (arrow) is remarkably preserved; $\times 0.28$.
- 7–9. Specimen in which the tissues are carbonized but not mineralized.
7. Longitudinal view in SEM of fractured surface with skeletal hyphae prominent and binding hyphae forming a meshwork; $\times 115$.
8. Transverse section showing all three hyphal forms; $\times 600$.
9. Longitudinal view in SEM of the binding hyphae closely adhering to the surfaces of the larger hyphae; $\times 600$.
- 10–14. *Prototaxites southworthii*.
10. Transverse section showing all three hyphal forms; $\times 600$.
11. Binding hypha with septal pore; $\times 1200$.
12. Actively branching generative hypha; $\times 125$.
13. Space “medullary space-dot” with coltricioid cluster; $\times 150$.
14. Higher magnification of the coltricioid cluster showing open tips of the branches; $\times 500$.



textural change is evident in the longitudinal section of *Prototaxites* (Plate II, 1a,b). The growth increment in *Prototaxites*, however, marks the formation of an amphigenous thickening hymenium, while the growth increment in *Ganoderma* is the supportive structure for the subtending poroid hymenium.

6. Ontogeny of the sporophore

A hypothetical description of the ontogeny of the sporophore of *Prototaxites* suggests that it began with the production of a mound of generative hyphae arising directly from some predetermined site on the mycelial mass (Fig. 12). The mound was probably 0.7–1.0 cm in diameter as suggested from the measurable diameters of the central cores of specimens from Gaspé and New Brunswick, Canada, northern Saudi Arabia and north Queensland, Australia. Upward growth of the generative hyphae continued, probably as a phototropic response, which is typical in the formation of a sporophore among many modern fungi. This primordial conico-cylindric shaft was the initial stage in the development of the sporophore in *Prototaxites*. Growth was perennial with additions of amphigenous thickening hymenia resulting in concentric ‘growth rings’ or increments to the diameter of the sporophore (Fig. 12). Nutrition for the continued growth of the sporophore is suggested as saprobic from a very extensive absorptive mycelium. The mycelium grew proportionately large at the

base of the sporophore forming large anchoring rhizomorphs. Growth probably was uninhibited and non-competitive with the vascular flora. A major limiting factor to its gigantism would have been the success or failure of the mycelium to supply adequate moisture and nutrients. The growth increments cannot be counted to determine the relative age of an individual as one would count growth rings in the tissue of a temperate woody plant. Instead, they indicate frequent reproduction under ideal growing conditions. Perennial fungi may develop more than one increment during a growing season. I personally have seen as many as four increments added to the growth of a large bracket fungus in one season.

7. Discussion

Prototaxites was the most bizarre and, for the greater part of its existence, the largest and tallest element in the terrestrial floras of the Devonian. Its height would have dominated the landscapes during the Early Devonian (Fig. 15) and early Middle Devonian but would have given way to the shrubs, arborescent lycopsids and progymnosperms in the Late Devonian. It is useful as an index fossil spanning the whole of the Devonian but cannot be used in determining smaller time/biostratigraphic units.

The redescription of *Prototaxites* as a fungus, quite obviously, has required a change in terminology from that which has been used in the past. Only the terms

PLATE IX

- 1,2. Specimen from New Brunswick.
2. Transverse ground thin-section of the center of the sporophore with generative hyphae radiating in all directions; $\times 35$.
3. Radial longitudinal section with incomplete clamp connection; $\times 900$.
- 3,4. Specimen from Queensland, Australia. (3) Surface with embedded plant fragments.
4. Embedded plant fragment with acicular leaves suggesting lycopsid affinities; $\times 1$.
- 5,6. Stipe of *Laminaria*.
5. Transverse section showing orderly contiguous rows of cells; $\times 50$.
6. Longitudinal section with relatively short contiguous cells and modified supportive cells at the center; $\times 50$. (7) Specimen of *Lactarius*. Transverse section of the stipe; prominent generative and binding hyphae interspersed with large lactiferous hyphae; $\times 250$.
- 8–13. Specimen of *Ganoderma lucidum*.
8. Transverse and longitudinal section through the body of the sporophore; $\times 38$.
9. Transverse section of the fundamental tissue of the sporophore, largely of heavily thickened hyphae; $\times 750$.
10. Longitudinal section through the fundamental tissue; small numbers of binding generative hyphae; $\times 825$.
11. Transverse section at growth increment; change in density and size of hyphae mark the transition; $\times 750$.
12. Radial longitudinal section at a growth increment; obvious change in anatomy; $\times 350$.
13. Contact point along margin of thickly agglutinated tissue; $\times 750$.



