



COMMENSAL BORINGS FROM THE MIDDLE DEVONIAN OF CENTRAL NEW YORK: ECOLOGIC AND TAXONOMIC REVIEW OF *CLIONOIDES*, *CLIONOLITHES*, AND *CANALIPARVA* N. ICHNOGEN.

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ABSTRACT—The examination of 730 borings within 88 brachiopod hosts from the Middle Devonian of central New York State revealed four ichnospecies belonging to three ichnogenera that have taxonomic histories riddled with confusion, controversy and contradiction. New observations of the ichnotaxa question long-held views of a simple morphologic differentiation between sponge borings and worm borings. *Clionoides* Fenton and Fenton, 1932 is here considered a sponge boring, which is comprised of a complex, multi-dimensional system of tunnels, shafts, canals, microterraced bowl-shaped structures and cone extensions, and is a senior synonym of *Paleosabella* (McCoy 1855) and *Vermiforichnus* Cameron, 1969a. *Clionolithes* Clarke, 1908 is a sponge boring possessing a rosette, branching network extending from a central node and is a senior synonym of *Nododendrina* Vogel et al., 1987 and *Ramodendrina* Vogel et al., 1987. The creation of *Canaliparva circularis* n. ichnogen. n. ichnosp. is needed to accommodate simple, vertically oriented, U-shaped tunnels that are indicative of worm activity. Paleoecologic evidence supports a commensal relationship between the endoliths and hosts based upon boring site frequencies in the hosts, boring patterns and five inter-specific co-occurrences between traces. These new data suggest greater diversity and ecologic complexity in ichnofaunal paleocommunities from the Middle Devonian than previously recognized.

INTRODUCTION

FOSSILIZED BIOTIC interactions reveal important information that permits interpretations of relationships among ancient organisms. When preserved within the fossil record, borers and their traces within the skeletons of host organisms provide direct evidence of such interactions. Although the Devonian Period documents a Paleozoic peak in traces (Taylor and Wilson, 2003; Bromley, 2004; Wilson and Palmer, 2006) and is known for its morphologically and behaviorally diverse suite of borings, many of these traces are constructed by uncertain trace makers resulting in an ichnotaxonomy that is particularly rife with confusing nomenclature and in some cases disregards taxonomic principles. Although the past 100 years have witnessed considerable progress in understanding Devonian endolithic traces, there still remains considerable confusion, contradiction and controversy as researchers attempt to identify the original trace makers, interpret the traces within a paleoecologic framework and establish a stable ichnotaxonomy.

Among potential trace makers of Devonian borings, clionaid sponges, spionid polychaete worms, phoronids, and several bryozoan clades (ctenostome, cryptostome, and cyclostome) are most commonly cited (see Taylor and Wilson, 2003 for a useful review). Many authors (Glaub and Vogel, 2004; Glaub et al., 2007) have supported a simple morphologic differentiation between borings, and have suggested that the majority of traces correspond exactly to the body outline of the boring organism, which produces species-specific features created by the trace maker. Teichert (1945) used simple morphologic criteria to distinguish between sponge and worm borings and suggested that more or less straight or simply curved, single or branching tubes are usually attributed to the activity of worms whereas more irregular excavations, often branching from a central node in a dendritic fashion, are attributed to sponge activity. This morphologic differentiation of traces has provided the

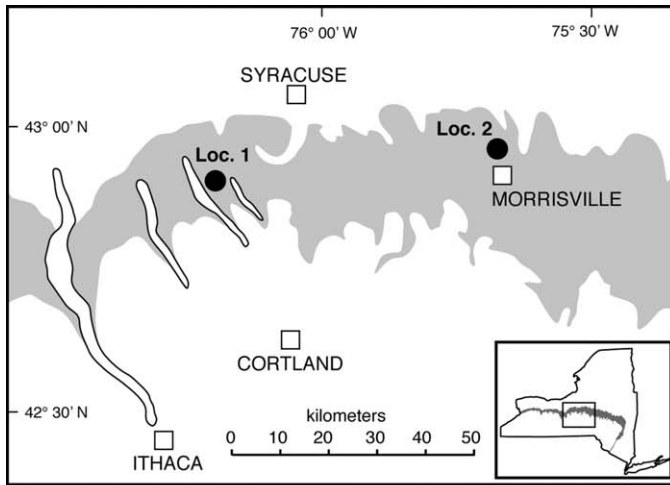
foundation for many interpretations of traces and trace making organisms; however, based on new observations within this study, their separation may not necessarily be as easily distinguishable as Teichert (1945) originally described.

In this paper, we describe and illustrate several ichnotaxa attributed to sponges and worms colonizing within exceptionally well-preserved brachiopod hosts from the Middle Devonian Hamilton Group of central New York State. Interpretations of ecological relationships between the host species and the traces produced by different endoliths are made based on boring site frequencies in the hosts, boring patterns and inter-specific co-occurrences between traces. Based on our observations of endolithic boring morphology, we propose new interpretations, which question long held views of Devonian sponge and worm ichnotaxonomy.

