Endolithic associations and their relation to facies distribution in the Middle Devonian of New York State, U.S.A.

KL AUS VOGEL, STJEPKO GOLUBIC AND CARLTON E. BRETT

LETHAIA


Microboringsof endolithic organisms (e.g. algae, fungi) provide valuable indicators of paleoenvironments. The present study documents the distribution of microborings in fossil skeletal substrates from a spectrum of shelf to basinal facies in the Middle Devonian of New York. Endolithic borings in brachiopod shells and corals were prepared using special embedding–casting method and were examined and photographed with SEM. About 13 distinct types of microborings were discovered, presumably produced by microorganisms (pro- and eukaryotic), sponges, bryozoans and worms. Brachiopod holdfast etchings are reported for the first time from Paleozoic rocks. Microborings are non-randomly distributed among Middle Devonian facies. The highest diversity and abundance of borings occurs in diverse brachiopod and coral-bearing calcareous mudstones; which appear to represent shallow, well-aerated and low turbidity environments. Microboring diversity and frequency decreases markedly into mudstones and siltstones recording higher turbidity as well as into dark gray to black basement shale facies. *Leiothyrella* brachiopods from probable deeper water, dysoxic environments display very low diversity of microboring assemblages. They include brachiopod pedicle borings and one endolithic which shows similarities to a modern cyanobacterium. If the latter is correctly identified, it brackets all of the studied facies within the photic zone. ☐ Endoliths, microborings, ichnofossils, bathymetry, biofacies, brachiopods, Devonian, New York State.

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This paper represents the first comprehensive study of small endolithic trace fossils from a spectrum of well-defined facies belonging to a single biostratigraphic unit. It aims to discern the relationship between fossil endoliths and depositional environments of ancient epeiric seas.

Reconstruction of the depth of deposition of fossil marine sediments is a long-standing problem. Many lithological and palaeontological criteria are available for recognition of shallow coastal waters, down to the normal or even storm wave base; however, there is a shortage of paleobathymetric indicators that would permit recognition of different depths below this event level. Accordingly, all sediments deposited below the storm wave base are usually called ‘deep-water deposits’, and it remains uncertain whether the depth of their deposition was within the euphotic or the aphotic zones. A refined depth scale that would include this distinction, would significantly improve palaeoecological analyses and reconstructions which may be of interest for regional structural geology as well as for the exploration of hydrocarbons and sedimentary ore deposits.

Attempts to use boring microorganisms, especially the photosynthetic ones (cyanobacteria and algae), for paleobathymetric reconstructions have already a long history (e.g. Pia 1937; Mägdefrau 1937; Hessland 1949; Boekshoten 1966; Swinchatt 1969; Wendt 1969; older literature is summarized by Golubic et al. 1975, and Kobluk & Kahle 1978). However, detailed analyses of microborings have been made possible only recently, after methods of resin casting and scanning electron microscopy of borehole casts became available (Golubic et al. 1970, 1983). Interpretation of fossil endoliths with respect to their value as paleoenvironmental indicators has been aided by the research on modern endoliths and their depth distribution. Important contributions dealing with shallow water coastal microendoliths are those by Schneider (1976),
LeCampion-Alsumard (1979) and Campbell (1983), those studying endoliths along shelf slope are by Lukas (1979), and Budd & Perkins (1980), and those studying deep-sea endoliths by Zeff & Perkins (1979), and Golubic et al. (1984).

A large number of fossil microendoliths and microborings have already been described, from the Precambrian (Campbell 1982; Knoll et al. 1986) up to the Pleistocene (e.g. Clarke 1908; Fenton & Fenton 1932; Mägdefrau 1937; Wetzel 1938; Peyer 1945; Teichert 1945; Hessland 1949; Schindewolf 1962; Jux & Strauch 1964; Müller 1968; Hántzschel 1975; Robba & Ostinelli 1976; Campbell 1980; Kobuk 1981), however, none of these studies analyzed the facies- and depth-related distribution of fossil borings within one and the same sedimentary basin and within the same biostratigraphic unit. This is what we did with the Middle Devonian of New York State.

In our selection of a model for this study, we have considered the following criteria: paleo-geography of the basin and the lateral facies sequence should be well-known and supported by persuasive evidence; the strata should range from shallow waters to deep waters; the tectonic and diagenetic overprint should be minimal and, finally, the outcrop conditions should permit easy access for collection of unweathered samples. We found the Devonian of New York State to offer almost ideal conditions for this study.

The field work and identification of brachiopods and corals as most common host substrates was conducted by C. E. Brett and K. Vogel, endolith cast preparation and evaluation of SEM images by K. Vogel and S. Golubic. S. Golubic and K. Vogel are responsible for characterization, description and interpretation of ichnotaxa.

Materials and methods

Geological samples were collected at several outcrops of the Hamilton Group (Givetian) of New York State: the easternmost in the Chenango Valley (Hamilton type area), the westernmost the Lake Erie cliff south of Buffalo (see Appendix). Additional materials from the Onondaga Group (Eifelian) of New York State were obtained on loan from the Museum of Natural History, Smithsonian Institution, Washington, DC. Samples from the Chemung Group (Frasnian) and of the Oriskany Sandstone (Siegenian) from Maryland and Pennsylvania respectively, were kindly made available by R. Thomas, Lancaster, PA. Whenever possible, samples were collected from different facies that have been deposited penecontemporaneously or within relatively short time intervals. For example, bored brachiopods and corals were collected from three different facies from the 'Bloomer Creek bed' of the Wanakah member, and from six different facies of the Windom member.

Specimens of brachiopods and corals were extracted from the rock, cleaned and examined by dissecting microscope at 25× (rarely 40×) magnification, using incident light. Under these conditions and with the surfaces of brachiopod shells or corals wetted, the endolithic traces can be easily detected. Selected material was further prepared using the casting–embedding technique (Golubic et al. 1970, 1983). The resin casts were exposed by dissolving the shell, examined by scanning electron microscopy (SEM) and photodocumented. The measurements and morphometric evaluation was carried out with the aid of a digitizing tablet and Sigma-Scan software (Jandel Scientific, Sausalito, CA) using IBM-PC.

More than 2000 specimens of brachiopods and corals were obtained from the seven distinctive facies of the Hamilton Group (marked I to VII in Fig. 3). The present study is based on morphological and morphometric evaluation of 600 SEM-photographs of 340 endolithic casts in 110 brachiopod shells and 15 corals from 39 samples (Fig. 2).

Hamiton biofacies and depositional environments

General setting

In western and central New York the Hamilton Group consists of black and gray shales, mudstones and siltstones, with minor, thin, but widespread carbonate and sandstone units (Cooper 1957). These marine deposits accumulated in anaerobic to fully oxygenated environments at the northern end of the Appalachian Basin following early phases of the Acadian orogeny (Kent 1985; Faill 1985; Woodrow 1985). Hamilton stratigraphy is shown in Fig. 1; most stratigraphic units display west to east facies changes reflecting increasing proximity to tectonic sediment source areas east of the present-day Catskill region. An area of active subsidence separated a relatively

sediment-starved muddy platform in the northwest from a more actively aggrading silty to sandy shelf in the southeast. The basin axis shifted from east (meridian of Cayuga Valley) to west (to Lake Erie area) during Givetian time.

Two types of cyclic facies motifs occur in the Hamilton strata: subsymmetrical, 3 to 5 m dark gray shale to light gray argillaceous limestone cycles from Lake Erie east to the Finger Lakes, and 5 to 20 m upward-coarsening, dark shale to siltstone–sandstone hemicycles in the eastern Finger Lakes region. Recent detailed study has demonstrated that the two types of Hamilton cycles are correlative and intergradational, and that the carbonate rich center beds are equivalent to the sandy caps of the coarsening upward hemicycle (Gray 1984; Grasso 1986; Brett & Baird 1985); both are responses to basinwide shallowing episodes; both carbonates and correlative, coarse siliciclastics represent shallow water facies.