Fig. 15. *Prototaxites*. A hypothetical reconstruction of the habit and habitat of the genus in Early Devonian time. It towered above all other land-life and had little competition for survival except from the burgeoning populations of fungivorous insects. Painting by Mary Parrish, Department of Paleobiology, Smithsonian Institute.

mycelia, mycelium, myceloid, hyphae and hypha have been occasionally used for want of algal terms in describing the anatomy of the genus. Generally, the descriptions of the cellular components of the tissue have included “meshwork composed of large tubes and small tubes” or “large thick-walled tubes in a matrix of small tubes”, or “tissue consisting of only two kinds of cells, large thick-walled and small thin-walled”. Based on the classification of the anatomy of a basidiocarp proposed by Corner (1932) (= sporophore of basidiomycetes), I have defined, in his mitic system, three types of hyphae from among the ‘tubes’ in earlier descriptions. Thus, the sporophore of *Prototaxites* is trimitic consisting of skeletal hyphae (also called ‘mycosclerids’; Wright, 1955), generative hyphae, and binding hyphae, for which I have given additional detail in the body of the descriptions. A hyphal form to which I have referred as coltricioid is a derivative of a generative hypha as found in the genus *Coltricia perennis* (*sensu* Corner, 1991). The hypha branches profusely and produces intricate clusters of thin-walled, septate lobes which, in my view, parallel the structures produced by the generative hyphae in the spaces, “medullary dots or rays”, in *Prototaxites*. This may be a misjudgment on my part, particularly in the presence of pores at the tips of the lobes of the hyphae, a character not described by Corner, but which I carry further by suggesting that

the coltricioid hyphae in the spaces in *Prototaxites* are secretory. They fill the spaces with hydrophilic or, at least, mucilaginous substances as a means of retaining moisture in the tissues. The space surrounding the coltricioid clusters is empty when the tissue is demineralized (Plate VIII, 13,14) but filled with organically stained quartz when viewed in ground thin-sections (Plate V, a,b). I have also illustrated dendrophyses (Plate VII, d) which are sterile hymenial accessories in basidiomycetous fungi. Growth increments (‘growth rings’) have received little attention other than to suggest that they represent some form of perennial growth. I have discussed their anatomy and have defined them as the site of the hymenium, which, in turn leads me to define the hymenium as amphigenous as one finds in the species *Clavaria pistillaris* (Corner, 1950). My hypothetical reconstruction of the ontogeny of the sporophore of *Prototaxites* is forthrightly based on that species. I am not fully satisfied with my definition of the reproductive bodies, however, the structures recur everywhere through the hymenium and appear to be morphologically parallel to the sterigmata that one might find in a modern basidiomycete. As an anatomist–morphologist of vascular plants this discourse has been an adventure into another discipline which is also exciting and demanding in clarity of terminology. Perhaps the most useful sources for definitions of terms for use

in the description and interpretation of the structural elements preserved in *Prototaxites* are contained in Ainsworth and Sussman (1965, 1966a,b), Hawksworth et al. (1995) and Alexopoulos et al. (1996).

Historically, subsequent to Dawson's original descriptions, *Prototaxites* has been subjectively identified with the algae, and yet, on a worldwide basis, the occurrences of the genus are in fluvial sediments. There are fewer occurrences of specimens in marine sediments (e.g. Kräusel, 1936; Kräusel and Weyland, 1934; Penhallow, 1893; Read and Campbell, 1939; Arnold, 1952; Chitaley, 1992), and those are generally in black shales that may represent deposition of fine-grained sediments in sea basins far removed from land surfaces. Dawson, from the very beginning of his descriptions and discussions, insisted that *Prototaxites* was a terrestrial plant and reconstructed it as a tree (Fig. 10). How was it possible to ignore all of the evidences of its occurrence in terrestrial sediments, in direct associations with vascular plants, and to follow by subjectively proclaiming that the genus was an alga (Carruthers, 1872); a terrestrial alga the magnitude of a tree, on land? From the outset of that proclamation and through all subsequent discussions of the genus, there has been little or no objective analysis of the anatomy of the algae with which *Prototaxites* has been classed. Transverse and longitudinal sections of the stipe of *Laminaria* are illustrated (Plate IX, 5,6) for comparison and contrast with the transverse and longitudinal sections prepared from "Specimen No. 5" of *Prototaxites* (Plate III, a,b). Seward (1898) and Schweitzer (1983) illustrated transverse sections of *Laminaria* and compared them favorably with the transverse section of *Prototaxites*. The transverse sections of *Laminaria* show contiguous rows of radially aligned cells while in *Prototaxites* the hyphae are free, randomly arranged, and held in position by the meshwork of smaller hyphae. Cells in the longitudinal section are uniformly relatively short, thin-walled and contiguous in *Laminaria* while the principal structural hyphae (skeletal — 'mycosclerids', *sensu* Wright, 1955) in *Prototaxites* are extremely long, thick-walled, aseptate and not contiguous. In my opinion, *Prototaxites* does not have the structural anatomy nor morphology of an alga. Chemotaxonomic analyses by Niklas (1976) concluded that the chemical constituents found in *Prototaxites*, certain fatty acids, cutin and suberin, differed from modern