GEOLOGIC AND PALEOECOLOGIC SETTING

The Middle Devonian Hamilton Group in central New York State represents a relatively thick succession of shelfal to basinal synorogenic marine sediments deposited along the eastern margin of the Appalachian foreland basin during the late Eifelian and Givetian (Cooper, 1930; Rickard, 1975; Brett and Baird, 1996). The Hamilton Group is predominantly composed of an eastward thickening wedge of clastic marine sediments with a minor carbonate component and passes eastward to coastal and fluvial dominated sequences of the Catskill Delta complex (Cooper, 1941; Etensohn, 1985).

The majority of specimens were collected from a small privately-owned quarry at Rose Hill in the Township of Marietta, Onondaga County, New York (Fig. 1) in which approximately 12 m of the Otisco Member of the Ludlowville Formation is exposed. The lower 6.7 m of the outcrop consists of fossiliferous, dark gray mud shale, which yields a diverse, abundant, and well-preserved marine fauna, including brachiopods, bivalves, trilobites, bryozoans, crinoids and anthozoans



Age	Group	Formation	Member	Lithology	
Middle Devonian	Givetian	Tully (pt.)	Lower	[Lithology: brick pattern]	
			Moscow	Windom	[Lithology: dotted pattern]
		Portland Point		[Lithology: brick pattern]	
		Ludlowville	Owasco	[Lithology: brick pattern]	
			Spafford	[Lithology: brick pattern]	
			Ivy Point	[Lithology: brick pattern]	
			Otisco	[Lithology: brick pattern]	
			Centerfield	[Lithology: brick pattern]	
		Skaneateles	Pompey	[Lithology: brick pattern]	
			Butternut	[Lithology: brick pattern]	
	Delphi Station		[Lithology: brick pattern]		
	Mottville		[Lithology: brick pattern]		
	Eifelian	Marcellus Subgroup	Oatka Cr.	Pecksport	[Lithology: brick pattern]
				Solsville	[Lithology: brick pattern]
				Bridgewater	[Lithology: brick pattern]
Chittenango				[Lithology: brick pattern]	
Cherry Valley				[Lithology: brick pattern]	
Union Springs	[Lithology: brick pattern]				
Onondaga (pt.)	Seneca	[Lithology: brick pattern]			

FIGURE 1—Generalized Middle Devonian stratigraphy of central New York and stratigraphy location of Rose Hill (Loc. 1) and Swamp Road (Loc. 2). Shaded area represents outcrop distribution of Hamilton strata.

(Ross et al., 2007). Approximately 5 m of fossiliferous, coarser-grained rusty brown silt-shale of the upper Otisco Member overlies the mudshale and contains an abundant and taxonomically rich fauna similar to that of the lower parts of the quarry. Within the base of the upper Otisco Member are several beds (each about 5 cm thick) rich in rugosan and tabulate corals that likely correlate to the Joshua Coral Bed (Ross et al., 2007). Specimens containing borings described here were collected in situ from both the lower and upper parts of the quarry and from recently eroded talus at the base of the quarry.

Additional specimens were collected from the Oatka Creek Formation (Marcellus Subgroup as per Ver Straeten and Brett, 2006) at a small hillside quarry at Swamp Road, approximately

3.5 km north of Morrisville, New York. This locality is well known for its diverse and exceptionally well preserved fauna (Rollins et al., 1971; Carter and Tevesz, 1978; Bailey, 1983) and is assigned to the Pecksport Member (Grasso et al., 1985). In the quarry, the Pecksport Member is composed of dark gray mud shale coarsening upwards into a medium-fine brown siltstone. Specimens reported herein were collected in situ from a distinctive shell bed dominated by *Spinocyrtia* brachiopods in apparent living position approximately 3 m above the base of the outcrop.

MATERIAL AND METHOD OF STUDY

Collections.—More than 1,000 articulated and disarticulated brachiopods, bivalves, and other macrofauna from both localities were collected and examined as potential hosts. Additional specimens from the State University of New York College at Cortland paleontological collections from both localities were included in the study. Unless otherwise noted, illustrated specimens and scanning electron microscope (SEM) stubs are curated within the collections at the New York State Museum, Albany (NYSM). Other repositories include: U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Division of Paleontology, American Museum of Natural History, New York (AMNH); Sedgwick Museum, Cambridge University (SMCU); and Institut für Geowissenschaften-Paläontologie, J. W. Goethe-Universität, Frankfurt (GPIF).

Of the material collected and examined, 103 specimens were found to contain borings with the majority (88 specimens) infesting only three host brachiopod taxa: *Athyris spiriferoides* (Eaton, 1831), *Spinocyrtia granulosa* (Hall, 1867), and *Mucrospirifer mucronatus* (Conrad, 1841). Borings were also found within the brachiopods *Rhipidomella penelope* (Hall, 1860), *Pseudoatrypa devoniana* (Webster, 1921), *Strophodonta demissa* Hall, 1867, and in a few species of bivalves, but due to their low abundance in both host individuals and endolithic traces, only the three major brachiopod host taxa are presented in this study.