Hamilton strata are noted for their well-preserved and diverse fossils which are found in recurring associations (Cleland 1903; Cooper 1930, 1933; Smith 1935). Recently, a large number of fossil ‘communities’ (also termed associations, or biosomes by some authors) have been recognized in the Hamilton Group (Grasso 1970, 1973, 1978, 1986; Brower et al. 1978; Gray 1984; Miller 1986; Savarese et al. 1986). Synthesis of these studies with recent facies mapping of the Hamilton Group had led to recognition of generalized biofacies, representing groups of closely
associated paleocommunities, that can be related to inferred environmental parameters (Brett et al. 1983; Gray 1983, 1984).

Spacial and paleoecological relationships among several recurring Hamilton brachiopod biofacies along a hypothetical gently sloping submarine ramp are depicted in Fig. 3. Adjacent biofacies on this diagram are those which most commonly border and intergrade with one another. The relative ordering of biofacies has been established on the basis of consistent vertical and lateral intergradation of fossil associations in five or six relatively complete sedimentary cycles of the Hamilton Group. The left hand side of the diagram represents typical ordering of fossil associations in dark shale to carbonate, regressive cycles of the Hamilton Group in western New York, while the right side reflects the typical vertical sequence of associations in the correlative upward coarsening cycles in the eastern Finger Lakes region. The lateral gradation of various portions of these two types of faunal cycles has been demonstrated in numerous sequences bounded by apparently isochronous beds.

The deeper–shallower polarity of biofacies has been established on the basis of several lines of evidence including: (1) facies geometry; for example black, 'Leiorhynchus'-bearing shales tend to occur nearest the presumed center of the Appalachian basin and to grade concentrically outward into gray Ambocoelita-rich shale; (2) position of biofacies within upward coarsening sedimentary cycles in which sedimentary structures (e.g. hummocky cross stratification) unequivocally indicate decrease in water depth upward; and (3) lateral gradation of fossil associations within single isochronous event beds or intervals, which display upslope biofacies sequences in the relative order shown in Fig. 3. Environmental factors responsible for bathymetric changes in biofacies may include oxygen levels (which should decrease in the deeper waters of a stratified basin), turbulence, light penetration, temperature, food supply, etc.

Absolute depths can only be approximated at present. Evidence for water depth is twofold: (1) indications of position of biofacies relative to normal and storm wave base (see Liebau 1980; Aigner & Reineck 1982; Aigner 1985, for approximations of these depths) utilizing a proximality spectrum for storm generated beds (see Brett et al. 1986b), and (2) evidence for position relative to the photic zone (e.g. indications of benthic algae or of visual systems in benthic organisms).

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Recognition of a spectrum of storm-generated layers ranging from amalgamated, winnowed coquinites to distal mud layers (Brett et al. 1986b), indicates that most Hamilton shell-rich facies were deposited between normal and storm wave base. A similar suite of storm-generated beds is forming today on shallow, storm-dominated shelf settings, generally at 10 to 50 m depths (Aigner & Reineck 1982). Hamilton dark shale facies generally display only the effects of weak storm-generated currents, rather than direct wave impingement and, therefore, probably accumulated at depths below the influence of all but the strongest storm waves. Most Hamilton facies, except for certain of the black shales possess abundant phacopid trilobites with large, well-developed eyes, as well as circumstantial evidence of benthic algae (herbivorous gastropods and bioimmuration of possible algal substrates; see Brett et al. 1986a). On these bases the entire spectrum of Hamilton biofacies probably was developed in relatively shallow, euphotic to dysphotic epicontinental sea environments ranging from perhaps about 10 m down to about 100 m; for detailed discussion see Brett, Baird & Miller (1986).

The sequence of depth-related biofacies within sedimentary cycles varies consistently from western to central New York. Certain, probably deeper water biofacies persist with little lateral change at an analogous position within any cycle from east to west. However, distinctly different shallow water biofacies substitute for another laterally at a given level within cyclothsms. For example, diverse brachiopod and coral biofacies in western New York typically grade eastward into Tropidoleptus-dominated associations. The same type of substitution also has been observed vertically between transgressive and regressive portions of a cycle at a particular location.

The horizontal axis of the diagram in Fig. 3 depicts along-strike differences in biofacies which are due to factors other than depth-related parameters. Consistent association of biofacies changes with the eastward thickening and slight coarsening of cycle members strongly suggests that this change is related to sedimentation-controlled features. We believe that turbidity was more critical than absolute rate of sedimentation or substrate. This type of biofacies gradation can occur without substantial change in thickness or lithology, which tends to rule out net sediment accumulation rate or substrate composition as the critical factors. However, the biofacies substitutions almost always coincide with circumstantial evidence for increased turbidity such as increased abundance of infaunal trace fossils and bivalves, loss of presumed turbidity-intolerant
organisms (i.e. corals) and increase in eye size of phacopid trilobites (Eldredge, in Eldredge & Gould 1977).

Biofacies description

Features of various Hamilton biofacies are summarized in the following sections adapted from Brett, Baird & Miller (1986; see that paper and Savarese et al. 1986, for detailed discussion and slightly more refined subdivision of biofacies). The Spinocyrtia–Psychopteria and Zoophycos biofacies are not included in this study, but are entered in Fig. 3 for the sake of completeness. These assemblages are typical of heavily bioturbated siltstones and sandstones of east-central New York State. They contain sparsely distributed and generally poorly preserved (moldic) specimens of bivalves and large brachiopods as well as pervasive Zoophycos spreiten. The fossils were found to be too difficult to extract and too poorly preserved to be useable in the study of endoliths. Procedings from offshore (deepest) to onshore (shallowest), the remaining biofacies can be outlined as follows:

I. 'Leiorhynchus'. – Low diversity (10–15 species) or even monotypic assemblages of poorly preserved leiorhynchid, chonetid and rare ambo- coelid brachiopods, nuculid bivalves, nautiloids, goniatites and Styliolina; invariably associated with black to dark gray, laminated shales. (The brachiopod genus Leiorhynchus is presently being revised (Sartenaer, pers. comm., 1986). The Hamilton species L.? limitare, and L.? multihastum undoubtedly belong to distinct genera other than Leiorhynchus; the Leiorhynchus facies is generally dominated by L.? limitare.)

Probably the deepest water assemblage (50–100 m); quiet, dysaerobic water settings, sediments anoxic near to the sediment/water interface; turbidity low to moderate; below storm wave base.

II. Ambocoelia–chonetid. – Low to moderate diversity (20–40 species) fossil assemblages, including abundant small free-living brachiopods (e.g. Ambocoelia, Devonochonetes scitulus); nuculid and modiomorphid bivalves, archeogastropods, phacopid trilobites; rare small inadequate cnidaries and blastoids, autopoikid corals. Dark to medium gray, concretionary, pyritic shales and mudstones.

Relatively deep (~50 m), quiet water, moderately oxygenated, with anoxic or dysoxic, non-sulfidic, shallowly burrowed substrates; near storm wave base; at least dysphotic zone.

III. Mucrospirifer–chonetid. – Moderate diversity (30–35 species) assemblages, often largely dominated by Mucrospirifer and Devonochonetes brachiopods and/or bivalves such as Cypricardella, Paleonello; also minor trilobites, typical of medium gray, commonly silty mudstones and muddy siltstones; concretions and pyrite nodules uncommon.

Depths variable, but similar to those inferred for the Ambocoelia-chonetid and Athyris biofacies, with which it interfingers; fairly high sedimentation and relatively high amounts of silt; abundant shallow burrowing; probably high turbidity and instable substrate.

IV. Athyris. – Moderate diversity (30–40 species) assemblages, including stereolasmatid corals, fenestrellid bryozoans, the brachiopods Athyris, Mucrospirifer, Devonochonetes, medium-sized protobranch modiomorphid and pteroid endobryssate bivalves, archeogastropods, phacopid trilobites and a few flexible and inadequate cnidaries. Common in medium gray claystones to silty mudstones, may be associated with carbonate concretions or with nodular pyrite; typically in shell-rich beds.

Moderate depths, within lower storm wave base (30–50 m), but normally rather quiet with low to moderate turbidity; bottom waters fully aerobic but upper sediments dysoxic.

