Septal Pores in *Prototaxites*, an Enigmatic Devonian Plant

Abstract. Prototaxites southworthii, *an Upper Devonian, nonvascular plant of unknown affinity that is commonly ascribed to the brown algae, has filaments with septal pores. These superficially resemble various pores and pit connections of the higher algae and fungi and suggest that very elaborate cell wall structure had evolved by Devonian times.*

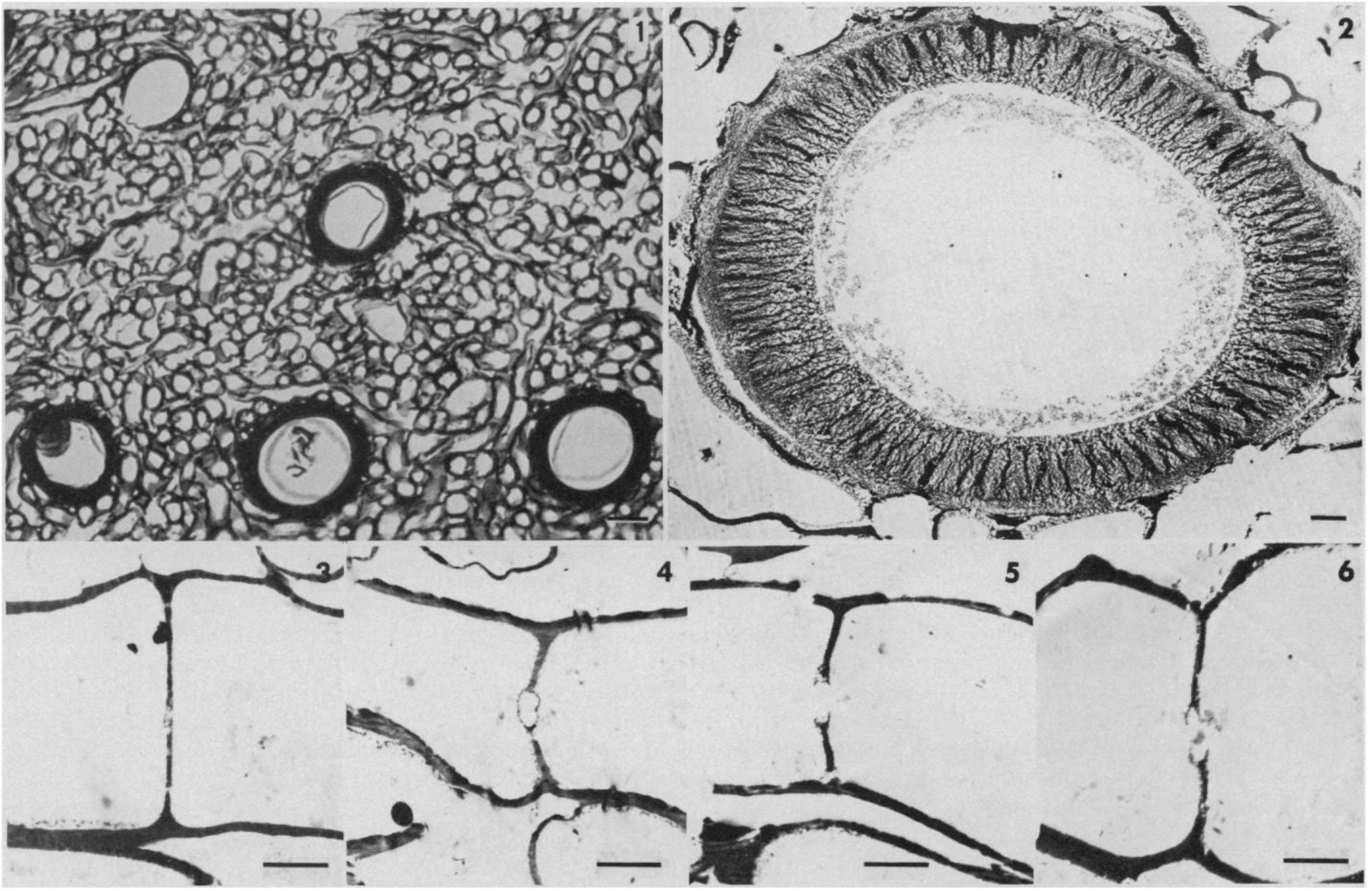
The affinities, habit, and habitat of *Prototaxites*, a Silurian-Devonian genus that was described from Gaspé, Canada, by Dawson in 1859 (*1*) and named because of a fancied resemblance to the tracheids of the modern yew (*Taxus*), has been the object of considerable discussion and speculation. Since Carruthers' work in 1872 (*2*), any affinity of *Prototaxites* with the conifers or other vascular plant groups has generally been disclaimed (*3*). The genus is commonly classified with the algae (*2, 4, 5*), usually, and more specifically, in or with the Laminariales and Fucales of the brown algae (*5, 11*). Resemblances have also been noted between *Prototaxites* and the Siphonales (especially Codiaceae) of the green algae (*2, 11*). Other workers believe that *Prototaxites* cannot justifiably be assigned to any group of recent seaweeds, and thus classify the plant in the Nematophytales described by Lang (*6–8, 10, 11*) or the Algomycetes described by Kräusel (*12*), groups that occupy an undetermined position in the plant kingdom. Finally, a fungal (*13*) or bryophytic (*14*) nature for *Prototaxites* has not escaped the imagination of botantists. Conversely to this furor, some researchers have not entered the systematic fray (*15*).