A total of 730 borings were found within the 88 infested hosts: 122 *Clionoides clarkei* (Cameron, 1969a) within 44 hosts, 123 *Clionolithes* ichnospecies Clarke, 1908 within 23 hosts and 485 *Canaliparva circularis* n. ichnogen. n. ichnosp. within 56 hosts. Since *Clionolithes* ichnospecies can only be differentiated at high magnifications (>50×), the abundance of both *Clionolithes radicans* (Clarke, 1908) and *Clionolithes cervicornis* (Vogel et al., 1987) are considered together.

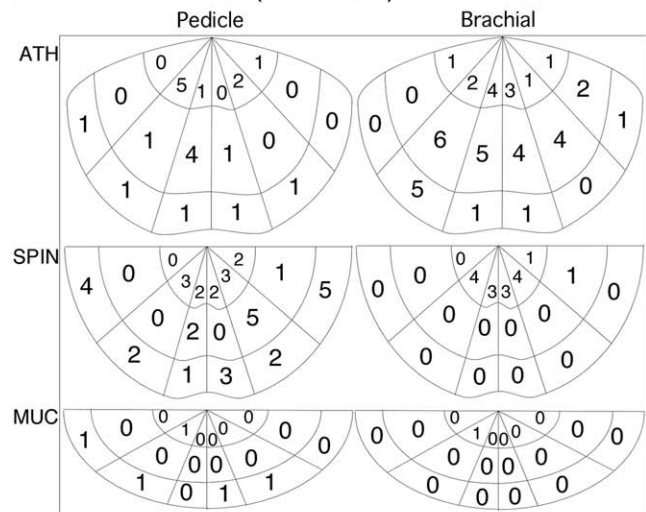
Examination techniques.—Brachiopod hosts were initially examined dry using binocular microscopy to determine the abundance and spatial distribution of borings on individual hosts. Traces were recorded as occurring within valve sectors (Fig. 2) following a modified version of the binning scheme of Kesling et al. (1980) and Sparks et al. (1980) to account for variability in size and taxonomic affinity of host species. Separate records of boring frequencies were tabulated for different host species, as well as for both pedicle and brachial valves (Fig. 2).

Select specimens were further prepared for examination as natural molds and artificial casts using a two-component epoxy embedding technique that impregnated hollow borings and strengthened sediment-filled casts. A dilute (10%) hydrochloric acid solution was used to remove the host skeletal matrix around the molds and epoxy casts, which revealed the 3-dimensional networks of the borings. These, and additional specimens, were mounted on standard aluminum stubs with carbon tape, and gold coated prior to imaging using New York State University College at Cortland's ISI DS-130C SEM at 15 kV and a working distance of 20 mm.

Clionoides clarkei (Cameron)

SYSTEMATIC ICHNOLOGY

Ichnogenus CLIONOIDES Fenton and Fenton, 1932



Type ichnospecies.—*Clionoides thomasi* Fenton and Fenton, 1932 by original designation; Middle Devonian, Iowa.

Diagnosis.—Widely spaced, branched, irregularly disposed, moderately curved tubes; circular in cross section; variable in length. Tunnels may terminate with tapering or swollen end, or maintain a uniform diameter; walls and floors smooth or perforated. Complex three dimensional network involving tunnels, shafts, canals, microterraced bowl-shaped structures and cone extensions may be present. All located within the upper and middle shell substrate of the host.

Included ichnospecies.—*Clionoides thomasi* Fenton and Fenton, 1932, *Clionoides clarkei* (Cameron, 1969a) and questionably *Clionoides frimbriatus* (Stephenson, 1952).

Remarks.—The ichnogenus and similar forms have a complex nomenclatural history, which stems from specimens collected and described by McCoy (1855) and Clarke (1908, 1921). Although summaries of the nomenclatural history have been previously published (Fenton and Fenton, 1932; Teichert, 1945; Cameron, 1969a), new observations require a review and clarification of the history of this ichnotaxon, which is described below and within Table 1:

McCoy (1855, p 260, pl. 1B. fig. 1, 1a) named and described the Silurian boring, *Vioa prisca* McCoy, 1855, and considered it to be the oldest known boring sponge trace.

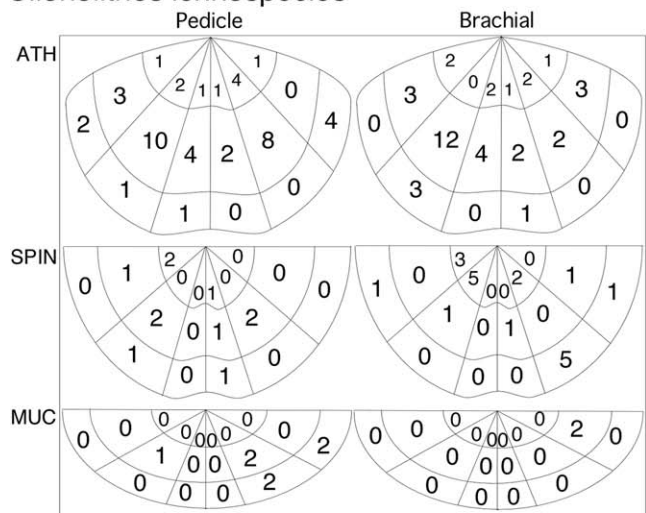
Clarke (1908, p. 168) also considered *V. prisca* (under the name *V. prisca*) as evidence of boring-sponge activity, but proposed the new ichnogenus *Clionolithes* Clarke, 1908 to replace *Vioa*, which was preoccupied. Clarke illustrated part of McCoy's original figure (pl. 8, fig.1) and several Devonian examples under *Clionolithes prisca* (McCoy, 1855) (Clarke, 1908, pl. 8, figs. 2–8, pl. 9, fig. 1).