V. Pseudotritypa (diverse brachiopod). – Moderate to high diversity (40 to 60+ species) fossil assemblages; contains the highest brachiopod diversity of any Hamilton unit, including various atyrids, spiriferids (Mediospirifer, Cyrtina, Elita, Nucleospira, Spinocyrtia), strophomenids (Sirophodonta, Pholidostrophia, Dowullina, Megastrophia), terebratulids (Centronella, and others); small- to medium-sized rugose corals (Stereolasma, Amplexiphyllum), fenestellid and fistuliporid bryozoans, various epi- and endobryssate bivalves, trilobites, cnidaries, blastoids. Primarily in medium to light gray, soft, commonly calcareous (marly) mudstone with abundant thin shell-rich layers; minor Zoophycos bioturbation.

Shallower (20–30 m), fully aerobic muddy to shelly-bottomed settings below wave base but
well within storm wave base; upper sediments aerobic; moderate to deep burrowing; turbidity and sedimentation rates generally low.

VI. TROPIDOLEPTUS. – Moderate diversity (30-50 species) assemblages, dominated by brachiopods (Tropidoleptus, Devonochonetes, Longispina, Mucrospirifer, Athyris, Meristella, Spinocyrtia). Pseudoastrypa and strophomenids may be present but usually rare; bivalves diverse and common, including Cypricardella, Modiomorpha, Psychopertia, and Glyptodesma; rugose corals rare or absent but the tabulate Pleurodictyum may be common and large; varied ramose and fistuliporoid bryozoans; placopid and proetid trilobites, often large; platycerat gastropods; high diversity of crinoids and blastoids. Typifies medium to light bluish gray, soft, bioturbated, blocky and moderately to sparsely fossiliferous mudstones or muddy siltstones; scattered coquinites, some with grading, gutter casts.

Analogous depths to Pseudoastrypa association, but with distinctly higher sedimentation rates and/or turbidity. Aerobic muddy to silty bottom areas, commonly affected by episodic storm waves.

VII. PENTAMERELLA–HELIOPHYLLUM. – Diverse (50 to 60+ species), coral-dominated fauna with many species of large turbinate and fasciculate rugosans (Heliophyllum, Cystiphyllodes, Eridiphyllum) and ramose to massive tabulates (Favoites, Alveolites, Cladophora); fenestrate, fistuliporoid and ramose trepostome bryozoans; brachiopods less common but represented by several genera, some of which (e.g. Pentamerella, Parazyga, Elita, Pentagonia) are largely confined to this facies; crinoids are abundant, but generally disarticulated; platycerat gastropods and large pteroid clams are locally common. May be biostromal; fossils commonly fragmented and heavily corroded. Associated with light gray, commonly soft, crumbly calcareous (marly) mudstone to nodular argillaceous limestone, or, rarely, calcareous siltstone.

Shallow, moderate to high energy settings approaching normal wave base (~20 m), well aerated, with abundant food supply; skeletal buildup on seafloor possibly inhibiting burrowing but favoring diverse epibiont communities; sedimentation rates very low.

Description of endoliths

In this section we describe 13 taxa of boring trace fossils. In the taxonomic treatment that follows, we subscribe to the basic principles of ichnological classification (Bromley & Fürsich 1980). Within this framework, we favor relatively wide and inclusive generic, and rather precise specific diagnoses. The shape and direction of the borings were determined from resin replicas as seen under SEM. Hence, the terms used in our descriptions refer to the inverted forms of casts rather than to the original hollow spaces. For the same reason holotypes are not preserved as borings, but rather as resin casts on SEM-stubs. They are stored in the collection of the Institute of Geology-Paleontology, J. W. Goethe University, Frankfurt a.M., W. Germany (GPIF). Ichnospecies are evaluated morphometrically: all measurements are expressed as ranges, and as means and standard deviation (M ± s; M = mean; s = standard deviation), followed by the number of observations within square brackets [n].

Rosette-shaped borings

A number of borings have a characteristic rosette-shape. These borings seem to start from a central point of entry from which they spread radially, parallel to, and immediately beneath the substrate surface resembling radiating boring traces, that were first described from Cretaceous belemnite rostra by Quenstedt (1849) under the name Dendrina. Mägdefrau (1937) described several species of Dendrina, but none of our taxa corresponds to any of the Cretaceous forms.

In 1908, Clarke described radiating boring systems from the Devonian of New York state and named them Clionolites. We have studied Clarke's (1908, 1921) descriptions and illustrations; however, they were insufficient for identification of borings observed in this study. Furthermore, the type material of Clionolites was too poorly preserved to provide adequate information. Thus we are forced to consider Clarke's names nomina dubia.

Olkenbachia Solle 1938 from the Devonian of Germany, according to Teichert (1945) a subjective synonym of Clionolites, may encompass three different morphotypes, here described as separate ichnogenera, Nododendrina, Rامođendrina and Plate dendrina. Neither the type
material of *Olkenbachia hirsuta* nor its illustration (iconotype) permit a decision as to whether this species corresponds to our *Nododendrina* or *Ramodendrina*. Preservation of the type materials of all *Olkenbachia* species is inadequate for direct observation, and preparation of resin casts for SEM study is not permitted. Hence, we consider Solle’s names as *nomina dubia* as well.

**NODODENDRINA n. ichnogen.**

*Etymology.* – nodum (L.) = node; dendron (Gr.) = tree.

*Diagnosis.* – Prostrate, rosette-shaped boring system with an enlarged node (pit) in the central area.

*Type species.* – *Nododendrina nodosa*.

*Comments.* – *Nododendrina* differs from other large rosette-shaped borings by its central node, by the high profile of the branch cross sections and by their dorsal spiny outgrowths.

**NODODENDRINA NODOSA n. ichnosp.**

*(Fig. 4)*

*Iconotype.* – Fig. 4C.

*Diagnosis.* – Rosette-shaped repeatedly branched systems, up to 1.5 mm in diameter (1.06 ± 0.33 [26]). Branches diverge radially, and immediately beneath the substrate surface from a central node (presumably at the original point of entry), with frequent anastomoses. The central nodes are 75–270 μm (163 ± 64 [10]) wide, and up to 300 μm high (207 ± 55 [10]). The node represents the deepest penetrating part of this endolithic. Radiating branches originate from the central node as high-crested ridges lowering gradually toward the periphery. The branches diverge in straight line, at angles ranging from 32° to 88° (63 ± 15 [63]), or are curved into U-shaped forks (Fig. 4B). The branches are high and narrow in cross section, 18–47 μm (30.74 ± 7.50 [100]) wide and 50–120 μm (87.05 ± 19.80 [88]) high, covered with larger and smaller spiny outgrowths. The outlines of these branches appear scalloped in both vertical and horizontal projections. Dorsal spines (i.e., those toward the interior of the brachiopod shell) end blindly, whereas the ventral ones form numerous connections with the shell surface (Fig. 4A, left).

*Comments.* – The density of branching varies from facies to facies and correlates positively with the frequency of anastomosing contacts. For example, the density of points of contact (both diverging and converging) between branches in Windom is only 10 points/mm², in Wanakah and Centerfield it reaches 40–50 points/mm² (comp. Figs. 4A and 4B).

*Occurrence.* – Facies II and IV.

*Number of specimens.* – 30.

**RAMODENDRINA n. ichnogen.**

*Etymology.* – Ramus (L.) = branch; dendron (Gr.) = tree.

*Diagnosis.* – Prostrate, rosette-shaped boring system with a branched trunk (tunnel) in the central area.

*Type species.* – *Ramodendrina cervicoris*.

*Comments.* – *Ramodendrina* differs from *Nododendrina* and *Platydendrina* by the circular cross section of its branches, and lack of anastomoses. It differs from other branched boring systems (e.g. *Talpina ramosa* Hagenow) by its consistently radiating pattern, flatness of the branching system, and size-distinction between primary, secondary and tertiary branches.

**RAMODENDRINA CERVICIORS N. ichnosp.**

*(Fig. 5)*

*Etymology.* – Cervicoris (L.) = like elk antlers.

*Iconotype.* – Fig. 5A.