algae but did not preclude an algal affinity. Lack of evidence of lignified supporting structures in the otherwise weak tissues and presumed erect habit would have imposed considerable stress in a terrestrial habitat. The presence of the compounds associated with a terrestrial habit raised the possibility that the genus could survive on land but did not prevent reiteration that the algal affinity was still possible. The anatomy, morphology and occurrences cannot be refuted so easily.

Schmid (1976) illustrated transmission electron microscope (TEM) sections obtained from demineralized hyphae of *Prototaxites southworthii* in which septal pores were evident. That was the first time that such an anatomical characteristic had been demonstrated in the genus and which served to suggest an affinity with the Fungi. The relationship was denied by the mycologists whom Schmid consulted even though the morphology of the pores was very similar to that of the septal pores in basidiomycetes. Median longitudinal sections of the septal pores in *P. loganii* were not obtained in ground thin-sections for direct comparison with TEM sections of *P. southworthii*. However, light microscope photomicrographs of septae in *P. loganii* compare well with the SEM photomicrograph of *P. southworthii* shown here. The purpose of the present study is to augment the anatomical evidence in support of the relationship of *Prototaxites* to the Fungi.

The presence of a fragment of "Specimen No. 5" in the Paleobotanical Collections of the U.S.N.M. was fortuitous. Penhallow's original thin-sections are missing and new sections could be prepared from the fragment. The slides prepared from the fragment of the neotype are the basic supportive components in the redescription of *Prototaxites*. Observations of the anatomy have involved direct comparisons with the anatomy of modern fungi and have required very little interpretation. The preservation of the cellular detail in the specimen is exceptionally good.

The interpretations for which support has been most difficult to obtain for describing *Prototaxites* as a fungus are the morphology of the genus as a whole, its nutrition, its habitat, and method of reproduction. The gigantic size has been the principal barrier to describing the genus as a fungus. Church (1919) commented that it could be considered a fungus, only to be ignored. The modern 'woody' fungus

Fomitopsis officinalis is reported to have lengths to 1 m and its wood-like texture lent itself to carving of totem figures by the shamans among the Northwest Coast Native Americans (Blanchette et al., 1992). *Prototaxites* was taller and generally greater in girth but might *Fomitopsis* attain larger sizes were it left undisturbed as was the situation with *Prototaxites*? Quite obviously I do not find the size to be a negative factor in defining the genus.

The nutrition of the genus with such a large sporophore was strongly questioned over the years and had little support for an answer until details were reported of the sizes of mycelia among species of *Armillaria* like *A. bulbosa* (Smith et al., 1992) which covered 15 ha and was estimated to be 1500 years old. Perhaps the mycelium of *Prototaxites* was even larger, but we do not have the fossil evidence for it. Sporophores produced on the mycelium of *A. bulbosa* are far smaller and more numerous than the huge and lesser numbered ones produced on the mycelium of *Prototaxites*. The longevity of *Prototaxites* in the fossil record, ± 50 million years, nearly the whole of the Devonian, gives one pause on how to explain such success in terms of the successes and failures among modern fungi. I will approach the subject in future discussions of the species of *Prototaxites*.

An extensive mycelium of *Prototaxites*, assumed here to have been a saprobe, would have obtained nutrients from large quantities of organic debris that had accumulated in well stabilized sites on flood plains of large streams. Evidence for its saprobic nutrition was obtained from the fragment described above in which debris of vascular plant tissues are embedded and invaded by hyphae (Plate VIII, 1,2). My opinion is that the land surface was far more densely covered by vegetation than heretofore assumed. This opinion is based on the allochthonous coals found on the south shore of Gaspé Bay, Quebec, as reported by Logan (1843) and Dawson (1859, 1869, 1871), and which remain exposed in that section of strata to the present time. Thin, allochthonous coaly layers as well as some richly carbonaceous zones of autochthonous plant debris occur on the north shore of Gaspé Bay. These evidences of significant quantities of plant debris suggest that there were adequate sources of nutriment for the growth of an extensive mycelium and the subsequent production of a large sporophore such as seen in *Prototaxites*.