Clarke (1921) concluded that *Clionolithes prisca* was produced by boring annelids. Clarke (1908) previously limited *Clionolithes* to the activity of boring sponges creating rosette forms and thus erected *Palaeosabella* Clarke, 1921, in which he included both previously illustrated (figs. 77, 94–100, 102) and newly illustrated material (figs. 78,79, 81–83, 101, 103).

Fenton and Fenton (1932) concluded that *Vioa prisca* was produced by a boring sponge and questionably placed McCoy's Silurian trace into the morphologically similar ichnogenus *Topsentia* Clarke, 1921 and referred to the forms as *Topsentia* (?) *prisca* (McCoy 1855). *Topsentia* has more recently been synonymized with *Entobia* Bronn, 1837; however, Tapanila (2006) suggested that *Topsentia* (?) *prisca* is morphologically different than *Entobia*. Although *V. prisca* lacks the central chamber indicative of *Entobia*, the cylindrical tunnels resemble the orientation of those that radiate from the central chamber in *Entobia*. We suggest that *V. prisca* remain ambiguous and should stay separate from *Entobia* and *Palaeosabella*. Once removing *V. prisca* from *Palaeosabella*, *Palaeosabella* becomes affiliated only with Clarke's (1908, 1921) specimens and is without a type specimen.

Fenton and Fenton (1932) introduced *Clionoides*, which was suggested as being produced by boring sponges. They originally described the ichnogenus as widely spaced tunnels, branching,

Clionolithes ichnospecies



Canaliparva circularis n. ichnogen. and ichnosp.

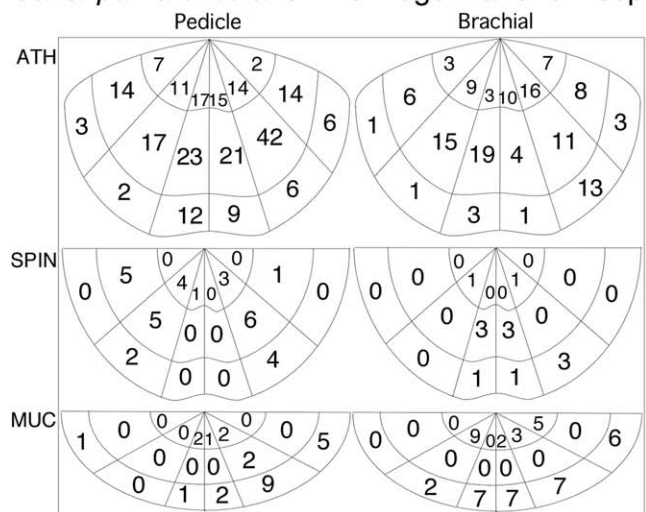


FIGURE 2—Grid count frequencies for *Clionoides clarkei*, *Clionolithes* ichnospecies, and *Canaliparva circularis* n. ichnogen. n. ichnosp. Host species

include ATH, *Athyris spiriferoides*; SPIN, *Spinocyrtia granulosa*; and MUC, *Mucrospirifer mucronatus*. Each half of the valve was divided into three sectors diverging from the beak: one sector adjacent to the hinge, a second near the fold/sulcus and a third sector including the fold/sulcus. The host shell was then divided concentrically into three more subsectors which measured 10 cm from the beak and 10 cm from the margin, with the middle sections changing in size based on the overall size of the host shell.

TABLE 1—Listing of borings and suggested ichnogenera synonymies.

Ichnotaxon	Synonymy	General description	Originator
<i>Clionoides</i> Fenton and Fenton, 1932*	<i>Palaeosabella</i> Clarke, 1921 ?Specus Stephenson, 1952 <i>Vermiforichnus</i> Cameron, 1969a	Tunnel (1 mm in diameter) with complex network of small shafts, canals, microterraced bowl-shaped structures and cone extensions.	Sponge
<i>Entobia</i> Bronn, 1837	? <i>Vioa</i> McCoy, 1855 <i>Topsentia</i> Clarke, 1921	Small branching tunnels extending from a central chamber.	Sponge
<i>Trypanites</i> Mägdefrau, 1932	(more research is needed to provide possible synonymies)	U-shaped tunnel/tube with consistent diameter throughout; not associated with shafts, canals, pits or cone extensions.	Worm
<i>Clionolithes</i> Clarke, 1908*	<i>Nododendrina</i> Vogel et al., 1987 <i>Ramodendrina</i> Vogel et al., 1987	Rosette network extending from a central node.	Sponge
<i>Canaliparva</i> n. ichnogen.*	<i>Specus</i> (Vogel et al., 1987)	Simple, small, vertically shallow U-shaped tubes	Worm

* traces found within this study.

irregularly disposed with moderate curvature and no trace of radial arrangement (Fenton and Fenton, 1932). The form possesses tunnels (0.5–1.5 mm in diameter), canals and perforations (Fenton and Fenton, 1932).