*Diagnosis.* – Rosette-shaped repeatedly branched systems up to 2.5 mm (1.50 ± 0.40 [10]) in diameter. Branches diverge from the main trunk (Fig. 5B, top), spreading radially in straight line or slightly curved; at angles ranging from 40° to 95° (64 ± 13 [50]). The main trunk is 80–250 μm wide. The primary branches (those proximal to the trunk) are 60–225 μm (133 ± 44 [24]) wide, the distal branches are 25–85 μm (52 ± 11 [100]) wide. The branches often adhere closely to the substrate surface (Fig. 5C). They have smooth
Fig. 4. Nododendrina nodosa n. ichnosp. Three growth forms.

A. In Alhyris, perspective view, Windom Member, facies V, Barnum Creek quarry (loc. 17), SEM 002.12585, GPFBo 1/3. □B. In Alhyris, densely branched anastomosing growth form. Wanakah Member, facies IV, 18 mi. Creek (loc. 1B), SEM 65.5010, GPFBo 1/2. □C. In Meiozoor, holotype. Wanakah Member, facies V, Lake Erie cliff (loc. 1A), SEM 003.12194, GPFBo 1/1. Note the central node and the high crested spiny radiating branches. Scale bars are 200 μm long.
and rounded surfaces, and are circular in cross section. They do not taper and have rounded, rarely pointed tips. Branch diameter decreases only slightly from primary to secondary and tertiary (distal) branches, and remains constant (or even increases slightly) between branching points. The branching varies in density, without anastomoses. The main aperture to the surface was not detected.

Comments. — It differs from *R. alcicornis* by the relatively constant width of its branches and their rounded tips.

Occurrence. — In facies IV to VII.

Number of specimens. — 18.

**RAMODENDRINA ALCICORNIS n. ichnosp.** (Fig. 6)

Eymology. — Alcicornis (L.) = like moose antlers.

**Iconotype.** — Fig. 6C.

**Diagnosis.** — Rosette-shaped repeatedly branched systems up to 2 mm (1.41 ± 0.34 [16]) in diameter (Fig. 6A). Branches diverge from the main trunk spreading radially, curved in a characteristic claw-like fashion (Fig. 6B), at angles ranging from 40° to 115° (72 ± 17 [50]). The main trunk is 75–190 μm (142 ± 40 [7]) wide. The primary branches range from 53 to 136 μm (95 ± 19 [50]), the secondary branches from 31 to 66 μm (51 ± 11 [50]), and the tertiary branches from 12 to 45 μm (26 ± 9 [37]) in diameter. They have smooth and rounded surfaces, and are circular in cross section. The branches taper toward pointed tips. There is a significant decrease in diameter from primary to secondary and tertiary (distal) branches, and the diameter between individual branching points remains constant or decreases. The branching varies in density, without anastomoses. The main aperture to the surface was not detected.

Comments. — *R. alcicornis* differs from *R. cervicornis* by its tapered claw-like distal branches.
**Fig. 6. Ramodendrina alcicornis** n. ichnosp. □A. In a spiriferid brachiopod together with *R. cervicornis* (c). Otisco Member, facies V-VI, Portland Point (loc. 20), SEM 015.11085, GPF IF Bo 1/7, scale bar 1 mm. CB. Detail of A (a), SEM 016.11085, scale bar 200 μm. □C. In *Mediospirifer*, holotype. Windom Member, facies V, Barnum Creek quarry (loc. 17), SEM 011.12585, GPF IF Bo 1/8. Note curved and tapered, claw-like distal branches, scale bar 200 μm.
Occurrence. – In facies V and V–VI.

Number of specimens. – 8.

**Platydendrina n. ichnogen.**

**Etymology.** – Platy (Gr.) = flat; dendron (Gr.) = tree.

**Diagnosis.** – Prostrate rosette-shaped system spreading parallel to, and immediately beneath, the substrate surface, with a large flat central area. Dorsal surfaces are smooth, whereas the ventral surfaces are beset by spiny outgrowths that connect to the substrate surface.

**Type species.** – *Platydendrina platycenrum*.

**Comments.** – *Platydendrina* is distinguished by a large flat central area, general flatness of its branches, and a rapid decrease in width from proximal to distal branches, and presence of anastomoses.

**Platydendrina platycenrum n. ichnosp.** (Fig. 7)

**Etymology.** – In reference to flat central area.

**Iconotype.** – Fig. 7A.

**Diagnosis.** – Palmate, repeatedly branched system, up to 3 mm (1.03 ± 0.56 [16]) in diameter. Central area is occupied by a large flat surface that gradually grades into the branches. Branches diverge at angles ranging from 32° to 100° (58 ± 16 [58]). The margins between branches are scalloped forming deep rounded embayments. The width of the primary branches at the base is 50–300 μm (134 ± 63 [66]), the secondary branches 20–60 μm (40 ± 11 [82]), whereas the tertiary (distal) branches are 5–20 μm (16 ± 8 [54]). Thus, there is a substantial decrease in width from the proximal to the distal branches (Fig. 7C). The branches end with tiny rhizoidal appendages only a few micrometers wide, which connect to the substrate surface (Fig. 7B). The anastomoses are common sometimes leaving rounded holes (Fig. 7A, lower left). The branches are depressed in cross section. The dorsal surfaces (interior with respect to the shell) of *Platydendrina* are smooth, whereas its ventral side is beset by spiny outgrowths that connect to the substrate surface.

**Comments.** – *Platydendrina platycenrum* shows some similarities to *Dendrina anomala* Mägdefrau 1937, described from Upper Cretaceous bel-
emnite rostra, and with *Entobia megastoma* (Fischer) Bromley & D’Alessandro 1984, but differs from them by the large central area and more regular palmate-radiating shape.

**Occurrence.** – In facies II to VII.

**Number of specimens.** – 17.

**HYELLOMORPHA n. ichnogen.**

**Etymology.** – Hyellomorpha (Gr.) = of the shape of *Hyella*, a modern boring cyanobacterium.

**Diagnosis.** – Prostrate, small (100–500 μm diameter) repeatedly branched rosette-shaped boring system, starting from a small central node.

**Type species.** – *Hyellomorpha microdendritica*.

**Comments.** – *Hyellomorpha* differs from all other rosettes by its small size.

**HYELLOMORPHA MICRODENDRITICA n. ichnosp. (Fig. 8)**

**Etymology.** – Microdendritica (Gr.) = like a small tree.

**Iconotype.** – Fig. 8B.

**Diagnosis.** – Rosette-shaped, repeatedly branched systems, up to 0.5 mm (0.24 ± 0.078 [49]) (Fig. 8A). Branches diverge radially, parallel to and immediately beneath the substrate surface, from a small central node (at the presumed point of entry). Anastomoses are common (Fig. 8C, upper right). The central node, approximately isodiametric 20–80 μm (50.26 ± 19.8 [16]) in diameter, represents the deepest penetrating part of the system. Branches diverge in straight line at angles ranging from 50° to 120° (76 ± 17 [21]), or are slightly curved, or change direction abruptly. The density of branching varies within samples. Branches are circular in cross section, with a diameter 8–19 μm (11.2 ± 2.8 [63]), at their distal ends swollen to a diameter of 10–30 μm (17.9 ± 5.3 [55]). The surfaces are smooth (except for substrate imprints).

**Comments.** – The shape and size of *Hyellomorpha* borings are similar to those produced by young thalli of the modern endolithic cyanobacterium *Hyella*. Body fossils of *Hyella* were identified in Late Precambrian strata, hence its occurrence in Devonian is not surprising.

**Occurrence.** – In facies I, II, IV and V.

**Number of specimens.** – 70.

**Bryozoan borings**

**ORBIGNYOPORA DEVONICA (Richards 1974) comb. n. (Fig. 9)**

**Diagnosis.** – Blimp-shaped autozoecial casts are 54–80 μm (64 ± 7 [17]) wide and 260–420 μm (324 ± 46 [11]) long. They are placed parallel to the substrate surface, or at a very low angle. This angle steepens abruptly at the main connection (opening) of the autozoecial cast with the substrate surface (at the anterior end of each zoecium). This connection (opening of the boring) is circular in cross section and 42–56 μm in diameter. Each autozoecial cast is ‘supported’ by a large number of accessory papillae (tubulets), of 5–10 μm diameter (Fig. 9A). The autozoecial casts appear to be ‘strung’ on very thin, mostly less than 10 μm wide filaments (stolon-tunnels), which run in straight course from one zoecium to the next. In some cases, a pair of secondary stolons arises at or near midlength of a zoecium, starting a network of interconnected zoecia (Fig. 9C). Heterozoecial casts occur on the same stolon networks as rare, very short, nearly ball-shaped to cylindrical, vertically positioned bodies, 110 to 200 μm (131 ± 17 [5]) wide and up to 200 μm (176 ± 24 [5]) high. They too send secondary papillae (tubulets) to the substrate surface (Fig. 9B).