Closely correlated with the problem of taxonomic affinity of *Prototaxites* is that of habit and habitat, whether marine (benthic or littoral), brackish, freshwater, or even terrestrial (*1–13*). An aquatic and generally marine habitat has been favored, usually by the proponents of a brown algal affinity, but the modern tendency [after Lang (*7*)] is to regard *Prototaxites* as terrestrial or, at least, as emergent aquatic. The plant was a behemoth; some specimens are as much as 1 m in diameter and 2.1 m long (*10*). Contributing to the obscure relationships and nature of *Prototaxites* is a total absence of reproductive structures and laminar and attachment organs (*1–15*).

Arnold (*10*) described in detail some exceptionally well-preserved, silicified material of *Prototaxites southworthii* from Kettle Point, Ontario, Canada. I examined the same material with the use of transmission electron microscopy and chemistry (*16, 17*) in an attempt to elucidate the relations and structure of the genus. The description below modifies and elaborates Arnold's (*10*) detailed study (*18*).

Prototaxites is a large, lacunose, pseudoparenchymatous mass that consists of two main types of elements: so-called hyphae or filaments (*19*), and so-called tubes (Fig. 1). The tubes (Figs. 1 and 2) are the large elements and are 19 to 50 μm in diameter, extend indefinitely, generally in a lengthwise direction, branch occasionally, and constitute as much as 50 percent of the bulk of the tissue. The walls of the tubes are thick and striate; the electron-opaque components of the wall anastomose (Fig. 2).

The filaments (or hyphae) (Figs. 1 to 6) constitute the small elements and are 4.75 to 9.50 μm in diameter, extend generally lengthwise, branch profusely, and inter-



Figs. 1 to 6. Transections of *Prototaxites southworthii*. Fig. 1. Pseudoparenchyma with filaments and large tubes (scale bar is 20 μm). Figs. 2 to 6 are transmission electron microscope images (scale bars, 2 μm). Fig. 2. Tube with investing filaments. Figs. 3 to 6. Septal pores of filaments; Fig. 3 is of the septum in the area next to the pore; Figs. 4 and 5 are of same septal pore apparatus, Fig. 5 through aperture, Fig. 4 close to it; Fig. 6 is through another aperture.

twine with each other. A hyphal sheath, generally one cell layer thick, usually completely invests the tubes (Figs. 1 and 2). The filaments have cross walls (septa) that are often far apart (121 μm in one case), such that the filaments appear to be coenocytic. The septa are complexly perforate (Figs. 3 to 6). An apparently elliptical aperture (Figs. 5 and 6) occurs in a border that encloses a cavity (Figs. 4 to 6; Fig. 4 is a section close to the aperture). The septal pores superficially resemble the circular bordered pits of conifers, without the pit membrane and torus of the latter. Despite the numerous reports of septate hyphae or filaments in fossil algae and fungi (*20*), including such complicated structures as fungal clamp connections (*21*), there are to my knowledge no previous reports of the occurrence of perforate septa in extinct plants.

Various types of pores and pit connections occur in the septa of the extant red algae (*22, 23*) and the higher fungi (*22, 24, 25*), but these structures are sufficiently different from the septal pores of *Prototaxites* to obviate any close relationship between these taxa. The perforate septa of *Prototaxites*, however, do show a closer resemblance to the dolipore septa of many Basidiomycetes (*22, 24*) or the similar septa of certain Mucorales (*25*) than to those of other modern groups. *Prototaxites* lacks both septal plugs, which are characteristic of the red algae and some fungi (*22*), and septal pore caps (parenthesomes), which are distinctive of many Basidiomycetes (*22, 24*).