Teichert (1945, p. 202) concluded that “no such species as ‘*Palaeosabella prisca* Clarke’ exists.” He further suggested that Clarke (1921) wrongly affiliated his specimens with McCoy’s, making *Palaeosabella* a monotypic ichnogenus with *V. prisca* as its probable type; therefore, *Palaeosabella* should be considered *nomina dubia*. Teichert (1945) tentatively synonymized *Palaeosabella* with *Topsentia*, but neglected to mention any details on *Clionoides*.

In a study on Late Cretaceous traces, Stephenson (1952) erected *Specus* (type species *Specus frimbriatus* Stephenson, 1952) as a sponge boring, which consists of tunnel casts that are circular in cross section, club-shaped (0.2–0.75 mm in diameter), straight, curved or irregular, which increase in size to a subhemispherical internal end. The orientations of *Specus* are highly variable, but possess a similar expanding boring pattern, which is prevalent in *Palaeosabella* (Clarke, 1921, fig. 99; Stephenson, 1952, pl. 8, figs. 5, 6). Stephenson (1952, p. 51), however, stated that “*Specus* should perhaps be regarded as a convenient form genus to which fossil borings of this kind may be referred to until more is known about the organism that produced them.”

Cameron (1969a) introduced the ichnogenus *Vermiforichnus* (type species *Vermiforichnus clarkei* Cameron 1969a), which he attributed to the activity of a spionid polychaete. Cameron (1967, 1968, 1969a) also described the pyritized remains of a worm (*Vermiforifacta rossinsi* Cameron, 1969a) resembling Recent *Polydora* (Galtsoff, 1964) in one of the borings, and concluded that it was the trace maker. Subsequently, Vogel et al. (1987) questioned the validity of the preserved worm as the trace maker and suggested that another organism may have produced the trace, perished, and the worm gained occupancy and was fossilized there. Blake and Evans (1973) noted that the simple tubes of *Vermiforichnus* were unlike any known Recent spionid boring, although later Pickerill (1976) described well preserved tubes as *Vermiforichnus*, which distinctively exhibited transverse segmentation suggesting a worm trace maker. Regardless of the validity of the relationship between the preserved worm and the boring, Cameron (1969a) incorrectly designated Clarke’s original specimens of *P. prisca* as the holotype (Clarke, 1921, fig. 81) and paratypes (Clarke, 1921, figs. 77–80, 82, 83, 95–103) for *Vermiforichnus* and correctly excluded McCoy’s specimen from his newly established ichnogenus.

Bromley (1972) synonymized *Specus*, *Vermiforichnus*, and six other ichnogenera with *Trypanites* Mägdefrau 1932. Similarly, Kobluk et al. (1978) synonymized *Specus*, four other ichnogenera and questionably *Vermiforichnus* with *Trypanites* and suggested various organisms as the originators of these

seemingly similar borings. Kobluk et al. (1978) suggested that *Palaeosabella prisca* (McCoy, 1855) be synonymous with *Vermiforichnus* and that *Trypanites* as the senior synonym for *Vermiforichnus* with the probable originator being a spionid. No descriptions of the borings were provided by Bromley (1972) or Kobluk et al. (1978). We suggest that *Vermiforichnus* should not be considered synonymous with *Trypanites* and should be limited to borings that are simple cylindrical tunnels and tubes that do not have a complex three dimensional assemblage of morphologic features.

Like *Clionoides*, *Trypanites* also has a complex nomenclatural history. Originally described by Mägdefrau in 1932, the cylindrical, single-entrance, pouch-shaped or U-shaped traces are present within a variety of hosts including brachiopods, bivalves, corals, stromatolites and are present within firmgrounds (Bromley, 1972; Kobluk et al., 1978; Frey and Seilacher, 1980; Pemberton et al., 1980). Bromley (1972), Kobluk et al. (1978), Kelly and Bromley (1984) and Wilson (2007) provide some insight on the nomenclatural problem, but much more is needed to fully describe the complexity surrounding the simple form, which is outside the scope of this paper.

Hoare and Walden (1983) suggested that large borings commonly found within the brachiopod host *Paraspirifer bownockeri* (Stewart, 1927) from the Silica Formation in northwestern Ohio be assigned to *Vermiforichnus clarkei* instead of *Clionoides*. They proposed that the borings were produced by polychaete worms instead of sponges, as many previous publications had suggested (Hoare and Walden, 1983).