**Comments.** – Devonian endolithic traces of this type can be compared in detail with borings of extant bryozoans. Although technically ichno-fossils, they contain sufficient information to characterize the biological taxon of the borer (Pohowsky 1978). These bryozoan borings had already been described from the Hamilton Group of the New York State by Richards (1974), and placed within the modern genus *Immergentia*.
Fig. 8. Hyellomorpha microdendritica n. ichnosp. □A. In Mediospinfer, together with bryozoan borings (b). Note the relatively small size of the rosettes and the central nodes, Wanakah Member, facies V, Lake Erie cliff (loc. 1A), SEM 10.12194, GPIF Bo 1/11. □B. Holotype, detail of A (h), SEM 011.12194. □C. In 'Lelorhynchus'. Note inflated branch tips (left) and the density of branching and anastomoses (right). Windom Member, facies II, Barnum Creek quarry (loc. 17), SEM 85.4323, GPIF Bo 1/12. Scale bars are 100 μm long.
Fig. 9. Orbignyopora devonica (Richards 1974) comb. n., bryozoan borings. □A. Autozoocodial cast in Athyris, note accessory 'papillae'. Wanakah Member, facies V, Lake Erie cliff (loc. 1A), SEM 018.12124, GPIF Bo 1/13. □B. Heterozoocodial cast, attached to a stolon, and with accessory 'papillae' connecting with substrate surface. In a spiriferid, Wanakah Member, facies V, Lake Erie cliff (loc. 1A), SEM 006.12194, GPIF Bo 1/14. □C. Two autozoocodial casts with primary and secondary stolon filaments. Windom Member, facies V, Barnum Creek quarry (loc. 17), SEM 031.12585, GPIF Bo 1/15. Scale bars are 100μm long.
Silén 1946 (Miocene–Recent). Richards named them *Immergentia devonica*. According to Pohowsky (1978), *Immergentia* is characterized by essentially vertical zooids. He erected the new genus *Orbignyopora* (?Silurian–Pliocene) for those non-pedunculate boring bryozoans with autozooccia lying throughout their entire length horizontally along stolon. Their lateral stolons arise at or near midlength of zooid, as they do in our samples. This position of stolon branching seems to be the only difference from *Ropalonaria* Ulrich 1879 (Ordovician–?Cretaceous), which is the oldest known boring bryozoan. In contrast to those of *Orbignyopora*, its stolons arise at or close to the aperture.

The majority of Recent boring bryozoans abounds in shallow water, although *Penetratia* and *Immergentia* have been collected from depths of over 400 m (Soule & Soule 1969).

**Occurrence.** — Facies II, and IV to VII. They are most abundant in facies V, but rare and shorter in facies II.

**Number of specimens.** — Numerous.

**Brachiopod pedicle borings**

*Podichnus centrefugalalis* Bromley & Surlýk 1973 (Fig. 10)

**Description.** — The casts of brachiopod pedicle borings appear as circular fields of cylindrical stubs (pits). Those in the center of a field are shorter and more or less perpendicular to the substrate surface; the marginal ones are longer and inclined outward (Fig. 10A, B). The diameter of the fields ranges between 100 and 1,500 µm. The stubs are at their base (at the substrate surface) 20–80 µm (50 ± 15 [79]) wide and 40–140 µm (81.51 ± 30 [42]) long, mostly conical (Fig. 10B). The number of stubs (pits) per field varies considerably: 10 to 50 (>100).

**Comments.** — Similar boring systems in modern and Cretaceous substrates have been described by Bromley & Surlýk (1973) under the name *Podichnus centrefugalalis*. On the basis of Recent-to-fossil comparison they interpreted these traces as etchings of brachiopod pedicles (holdfasts). Nekvasilova (1975, 1976) described corresponding traces from the Cretaceous of Czechoslovakia, and Malkowski (1975) from the Triassic of Poland. Brett & Mottrell (1982) reported similar pits from latex-cast mollusk shells, also from the Hamilton group. These are the first definite reports of *Podichnus* from the Paleozoic. The occurrence of these traces on *Leitorhynchus* (?)
Worm borings

**SPECUS FIMBRIATUS** Stephenson 1952 (Fig. 11A)

**Description.** – The casts of worm borings are straight or curved unbranched cylinders with smooth surface and rounded, sometimes slightly swollen tips. They are upright, inclined or parallel to the substrate surface, 180–310 μm (236 ± 31 [21]) wide and up to 5 mm long.

**Comments.** – Some growth features may depend on the constraints given by the host shell (steno-
morphy, Bromley & D'Alessandro 1984). For instance, the inclination of the borings with respect to the substrate surface apparently depends on the thickness of the host shell. Several worm borings may start at the same growth line or at the shell margin.

Stephenson (1952) described simple cylindrical to club-shaped borings, circular in cross section under the name *Specus fimbriatus*. He classified it provisionally among sponges. Devonian worm borings are similar with respect to size, shape, orientation and course within the host shell, and slightly inflated tips. They differ from Stephenson's forms by being more consistently cylindrical, i.e. less variable in diameter.

Unbranched (occasionally forked) cylindrical borings have been described much earlier in Upper Cretaceous belemnite rostra under the name *Talpina solitaria* Hagenow (Quenstedt 1849). Mägdefrau (1937) revised this genus (to include only repeatedly ramified forms) and erected the new genus *Nygmites* for simple tubes. *Nygmites solitarius* (Hagenow) Mägdefrau was described to gradually narrow distally. In contrast, a re-examination of the original material by Voigt (1972) revealed that the distal parts of these borings actually widen and flatten, including occasional bifurcation. The genus *Nygmites* also included club-shaped forms (*N. pingens, N. sacculus*), which were later separated by Voigt (1972). (Ichnological nomenclature for clavate forms was discussed by Kelly & Bromley 1984.)

Mägdefrau (1932) described unbranched 'borings' under the name *Trypanites*. Bromley (1972) redefined this ichnogenus to include clavate forms. Recently, Kelly & Bromley (1984) suggested reserving this name for cylindrical borings in hard substrates (as opposed to *Skolithos* in unconsolidated sediments). From the original description, however, it is clear that *Trypanites* refers to burrows in mudbanks which later consolidated into rock. The use of the same name for true borers by Müller (1956, cited in Bromley 1972) does not change the original meaning. We are provisionally using the name *Specus fimbriatus* Stephenson for the Devonian borings, although this ichnotaxon refers to elongated club-shaped rather than strictly cylindrical borings (see Kelly & Bromley 1984).

Cameron (1969a) described worm borings from the Devonian of New York State and the Ordovician of Ohio under the name *Vermiforichnus*. He also discovered a body fossil of a worm (with its soft parts preserved) within one of these boreholes (Cameron 1967; 1969a) and attributed it to a polychaete similar to modern *Polydora*. He interpreted it as the producer of the boring and described it under the name *Vermiforacta rollinsi*. Blake & Evans (1973) criticized this interpretation, because the cross section of the *Vermiforacta* borehole was circular and thus different from the borings of modern *Polydora*, which are U-shaped or at least elliptical in cross section. Cameron (1969b) published size frequency histograms of worm-boring diameters in two Devonian and one Ordovician formation. Both Devonian histograms are bimodal, with primary modes between 0.5 and 1 mm, and secondary modes between 0.2 and 0.3 mm. We suggest that his measurements included more than one taxon. The Devonian *Specus fimbriatus* corresponds to the 0.2-0.3 mm modes, whereas, according to Cameron's description, the *Vermiforacta* borings (1.2 mm wide) fall into the larger mode. Müller (1968) described 10 groups of worm borings from the lower Devonian of Germany. Form and size of our specimens correspond to her group I, which she named *Conchifora zylindriformis zylindriformis*.