Additional evidence supporting the hypothesis of saprobic nutrition in *Prototaxites* comes from the occurrence of the genus on the south shore of Chaleur Bay, New Brunswick (USNM Loc. #14256). The specimen (USNM #510099; Plate III, 5,6) was in direct association with a highly altered shale containing coaly masses of spinous plant remains (aff. *Sawdonia* spp. or *Psilophyton* spp.) The effects of the igneous intrusion above the shale stratum altered the preservation of the vascular plants but did not alter the silicified tissues of *Prototaxites*. This richly organic stratum may have been the site for the growth of part of the mycelium, however such delicate structures as mycelia may have been obliterated by the effects of the igneous intrusion. No hyphae have been observed in thin sections nor in macerations of the matrix. The occurrence of the genus in association with such an organically rich stratum may lend credence to the saprobic nutrition of the genus although evidence of an extensive mycelium is lacking.

Reproduction has been the most difficult to characterize in *Prototaxites*. In my early attempts to understand the nature of the borders of the growth increments I concluded that they represented the hymenium, the spore bearing layer of the sporophore. Ground thin-sections between 30 and 60 μm in thickness were prepared longitudinally and tangentially to growth increments. Recurring structures, viewed under oil immersion, appeared to be clusters or rows of inflated sterigmata with elongate spicula (Fig. 13; Plate VII, a–c). I have not been able to determine what other structure they might represent within a hymenium. Basal cells, metabasidia, in association with the structures interpreted as sterigmata, were not distinguishable from among other remnants of collapsed cells. Their disruption or collapse may have been the result of the pressures and crowding by the intrusive growth of mycelia through the hymenium as expanding growth of the sporophore continued. Both the morphology and site of occurrence of the structures interpreted here as sterigmata suggest that they may be described as remnants of reproductive structures. They resemble most closely parts of reproductive structures found in basidiomycetes, and a hypothetical reconstruction of a basidium bearing them is offered in Fig. 13d. No spores were found in the prepared sections, such might be expected since

the latest formed hymenium would have been exposed on the surface of the sporophore and unprotected from winds and rain.

There is evidence of very active fungivory in the specimen of *P. southworthii* described by Arnold (1952) from the late Upper Devonian. That activity has been corroborated in a second, undescribed specimen in the USNM Paleobotanical Collections (USNM #510202) which was donated by Mr Southworth after whom the species was named. Sections cut from the specimen reveal mazes of galleries containing coprolites and frass composed only of hyphal fragments left by the feeding activities of an unknown insect. The feeding took place while *Prototaxites* was living as evidenced by the regrowth of hyphae into and sealing of many of the galleries. Was it fungivory that drove the genus into extinction at the end of the Devonian? Perhaps its habit became greatly reduced in adaptation to a new habitat among the shrubs and forests which were rapidly dominating the landscapes. May it have changed its source of nutrition? Those questions cannot be answered readily from the fossil record of organisms so fragile as the fungi.

If fragility is a problem in the preservation of a fungus as a fossil, why is it that *Prototaxites* is so well preserved? In the stratigraphic section in Gaspé Bay, a 'log' is commonly found, in place of burial, resting on what had been mats of vascular plant remains. The surrounding plants are compressed and carbonized while *Prototaxites* is the only specimen in which cellular details are preserved. The preservation of the genus was the result of impermeation by ambient silica-rich solutions in the sediments in which it was buried. The subsequent process of silicification of its tissues parallels some of the stages in the petrification of woody tissues. Unfortunately, the silicification of the two tissues cannot be compared fully because of the differences in the organic composition of their cell structures. Most of the studies of the processes of petrification have traced the reactions between silicic acid and the cellulose in vascular tissues (Carson, 1991; Karowe and Jefferson, 1987; Leo and Barghoorn, 1976; Siever and Scott, 1963; Sigleo, 1978; Stein, 1982).