In a larger work on Devonian endoliths and microborings from New York, Vogel et al. (1987) suggested that Cameron (1969b) identified only one of two worm ichnospecies within his study. The bimodal histogram of endolith tube diameters illustrated by Cameron (1969b, fig. 5b) was hypothesized as indicating a seasonal or yearly population structure but was later interpreted by Vogel et al. (1987) to indicate two distinct ichnospecies attributed to worms: *Specus* being smaller in size (0.2–0.3 mm in diameter) and *Vermiforichnus* being larger in size (~1.2 mm in diameter). However, as noted above, *Specus* (as described by Stephenson, 1952) possesses forms that are much larger (~1 mm in diameter) than the ones identified by Vogel et al. (1987).

Plewes (1996) and Bromley (2004) reinstated *Palaeosabella* and deemed it a useful name and a senior synonym for *Specus*. Bromley (2004) defined *Palaeosabella* as tubes, which slightly expand distally, and further stated that specimens identified by Clarke are *Palaeosabella* and not *Trypanites*. Bromley (2004) also suggested that many forms described as *Vermiforichnus* belong to *Palaeosabella* or *Trypanites*, and those considered *Vermiforichnus* by Pickerill (1976) belong to *Trypanites*.

Wilson (2007) described *Palaeosabella*, *Trypanites*, *Clionoides* and *Vermiforichnus*, and noted the key morphological features distinguishing each. *Palaeosabella* slightly enlarges distally,

while *Trypanites* maintains a consistent diameter throughout the length of the form (Wilson, 2007). *Clionoides* describe tubular borings with irregular branches that are attributed to sponge activity (Wilson, 2007). *Vermiforichnus* possess distinctive transverse segmentation when well preserved and was named after the soft-bodied fossilized worm trace maker, *Vermiforafacta* (Wilson, 2007).

Wilson (2007) and others (Taylor and Wilson, 2003; Wilson and Palmer, 2006) have described forms attributed to *Palaeosabella* from the Ordovician of Ohio. Wilson and Palmer (2006) suggested that *Palaeosabella* (here considered *Clionoides*) resembles *Trypanites* and the two may be indistinguishable from one another unless a slightly clavate terminus is observed. Since the genus *Palaeosabella* is here considered *nomina dubia*, many of these previously described traces belong to either *Clionoides* or *Trypanites* based on morphologic characteristics.

In summary, Clarke (1921) proposed the ichnogenus *Palaeosabella*, but wrongly affiliated *P. prisca* (McCoy) with the ichnogenus. Since *Palaeosabella* was defined by ambiguous forms, it is without a holotype and becomes *nomina dubia*. However, we suggest that Fenton and Fenton (1932) failed to see the similarities between Devonian *Palaeosabella* and their newly established ichnogenus *Clionoides*, and that the two should be considered synonyms, under the sponge boring ichnogenus *Clionoides*. *Vermiforichnus* and *Specus* become probable junior synonymies of *Clionoides* but exclude forms described by Pickerill (1976) that exhibit distinct transverse segmentation, which is indicative of worm activity, and those described as *Specus* by Vogel et al. (1987) which possess small cross-sectional diameters (see Systematic Ichnology Section on *Canaliparva* n. ichnogen. for further details). *Trypanites* should remain separate from *Clionoides* and should describe cylindrical tunnels and tubes that maintain a consistent diameter and lack three dimensional networks.

Clionoides is limited to tunnels with an average diameter of 1 mm that occasionally branch (7.9%). As stated above, *Clionoides* exhibits a variably swollen terminus that may be or may not be expanded; tunnels may maintain a consistent diameter (Fig. 3.2, 3.8), or be slightly swollen (Fig. 3.7) or bi-clavate (Fig. 3.9, 3.10). It is therefore important to examine all borings on a specific host as well as the entire population within the locality to determine variability of ichnotaxonomic traits. Tunnels are oriented parallel to the shell surface and are within the upper and middle shell substrate with tunnel apertures infrequently preserved. Tunnels predominantly extend from the hinge/umbo of brachiopod hosts and radiate towards the anterior margins of host valves (Figs. 3.1, 3.2, 4.1), but are not limited to this orientation (Fig. 3.3–3.5, 3.7). Well preserved specimens may exhibit an array of three dimensional forms including microterraced bowl-shaped structures, (Fig. 4.3) vertical shafts, canals (Fig. 4.2) and perpendicular cone shaped extensions off the main tunnel (Fig. 3.10–3.12) which were originally described as perforations by Fenton and Fenton (1932, pl. 8, figs. 1, 2). Although cone extensions/perforations are indicative of the ichnogenus, some individual tunnels preserved on the holotype, paratypes, and our Hamilton specimens possess smooth, un-perforated surfaces alongside tunnels with perforations (Fig. 3.11; Fenton and Fenton, 1932, pl. 7, figs. 1, 2) suggesting significant variability within the ichnogenus.