Modern *Polydora* has been reported to occur to a depth of 50 m (Beokschooten 1966), and *Dodecaceria concharum* reaching depths of about 400 m (Hartmann-Schröder 1971). The distribution of these *Vermiforichnus* in the Upper Devonian Genesee Group of New York State was described by Tayer (1975) as most abundant on the delta platform but rare in prodelta, basinal and open shelf facies.

**Occurrence.** – Facies I-VII.

**Number of specimens.** – Numerous.

**SPECUS (?) sp.** (Fig. 11B, C)

**Description.** – The casts of these borings are straight or curved cylinders that are frequently bifurcated or laterally branched with one bifurcation per cylinder, which can occur proximal or distal to the point of entry. They are upright, inclined or parallel to the substrate surface, 80-134 μm (128 ± 25 [33]) wide and up to 1 mm long.

**Comments.** – Müller (1968) described bifurcating worm borings, but her specimens branch in the
opposite direction, having two or more apertures (they are also wider than our specimens, having a mean diameter of 0.45 mm). They differ from *Nygmites solitarius* (Hagenow) Mägdefrau 1937 (sensu Voigt 1972) by the lack of flat widening. Our specimens also differ from *Tulpina* (Hagenow) Mägdefrau em. 1937, and *Conchoatra* Teichert 1945 because they never form networks. The possibility that bifurcation is produced by a second organism using an old boring as a favorable larval settlement site (R. G. Bromley, pers. comm. 1986) seems unlikely because bifurcation consistently correlates with smaller diameter borings.

**Occurrence.** — Facies I–VII (in I rare).

**Number of specimens.** — Numerous.

### Swellings and filaments

There are two groups of borings that do not belong in any of the ichnotaxa described. Their casts can be tentatively classified simply as swellings and filaments.

**‘DODGELLA-like swellings’ (Fig. 12)**

**Description.** — Small borings of unknown affinity and globular (35–40 μm), pear-shaped (30–35 × 50 μm) or ellipsoidal (30 × 40 μm) shape are all grouped together as ‘Dodgella-like swellings’. Some of these are sessile, others rest on a single stalk (Fig. 12B), or on multiple rhizoidal pedicles. Most of them are simple, a few are composite into a cluster of closely compacted or aligned bodies. They are frequently, but not always, associated with thin hyphae-like filaments 3–8 μm in diameter.

**Comments.** — These borings obviously represent a heterogeneous group which presently cannot be resolved in individual taxa due to paucity of well preserved samples. The similarity of a number of these borings to modern *Doddella* is striking. *Doddella* has been described by Zebrowski (1936) as a cladochytrid (lower fungi); this classification, however, awaits re-evaluation and revision.

**Occurrence.** — Facies IV–VII.

**Number of specimens.** — Numerous.

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**Fig. 12. Dodgella-like swellings.** □A. Swellings and sessile spheres of different sizes with hyphae-like filaments, in *Mediostriatia*. Centerfield Member, facies V–VI, Hall’s Landing (loc. 21), SEM 86.1811, GIF1 Bo 1/21, scale bar 100 μm. □B. Pear-shaped swelling on a pedicle, in *Spinocyrtia*. Windom Member, facies V, Barnum Creek quarry (loc. 17), SEM 017.12585, GIF1 Bo 1/22, scale bar 10 μm.

### ‘Reticulate filaments’ (Fig. 13A)

**Description.** — Irregular three-dimensional lattice of densely branched and anastomosing filaments. Diameter of network patches is up to 300 μm.
The filaments are fairly constant in diameter (5–10 µm), have an irregularly meandering course, and rounded tips.

**Occurrence.** – Facies IV–V.

**Number of specimens.** – 6.

**'Spiny filaments' (Fig. 13B)**

**Description.** – Irregular three-dimensional lattice of densely-branched and anastomosing filaments. Diameter of network patches is up to 400 µm. The filaments vary strongly in diameter (8–15, up to 50 µm), and are beset with spine-like projections extending in all directions. Network patches are sometimes interconnected by straight filaments.

**Occurrence.** – Facies VII.

**Number of specimens.** – Several systems in two hosts.

**'Smooth filaments' (Fig. 13C)**

**Description.** – Mostly straight filaments (tunnels), circular in cross section, running immediately below and parallel to the substrate surface. The width of the filaments remains rather constant through their entire length 50–70 µm (65 ± 12 [63]). They terminate with rounded tips. Ramifications monopodial, with single or opposing lateral branches. Branching at angles mostly between 60° and 90° (87 ± 29 [17]) without thickening at the branching points.

**Comments.** – Some similarity exists with the 'tubular branching borings' described by Zeff & Perkins (1979, Figs. 11 & 12). As the only difference their tips are inflated.

**Occurrence.** – Facies VII.

**Number of specimens.** – Many galleries within one host.

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Fig. 13. Filamentous boring casts. □A. 'Reticulate filaments', in a strophomenid brachiopod, Wanakah Member, facies IV, Wheeler Gully (loc. 11), SEM 85.4128, GPF Bo 1/24, scale bar 50 µm. □B. 'Spiny filaments' in coral, Centerfield Member, facies VII, Browns Creek (loc. 8A), SEM 85.3310, GPF Bo 1/25, scale bar 50 µm. □C. 'Smooth filaments', in *Athyris*, Wanakah Member, facies VII, Pond Brook (loc. 4), SEM 85.3626, GPF Bo 1/26, scale bar 200 µm.
Distribution of endoliths

Distribution of major categories of endolithic borings in brachiopod shells and corals sampled from seven Hamilton biofacies (see chapter on facies) is summarized in Fig. 14. The approximate percentages of infested shells, as listed here, represent ranges of values from several different collections (see Fig. 2 for distribution of collections). Relative abundance and diversity of endoliths are variable among the facies in a consistent pattern. The abundance of borings, both in terms of the percentage of shells bored, and number of borings per shell, is low in the inferred deepest water facies and generally increases into shallow water facies (see Fig. 3). At most, only 5% of all shells in facies I and II are bored. The highest frequency of occurrence (30-80% of all shells in about 10 different collections) and boring density occurs in facies IV and V.

Surprisingly, the abundance was found to be lower (only up to 10%) in facies VII, which is interpreted as a relatively clear, shallow water environment, probably slightly shallower than facies IV and V. Abrasion and/or corrosion of skeletons, commonly observed in this facies, may have obliterated delicate surficial traces. A few pelmatozoan and coral grains obtained from this facies appear to have micritized surfaces. Also, many of the larger corals and brachiopods from this facies are covered with networks of epibionts, including bryozaans, aluporoid corals, inarticulate brachiopods, and cornulitids. Thus, the impoverishment of endoliths also might be partially explained by spatial competition from these epibionts (see Golubic et al. 1975). Facies III and VI probably were deposited at similar depths to IV and V, respectively. However, the frequency of endoliths is consistently lower on shells from facies III and VI, than on their counterparts. In some samples from facies VI the percentage of borings is only 2%. This is true even in outcrops where the two analogous facies are closely interbedded.

Diversity, expressed as the number of ichnotaxa (excluding brachiopod pedicle borings), is lowest in facies I (2 taxa), but increases significantly into inferred shallower water facies, within typical calcareous upward-shallowing sequences of western New York: facies II (5 taxa), IV (8), V (9), and VII (8). A corresponding increase in diversity of endoliths into shallower

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Fig. 14. Distribution of endoliths through facies categories I-VII. The percentage of infestation is an estimate.
water is also observed in shells derived from correlative upward-coarsening sequences; however, given biofacies display lower diversities than their counterparts from more condensed, calcareous facies: facies I (2 taxa), III (2), VI (7). Particularly notable is the absence of the probable algal boring *Hyelomorpha* from facies III and VI, despite its common occurrence in facies I, II, IV and V. As noted above (see Fig. 3), facies III corresponds approximately to facies II and IV, while VI is a bathymetric analog of V, but facies III and VI probably represent environments with higher sedimentation rates and/or more turbid water.