The openly porous but firm structure of *Prototaxites* suggests that it would not be easily compressed and could become waterlogged quite readily when buried in sediments saturated with water. Anoxic

conditions would slow the activity of most organisms of decay. Degradation of various cell contents and structures would begin and the soluble by-products would enter the ambient water. Degradation of the proteinaceous contents of the hyphae might have been a source of ammonia and ammoniacal compounds. Their addition to the ambient groundwater, in which salts of alkaline earth metals were probably already present, would have increased the alkalinity of the solution to a level conducive to an increase in the concentration of dissolved silica. The relatively concentrated solution of silica migrated into the tissues and met with gradual acidic changes in pH whereupon precipitation of the silica began. Initially the precipitate covered the walls of the hyphae. As the enrichment of the solution of dissolved silica continued, the precipitation of silica in the tissues filled the voids and embedment was complete. The initial form of the silica was amorphous but through time crystallization occurred and the end member was low quartz. The quality of preservation of cell details depends on the size and morphology of the crystals, and one can find all levels of crystal size in the tissues of *Prototaxites*. *Celluloxylon* (Dawson, 1881a,b) was a genus based on a fragment of *Prototaxites* in which the crystals were of such large sizes that their development disrupted the tissues completely. They were separated from one another by thin films of carbonized residues of tissues, and in ground thin-sections produced an image resembling cell structures. Silica precipitated in the softened mucilaginous thickenings in the skeletal hyphae and subsequently crystallized. Schmid (1976) illustrated a skeletal hypha in which bladed crystallization of quartz disrupted the otherwise uniform texture of the thickening on the hyphal wall. It is an unusual example of mineral emplacement in an organic substance.

As a brief addendum to the story of Dawson's specimens marked with a large white #5, there is a second specimen in the USNM Paleobotanical Collections. It is in the Paleobotanical Collections of the American Museum of Natural History which were given totally to the USNM in exchange for a large and comprehensive collection of invertebrate fossils in 1955.

The early history of that paleobotanical collection includes an exchange between Dawson and the museum (Dawson, 1882c). Among the several specimens we

can attribute to Dawson's exchange are two fragments of *Prototaxites*. One is marked with an obvious #5 and resembles some of the others collected by Dawson in 1869 which are housed in the collections of the Peter Redpath Museum. The other specimen is from the Bordeaux Quarries (Dawson, 1881a). The second #5 specimen in the USNM collections is mentioned primarily so that it will not be confused with the fragment of the neotype.

8. Conclusion

Hypothetically, *Prototaxites* was heterotrophic, absorptive, and saprobic in nutrition; possessed an extensive filamentous perennial soma of persistently dikaryotic, septate and aseptate hyphae; reproduced by spores on an enormous phototropic amphigenous sporocarp or possibly by fragmentation of the soma.

The hypotheses may never be satisfied from the fossil record but the existence of a huge organism faithfully preserved by the impermeation of minerals has been the source of anatomical data which are tangible. The anatomy of the genus compares favorably with that of the present day woody fungi but its size, as mentioned before, has deferred consideration of any relationships. Thorough analysis of the cell structures in well preserved specimens can only lead to the conclusion that *Prototaxites* is an extinct form of fungus with sporophores that exceed comparable forms living today and exceed the imagination as well. There was a time when the size of the dinosaurs was not readily conceived nor believed, but as knowledge of their structures, habits and habitats increased they soon became 'real'. They are now accepted, so much so, that young children identify them by genus well before they are doing multiplication tables. So is it not possible to accept *Prototaxites* as a gigantic fungus on the evidence at hand? It survived through nearly the whole of the Devonian Period where, at the end, it was probably driven into extinction by predatory fungivores and competition with larger vascular plants. Once more, hypotheses.

However, the tangible evidence in the structures preserved in *Prototaxites* support the interpretation of its classification with the Fungi. In spite of its bizarre form, it can become credible as more and more evidence is described for the diversity and anti-

quity of the Fungi. Recent discovery and description of an exceptionally well preserved ascomycete in the Lower Devonian Rhynie Chert (Taylor et al., 1999) establishes a remarkable lineage with the Euascomycetes, members of which may be cursed today as plant pathogens or valued for their products of fermentation. In another report, the remains of fungi even older than the Rhynie Chert ascomycete and the Gaspesian basidiomycete, *Prototaxites*, are described from a mid-Ordovician dolomite, which is about 460 million years old (Redecker et al., 2000). The fossils are compared with the Glomales of the Zygomycetes, a group of fungi that are widely dispersed today as symbionts with terrestrial plants. Their greatest significance is the part that they may have played in facilitating the colonization of land by plants. These reports are the beginnings in discovery of tangible fossil evidence that suggests a very early origin and subsequent early diversification of successes or failures among the Fungi.

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