Clionoides possess features that bring into question Teichert's (1945) simple morphological differentiation between borings produced by sponges and worms. According to Teichert (1945), the cylindrical tunnels that make up *Clionoides* suggest that the form was created by a boring worm; however, the canals and microterraced texture within the uppermost shell surface are the

most diagnostic features produced by modern boring sponges (Cobb, 1969, 1975; Futterer, 1974; Sparks et al., 1980; Calcinaï et al., 2008). The cone extensions off the main tunnels are also not characteristic of modern and ancient worm borings. However, one brachiopod host within this study (Fig. 4) possessed *Clionoides* that may suggest the forms are tubes (with a lining) instead of tunnels based on a gap between the sediment filled boring and the shell substrate. If true, the lining may have preferentially been dissolved away leaving the gap, which suggests the structure was produced by a worm. A secondary boring organism would have then created cone extensions, canals, shafts and micro-terraced bowl structures. However, the majority of hosts containing *Clionoides* do not possess this gap. We suggest that due to the consistency and complexity of the three dimensional assemblage of multi-diameter tunnels, shafts, canals, microterraced bowl-shaped structures and cone extensions, the borings were not created by multiple organisms at separate times.

CLIONOIDES CLARKEI (Cameron, 1969a)

Figures 3, 4

- non1855 *Vioa prisca* MCCOY, p. 260, pl. 1B, fig. 1, la.
 1908 *Clionolithes (Vioa) prisca* CLARKE, p. 168, pl. 8, figs. 2–8, pl. 9, fig. 1.
 1921 *Palaeosabella prisca* CLARKE, p. 91, figs. 77–83.
 1969a *Vermiforichnus clarkei* CAMERON, p. 190, figs. 1, 2.
 1969b *Vermiforichnus clarkei* CAMERON, p. 693, pl. 1D–1O, figs. 1, 7.

Diagnosis.—Complex three dimensional network involving tunnels, shafts, canals, microterraced bowl-shaped structures and cone extensions. Main tunnels are cylindrical, straight to moderately curved, circular in cross section, of generally small diameter (~1 mm), variable in length; branching/forking infrequently; walls and floor smooth. Cone extensions penetrate at floor of tunnels but may be absent. Tunnels may terminate with tapering or swollen end, or maintain a uniform diameter. All located within the upper and middle shell substrate of the host.

Description.—Straight to slightly curved cylindrical tunnels of variable lengths, with large diameters (mean diameter of 1 mm), circular cross sections (Fig. 3.6) and slightly swollen (Fig. 3.7), tapered, or uniform diameters at terminus (Fig. 3.2, 3.8); bi-clavate terminus very rare (Fig. 3.9, 3.10). Tunnels are located within the primary and secondary shell substrate, oriented parallel to the shell surface; rarely branching (7.9%), widely spaced and occasionally overlapped or crossed; predominantly oriented radiating/fanning sub-parallel from the umbo and perpendicular to host commissure. Some borings exhibit evenly spaced, cone extensions branching from main tunnel (Fig. 3.10–3.12). Canals (possess slightly larger, bowl shaped apertures) and shafts (without bowl-shaped apertures) adjacent to the tunnels (~0.14 mm in diameter) (Fig. 4.1, 4.2) and microterraced, bowl-shaped structures (0.29–0.66 mm diameters) (Fig. 4.3) are preserved within some hosts.

Types.—Cameron (1969a) designated the holotype and paratypes of *Vermiforichnus clarkei* to Clarke's original specimens, as well as several of his newly collected specimens (Clarke, 1921, figs. 77–83, 95–103; holotype: NYSM 7843; paratypes NYSM 7832–7839, 7841–7846, and AMNH 28471); Lower and Middle Devonian, New York.

Occurrence.—Common from the Rose Hill Quarry (Otisco Member, Ludlowville Formation) and Swamp Road (Pecksport Member, Oatka Creek Formation), Hamilton Group, New York. Clarke's (1921) specimens were collected from the Oriskany Sandstone at Knox, New York, other Middle and Upper Devonian localities (Hamilton and Chemung Groups) from central New York and the Grande Grève Limestone, Gaspé, Quebec.