Hence, two distinctive types of distributional patterns are observed for endoliths in Devonian shells. First, decline of abundance and diversity of endolithic ichnotaxa into the deepest part of the basin. Second, borings are more common in calcareous mudstones typical of western New York than in shells derived from analogous but thicker, non-calcareous and/or siltier counterparts that characterize the eastern Finger Lakes region; this gradient is probably related to sedimentational rather than depth differences. In terms of direct causes, decreased abundance of endoliths may have resulted from one or more of several possible factors, including deficiency of suitable substrates, deficiency of oxygen, and/or deficiency of light.

**Scarcity of host substrates.** – Relatively low densities of large shells in some of facies I might be considered as a possible explanation for the low diversity of endoliths. However, in many layers, medium-sized brachiopod shells are abundant; yet these beds do not yield common endoliths. Moreover, styliolitid shells are common at most levels, even where other shells are absent. Modern pteropod shells, and shell fragments of comparable size, are colonized by abundant and diverse endolith assemblages (Hook et al. 1984). Hence there were sufficient substrates to sustain populations of endoliths and lack of substrate cannot explain the low diversity and abundance of borings.

**Low residence time of shells on the seafloor.** – High sedimentation rate appears an equally unlikely explanation for scarcity of endoliths in facies I. Brachiopod shells in facies I are mainly disarticulated and commonly are concentrated in thin lags and stringers, generally indicating low rates of burial. Shells were evidently exposed long enough to be colonized by boring worms and *Hyelomorpha*-producing endoliths; their exposure time at the sediment–water interface should have sufficed for colonization by other endoliths if such were present in the environment. Rapid burial of skeletons may have been a factor in producing the scarcity of microborings in shells of facies III and VI; many of the fossils in these facies display excellent preservation and little epibiont overgrowth, suggesting rapid burial. However, even shell pavements found within these facies (e.g. *Tropidoleptus* or *Mucospirifer* shell beds) show relatively low boring densities and diversities, so this is not a complete answer.

**Deficiency of oxygen.** – Low oxygen (dysoxic) condition characterized facies I, and probably II in part, although the seafloor was aerated enough to permit survival of *Leiorhynchus* brachiopods and boring worms. Leiorhynchids have frequently been interpreted as being epipelic, because of their abundance in black shales. However, the occurrence of Hamilton *Leiorhynchus* in *in situ* clusters, evidence from pedicle borings that they were attached to one another, their restriction to dysoxic facies, and resemblance of their endolith assemblages to those on unquestionably benthic brachiopods of facies II, all indicate a benthic mode of life. Slight oxygen depletion actually stimulates growth of some modern cyanobacteria. This may have been the case with the microorganism that produced *Hyelomorpha* borings. Assuming that oxygen-requirements of Devonian organisms were similar to those of the modern counterparts, it is to be expected that more sensitive taxa (e.g. bryozoans, sponges) would be excluded from dysoxic zone. Thus, this factor may partly account for the low diversity in facies I. It cannot be invoked to explain low diversities in III and VI, however, as these facies include diverse and large benthic fossils.

**Depth and light limitation.** – The facies-related gradient in endolith diversity suggests the possibility of bathymetric controls on the distribution of these organisms. Unfortunately, morphological comparisons between modern and Devonian microborings provide only limited clues as to the taxonomic identity and ecological requirements of Devonian endoliths. Boring bryozoans and worms can be clearly identified, but the distribution of their modern counterparts does not provide precise depth inference. Modern
boring bryozoans and worms range from tens down to several hundreds of meters. *Platyden-drina* shows some similarity to the sponge boring *Entobia megastoma* (Fischer) Bromley & D'Alessandro 1984. Today, most boring sponges occur at depths of less than 100 m, but several species advance down to more than 1400 m (Bromley 1970). The biological affinities of the other rosette-shaped borings, except *Hyellomorpha*, is unknown.

*Hyellomorpha* resembles borings of modern *Hyella*, a photoautotrophic endolith, although an identification based on this comparison is tenuous. Borings and body fossils of *Hyella* have been recognized in silicified ooids of late Precambrian age 700–800 My (Campbell 1982; Knoll et al. 1986), and its presence in Devonian seas is to be expected. We conclude that *Hyellomorpha* was probably produced by a photoautotroph, and, as such, its presence places the strongest constraints on water depth.

The penetration of light in the waters of modern oceans varies latitudinally and regionally. Deepest penetration of light, as well as of photoautotrophic endoliths is observed in oligotrophic, tropical oceans. Particular species of photoautotrophic endoliths, specialized to utilize low light, were recovered live from depths of over 200 m in clear waters of the Mediterranean Sea (Fredj & Falconetti 1977) and the Straits of Florida (Lukas 1979); they were reported to extend to 80–110 m on the Puerto Rico slope (Budd & Perkins 1980). Most photoautotrophic endoliths, however, are restricted to much shallower waters, where they occur in abundance. *Hyella* extends from the intertidal zone downward to about 100 m in clear, oligotrophic seas (Lukas & Golubic 1983). The extent of the photic zone, and accordingly the distribution of photoautotrophic endoliths in eutrophic areas of upwelling, in turbid coastal waters (e.g. near estuaries) and generally in higher latitudes is much shallower.

According to most recent reconstructions (Kent 1985; Faill 1985; Ettensohn 1985; Woodrow 1985) the paleolatitude of the northern Appalachian Basin during the Middle Devonian was within a few degrees of the equator. However, the abundant influx of terrigenous sediment, associated with the prograding Catskill deltaic complex, must have decreased light penetration considerably. Moreover, the prevalence of black, organic-rich sediments, commonly with abundant tasmanitids, in deeper portions of the basin, suggests that Devonian seas were relatively eutrophic; high primary productivity also would have reduced water clarity. Hence, if our interpretation of *Hyellomorpha* is correct, even the deepest studied facies of the Middle Devonian were deposited within a shallow euphotic zone, at less than 100 m.

In modern shallow water environments photoautotrophic euendoliths (algae and cyanobacteria) are capable of deep penetration resulting in total destruction of shells and skeletal fragments, starting from the surface of a grain and forming an inwardly expanding micritic envelope (Bathurst 1966). Such micritization is rare in the studied Devonian fossils, but does appear to be present in crinoid grainstones, which have been interpreted as the shallowest water facies of the Hamilton Group (Savarese et al. 1986). However, these facies were not included in the present study owing to the poor preservation and difficulty of extraction of fossils.

With depth approaching the limit of light penetration, algal borings become shallower and confined to the substrate surface (Budd & Perkins 1980). Light-independent heterotrophic endoliths as a rule, are also confined to the surface layers of the substrate. Thus, the shallow subsurface position of borings does not necessarily indicate light limitation (although for *Hyellomorpha* this mode of development is suggestive of such limitation). The absence of deep borings in most Hamilton facies may indicate that these sediments accumulated at depths greater than about 10 to 20 m. In modern oceans the limit for abundant deep and micritizing (algal) penetration is encountered in shallows of less than 20 m in tropical (Swinchatt 1969), as well as arctic, waters (15–26 m; Bromley & Hanken 1981).

Reduced quantity and diversity of endoliths in facies III and VI, as compared with facies II, IV and V (which were deposited in similar water depths), may be best explained by higher turbidity of these environments (represented by III and VI). Increased turbidity may have adversely affected filter-feeding organisms as well as diminishing light penetration. The latter effect may account for the absence of *Hyellomorpha* from these facies.

Conclusions

Examination of over 2000 brachiopods and corals, derived from a spectrum of 7 facies in the
Middle Devonian Hamilton Group has revealed about 13 new ichnotaxa of endolithic borings produced by algae, sponges, ctenostome bryozoans, worms, and organisms of unknown affinity. Relatively few microborings can be clearly matched with extant endolithic borings. In general, the density of borings per shell is also considerably lower than that found in most modern shell substrates.

Most of the Devonian endolithic borings represent new ichnospecies, and four new ichnogenera of rosette type borings are described: *Nododendrina*, *Ramosendrina*, *Platyendrina* and *Hyellomorpha*. The formerly described ichnogenera *Clionolites* Clarke 1908, *Olkenbachia* Solle 1938, and *Trypanites* Mâgédefrau 1932, are reviewed and are considered to be *nomina dubia*. The ichnogenus name *Specus* Stephenson 1952 is suggested for large cylindrical worm borings. An interesting spinoff of this study is discovery of the oldest known brachiopod pedicle borings.