The septal pores of *Prototaxites* might represent an "evolutionary experiment," perhaps leading toward the type of septal structure that is characteristic of the more specialized algae and fungi. Alternatively, one should not dismiss the possibility of convergent evolution of pitlike systems that are comparable to those of the tracheary elements of vascular plants, especially since other members of the Nematophytales (*Nematothallus* and *Nematoplexus*) (*7, 8*) have spirally or annularly thickened tubes that simulate the water-conducting elements of the higher plants (*26*). The Silurian and Devonian are now known to have been very active periods of evolution for multifarious plant groups and structures (*26, 27*).

The large tubes of *Prototaxites* (Fig. 2) have no counterparts in the plant kingdom. Any resemblance to sieve-filament elements, trumpet hyphae (filaments), mucilage canals, and thick-walled hyphae of the brown algae, particularly the seaweeds Laminariales and Fucales, is strictly superficial (*28*).

Prototaxites remains a taxonomic and structural enigma. Indeed, mycologists who have seen my portfolio of transmission electron micrographs have denied any relation of *Prototaxites* to the fungi, whereas phycologists have similarly excluded the algae. I believe that the concept of Nematophytales (*7*) as a bizarre group of uncertain relationship seems best supported. The complex ultrastructure of not only the walls of the large tubes of *Prototaxites*, but also of the perforate septa of the filaments suggests that in the nonvascular plants, as in the vascular plants (*16*), very elaborate cell wall structure had evolved by Devonian times.

RUDOLF SCHMID
Department of Botany, University of California, Berkeley 94720

References and Notes

1. J. W. Dawson, *Q. J. Geol. Soc. London* **15**, 477 (1859).
2. W. Carruthers, *Mon. Microsc. J.* **8**, 160 (1872).
3. However, the notion that *Prototaxites* is a vascular plant of some sort has persisted: for example in L. Emberger, *Les Plantes Fossiles dans Leurs Rapports avec les Végétaux Vivants* (Masson, Paris, 1944), but not in his second edition (1968); J. Grüss, Nematophora fascigera *gen. nov., eine Devonalge als Vorläufer der Gymnospermen* (Tauber-Verlag, Berlin, 1924); *Palaeobiologica* **1**, 487 (1928); W. Schmidt and M. Teichmüller, *Geol. Jahrb.* **69**, 89 (1954).
4. R. Kräusel, *Fortschr. Geol. Rheinl. Westfalen* **12**, 25 (1964).
5. J. H. Johnson and K. Konishi, *Colo. Sch. Mines Q.* **53**, No. 2 (1958); ______, R. Rezak, *ibid.* **54**, No. 1 (1959).
6. W. C. Darrah, *Chron. Bot.* **6**, 52 (1940).

W. H. Lang, *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* **227**, 245 (1937); *J. Linn. Soc. Lond. Bot.* **52**, 535 (1945). It should be noted that the concept of a phylum or division Nematophyta originated with A. Chiarugi [*Nuovo G. Bot. Ital. (Nuova Ser.)* **40**, 590 (1933); *Missione Scientifica della Reale Accademia d'Italia a Cufra* **3**, 291 (1934)], who, however, considered this group algal; see Darrah (*6*).

8. A. G. Lyon, *Trans. R. Soc. Edinb.* **65**, 79 (1962).
9. J. M. Schopf, *Geol. Soc. Am. Mem.* **67**(2), 709 (1957).
10. C. A. Arnold, *Palaeontogr. Abt. B Palaeophytol.* **93**, 45 (1952); *8th Congr. Int. Bot. Paris 1954 Rep. Commun.* (1954), sect. 5, p. 137.
11. The workers that accept either a nematophytalean or, especially, an algal assignment for *Prototaxites* are legion and include most of the notables in paleobotany of the past century (*4–10*).
12. R. Kräusel, *Palaeontogr. Abt. B Palaeophytol.* **86**, 113 (1941); see appraisal in Schopf (*9*).
13. A. H. Church, *Thalassiophyta and the Subaerial Transmigration* (Oxford Univ. Press, London, 1919). Many authors have denied such a relationship; see especially Kräusel (*12*) and W. Schmidt, *Palaeontogr. Abt. B Palaeophytol.* **104**, 1 (1958).
14. D. H. Campbell, personal communication in Darrah (*6*).
15. F. Stockmans, *Mém. Mus. R. Hist. Nat. Belg.* **93**, 1 (1940); ______ and Willière, *Bull. Mus. R. Hist. Nat. Belg.* **14**(55), 1 (1938).