Hamilton microborings display a gradient of increasing abundance and diversity from black 'Leiorthycon'-bearing shale facies I (3 taxa), to coral and brachiopod biofacies V (10 taxa), VII (9 taxa). In presumed clear water calcareous biofacies this general increase in diversity probably parallels a depth gradient. A surprising result is the drop in microboring abundance (but not diversity) in shallow biostromal biofacies VII. However, extensive corrosion and apparent micritization of shells and coral from these facies may have damaged skeletal surfaces and partly eradicated delicate traces. Competition by epibionts may also have excluded microborings.

Previous bathymetric inferences for Hamilton facies are rather strongly supported by endolithic distribution. The occurrence of the probable algal boring *Hyellomorpha*, in even deepest water black shale facies, indicates that the full facies spectrum was deposited in the photic zone, probably less than 100 m. Furthermore, an uppermost depth limit of 10–20 m can also be surmised from the absence of deep, vertically penetrating borings in biofacies I through VII. Hence, the evidence from microborings is consistent with the previously inferred depth range of about 10 to 100 m.

Another, very significant conclusion of this study is that non-calcareous, commonly silty, shallow water biofacies III and VI (i.e. *Mucrosipirifer* and *Tropidoleptus*) display considerably lower abundance and diversities of microborings than do more condensed, calcareous biofacies (IV and V). Furthermore, *Hyellomorpha* was found to be absent from non-calcareous facies. These observations are consistent with previous inference of relatively high turbidity in the *Mucrosipirifer* and *Tropidoleptus* facies. This correspondence suggests the potential use of microborings as an indicator of relative water clarity in cases where depth can be inferred independently, although such application requires more rigorous confirmation in modern environments.

Thus this preliminary study of Devonian endolithic traces demonstrates the potential application of such trace fossils in paleoecology. We anticipate that the inventory of microborings and its relation to well-defined facies types will become an important tool in the reconstruction of other sedimentary basins (see Vogel et al. 1984).

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**References**


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Appendix

Locality register (all quadrangles 1:24,000)

1A Eden Quadrangle - Erie lakeshore bluffs S of the mouth of Eighteenmile Creek 4.0-5.5 km SW of Wanakah, Erie Co., NY (Wanakah, Tichenor & Windom Members).

1B Eden Quadrangle - banks of Eighteenmile Creek 0.8 km E (upstream) from NY Rt. 5 overpass, North Evans, Erie Co., NY (Wanakah, Tichenor & Windom Members).

2 Buffalo Northeast Quadrangle - floor of large, abandoned Penn Dixie Cement Co. shale pit, 0.5 km NE of the junction of Big Tree and Buy View Roads, Blasdell, Erie Co., NY (Wanakah, Tichenor & Windom Members).

3 East Aurora Quadrangle - bank of Buffalo Creek N and S of (upstream from) old Bullis Road bridge 3 km W of Marilla, Erie Co., NY (Wanakah, Jaycox, Tichenor, Deep Run, Menteth, Kashong & Windom Members).

4 East Aurora Quadrangle - banks of Pond Brook 0.4 km SE of its confluence w. Buffalo Creek, near intersection of Bowen and Chair Factory Roads, Elma, Erie Co., NY (Lower Wanakah Member).

5 East Aurora Quadrangle - cap of small falls in Cayuga creek, 0.4 km S of Clinton Road (Rt. 354) bridge and just W of Eastwood Road, Alden, Erie Co., NY (Geneseo Shale).

6 Corfu Quadrangle - low banks and bed of Eleven Mile Creek 0.5 km E of Harlow Road and 1.9 km NE of intersection of Harlow Road and US Rt. 20, Darlen, Geneseo Co., NY (Ledyard Shale).

7 Batavia South Quadrangle - low cuts along (abandoned) Delaware, Lackawanna and Western Railroad immediately E and W of Center Road, 3 km N of Bethany Center, Geneseo Co., NY (Centerfield Member).

8A Geneseo Quadrangle - waterfalls and banks of Browns Creek, 0.5 km W of trestle for Geneseo and Wyoming Railroad, York, Livingston Co., NY (Levanna & Centerfield Members).

8B Geneseo Quadrangle - Banks of creek and low waterfall in Spezzano Gully, 0.5 km W of NY Rt. 35 and 2.4 km S of the junction of NY Rts. 36 and 63, Livingstone Co., NY (Windom Member).

10 Leicester Quadrangle - shale dumps and rail road cut along Geneseo and Wyoming Railroad; 0.3-0.5 km S of NY Rt. 63, and 0.2 km N of buildings for International Salt Co., Retsof mine, just SW of Retsof Corners, Livingstone Co., NY (Kashong Member).

11 Geneseo Quadrangle - high waterfalls and banks of Wheeler Gully (north fork of Jaycox Creek) 0.2-1.6 km W of (downstream from) NY Rt. 39, 3.5 km N of Geneseo, Livingstone Co., NY (Centerfield, Ledyard, Wanakah, Jaycox, Tichenor Deep Run, Menteth & Kashong Members).

12 Canandaigua Lake Quadrangle - banks of Menteth Gully 0.3-1.0 km W of (upstream from) West Lake Shore Road overpass 2.4 km SE of Chisire, Ontario Co., NY (Deep Run, Menteth, Kashong & Windom Members).

13 Canandaigua Lake Quadrangle - banks and bed of unnamed creek (locality called Reed Gully), 0.1-0.5 km W of NY Rt. 364, beginning at bridge 0.2 km S of junction of Rt. 364 and Hall Road, Gorham, Ontario Co., NY (Kashong & Windom Shale Members).

14 Geneva South Quadrangle - high falls and adjacent shale banks along Kashong Creek 0.2-1.4 km W of NY Rt. 14, Bellona, Yates Co. NY (Ledyard, Wanakah, Jaycox, Tichenor, Deep Run, Menteth, Kashong & Windom Members).

15 Romulus Quadrangle - quarry (town dump) immediately S of Poorman Road, 0.5 km W of Fayette, Seneca Co., NY (Levanna & Centerfield Members).

16 Ovid Quadrangle - creek banks along Bloomer and Mack Creeks, near the east edge of the Quadrangle, 3.2 km E of Hwy Corners, Seneca Co., NY (King Ferry, Tichenor, Deep Run, Menteth & Kashong Members).

17 Sheldrake Quadrangle - shale pit on south side of Barnum Creek just W of NY T89 and 0.2 km S of Ovid/Romulus townline, Seneca Co., NY (Windom Shale).

18 Sheldrake Quadrangle - shale pit (Hubbard quarry) immediately E of NY Rt. 89 and 0.1 km N of Lively Run, Cowert, Seneca Co., NY (Geneseo & basal Sherburne Members).

19 Sheldrake Quadrangle - exposures on east shore of Cayuga Lake, at Stony Point, 2.7 km S of Aurora, Cayuga Co., NY (Centerfield Member).

20 Ludlowville Quadrangle - cliff exposures along railroad cut on east shore of Cayuga Lake and adjacent creek banks along Gulf Creek, 300 m E of Portland Point, Cayuga Co., NY (Otisco, King Ferry, Portland Point & Windom Members).

21 Spafford Quadrangle - cliff exposures along east shore of Skaneateles Lake at Halls Landing, S of Ten Mile Point, Onondaga Co., NY (Centerfield (=Chenango) & Otisco Members).

22 Spafford Quadrangle - roadcut cliffs adjacent to Skaneateles Lake 0.2-0.3 km NW of Jenny Point, toward Spafford, Onondaga Co., NY (Otisco Shale Member).
23 Tully Quadrangle – exposures on east branch of Butternut Creek, 0.9 km WSW of the junction of Berry and Stebbins Roads, near Apulia, Onondaga Co., NY (Chenango Member).

24 West Eaton Quadrangle – large shale borrow pit (Pierreville quarry) on Soule Road 0.2 km W of intersection w. Bradley Brook Road, Lebanon, Madison Co., NY (Windom Member).

SM1, SM2, Collection of Smithsonian Institution, Washington, DC, Onondaga limestone, Edgecliff Member, Williamsville, Erie Co., NY. SM1: Heliothylum 'USNM exc. 103'; SM2: Siphonophrentis, 'USNM 135719'.