R. Schmid, *Am. J. Bot.* **54**, 720 (1967).

17. The material was desilicified in concentrated hydrofluoric acid and then prepared for transmission electron microscopy as outlined by Schmid (*16*). Chemical tests are being performed by V. J. Vreeland.
18. My findings from electron microscopy largely corroborate Arnold's (*10*) light microscopic data. A detailed account is in preparation.
19. These terms are used interchangeably in descriptive accounts of *Prototaxites*. Hypha, filament, septal pore, and similar terms thus bear no implications with regard to taxonomic relationships.
20. See bibliographies in H. P. Banks, K. I. M. Chesters, N. F. Hughes, G. A. L. Johnson, H. M. Johnson, L. R. Moore, in *The Fossil Record*, W. B. Harland *et al.*, Eds. (Geological Society of London, London, 1967), p. 163; J. H. Johnson, *Colo. Sch. Mines Q.* **62**, No. 4 (1967); B. H. Tiffney and E. S. Barghoorn, *Occas. Pap. Farlow Herb. Cryptogam. Bot. Harv. Univ.* **7**, 1 (1974).
21. R. L. Dennis, *Science* **163**, 670 (19 *Mycologia* **62**, 578 (1970).
22. V. Demoulin, *Bot. Rev.* **50**, 315 (1974). Demoulin gives a good bibliography of pit connections in red algae and septal pores in Basidiomycetes, Ascomycetes, and several "Phycomycetes."
23. T. Bisalputra, *Can. J. Bot.* **44**, 89 (1966); ______, P. C. Rusanowski, W. S. Walker, *J. Ultrastruc. Res.* **20**, 277 (1967); J. G. Duckett, J. S. Buchanan, M. C. Peel, M. T. Martin, *New Phytol.* **73**, 497 (1974); R. E. Lee, *Br. Phycol. J.* **6**, 29 (1971); J. Ramus, *J. Phycol.* **5**, 57 (1969).
24. C. E. Bracker, *Annu. Rev. Phytopathol.* **5**, 343 (19 ______ and E. E. Butler, *Mycologia* **55**, 35 (1963); M. D. Coffey, B. A. Palevitz, P. J. Allen, *Can. J. Bot.* **50**, 231 (19 T. T. Ellis, M. A. Rogers, C. W. Mims, *Mycologia* **64**, 681 (1972); D. R. Jones, *Trans. Br. Mycol. Soc.* **61**, 227 (1973); R. T. Moore, *J. Gen. Microbiol.* **87**, 251 (1975); ___ and J. H. McAlear, *Am. J. Bot.* **49**, 86 (1962); ______, R. Marchant, *Can. J. Bot.* **50**, 2463 (1972).

G. L. Benny, *Mycologia* **64**, 854 (1972); T. W. K. Young, *Ann. Bot. (Lond.)* **33**, 211 (1969).

26. H. P. Banks, *Rev. Palaeobot. Palynol.* **20**, 13 (1975). Banks refutes the notion that such tubes are tracheids.
27. ______, in *Evolution and Environment*, E. T. Drake, Ed. (Yale Univ. Press, New Haven, 1968), p. 73; *Palaeontology* **15**, 365 (1972); *Taxon* **24**, 401 (1975); W. G. Chaloner, *Biol. Rev. Cambridge Philos. Soc.* **45**, 353 (1970).
28. Refutative criteria parallel those noted by Banks. (*26*) for the tracheidal nature of differentially thickened tubes of the Nematophytales.

29. I thank numerous mycologists, phycologists, and paleobotanists, especially T. L. Phillips, V. J. Vreeland, and S. M. Wolniak for valuable discussions, and C. A. Arnold for the loan of his holotype material of *Prototaxites southworthii* for reinvestigation.

11 September 1975; revised 31 October 1975

Premature Specification of the Retina in Embryonic *Xenopus* Eyes Treated with Ionophore X537A

Abstract. *Eyes excised from* Xenopus *embryos at stages 24 to 25 were cultured for 4 to 6 hours in a medium containing the ionophore X537A or in a control medium. The eyes were implanted either upside down or normally in host embryos at stages 28 to 30, and their retinotectal projections were mapped after metamorphosis. Treatment with X537A prevented realignment of retinal axes in eyes implanted into hosts that were capable of producing retinal axial alignment in all control eyes.*

During development, the ganglion cells of the retina project their axons into the brain to form an orderly pattern of connections in the midbrain tectum. The spatial order of the ganglion cells in the anteroposterior (AP) and dorsoventral (DV) axes of the retina is duplicated in the order of axon terminals in the AP and DV axes of the tectum. Although the way this happens is largely unknown, the polarity of the projection in the AP and DV retinal axes is determined (specified) in the early em-