Remarks.—The ichnospecies is distinguishable from others

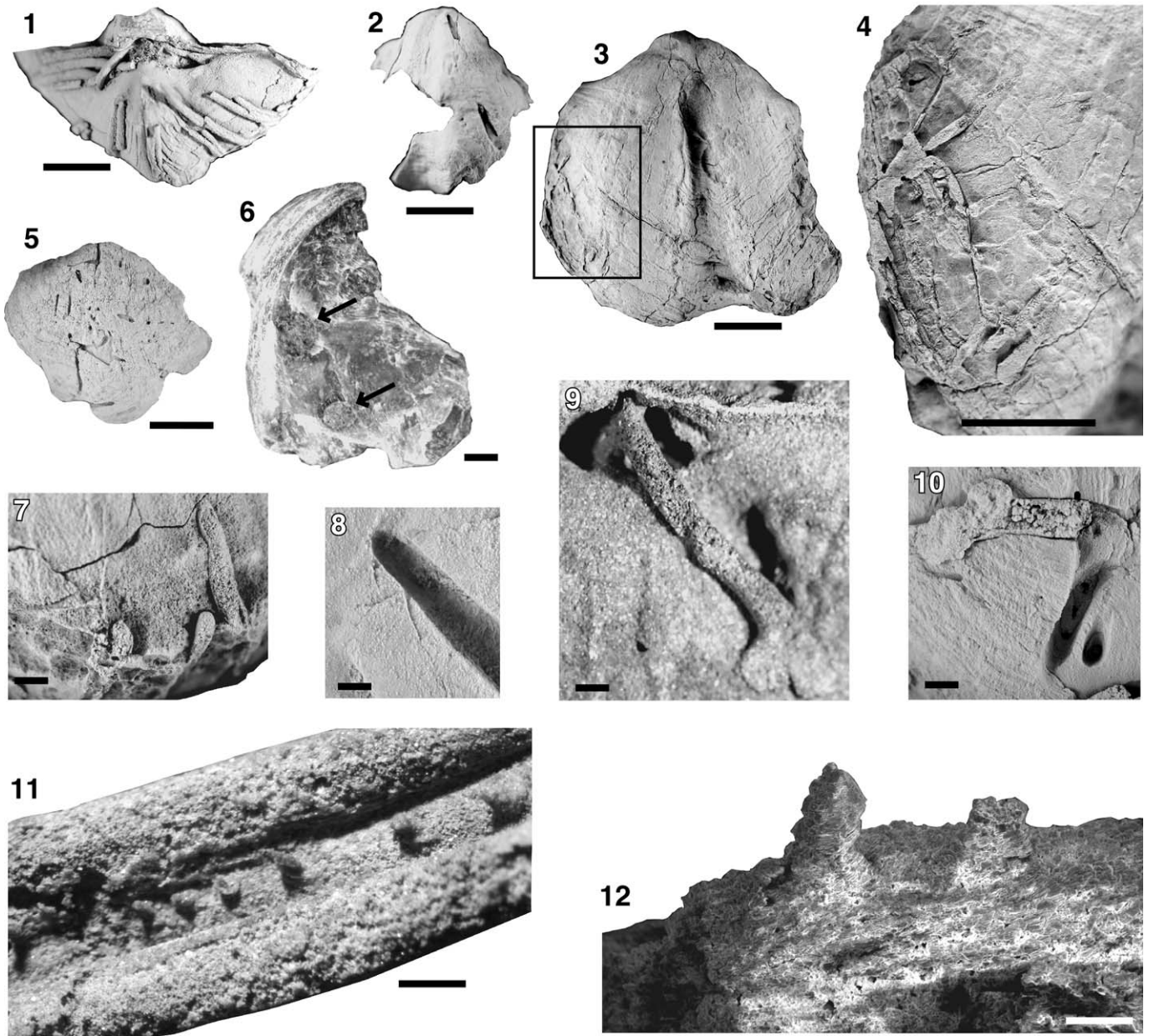


FIGURE 3—12, *Clionoides clarkei*. 1, cast within *Spinocyrtia granulosa* from the Hamilton Group of New York; re-illustrated from Clarke (1908; pl. 8, fig. 5), NYSM 7835, scale bar=1 cm; 2, boring oriented parallel to the commissure and radiates from the umbo, NYSM 18203, scale bar=1 cm; 3, cast radiating upward to the umbo, NYSM 18204, scale bar=1 cm; 4, enlarged view of 3; 5, tunnels oriented at many different angles within a shell of *Athyris spiriferoides*, NYSM 18205, scale bar=1 cm; 6, cross sectional view of two sediment filled borings in the umbo of a shell of *S. granulosa*, arrows point to the cross sections of sediment filled tunnel, NYSM 18206, scale bar=1 mm; 7, magnified view of casts along the commissure of a *S. granulosa* host, NYSM 18207, scale bar=1 mm; 8, empty boring with consistent diameter throughout the length of the boring, NYSM 18208, scale bar=1 mm; 9, re-illustration of a similar bi-clavate cast of *C. clarkei* in a *Protolrptostrophia perplana* (Conrad, 1841) from the Hamilton Group of New York from Clarke (1908), NYSM 7836, scale bar=1 mm; 10, branching tube in *A. spiriferoides*, one gallery is empty and the other, which is bi-clavate, is sediment filled; equidistant perforations present along the base of the empty boring, NYSM 18209, scale bar=1 mm; 11, sediment filled tube within *S. granulosa* revealed after dissolution of shell with acid; the three borings touch and run parallel to each other, but do not cross; the center boring possesses cone extensions, NYSM 18210, scale bar=1 mm; 12, SEM images of tube with vertical extensions, NYSM 18211, scale bar=100 μ m.

described later in this paper, based on their large size of tunnel lengths and diameters, and the complexity of the three dimensional morphologic network involving tunnels, shafts, canals, microterraced bowl-shaped structures and cone extensions. The slightly curved, occasionally branching tunnels are oriented most frequently radiating/fanning from the host umbo, perpendicular to the commissure. The cone extensions penetrate downward from the large main tunnel and cannot be seen without interior views of the tunnels or the destruction of the specimen.

The cone extensions are distinctive to *Clionoides clarkei* and are not observed in other ichnospecies apart from *Clionoides thomasi* Fenton and Fenton, 1932 (as perforations). *Clionoides clarkei* is morphologically similar to *C. thomasi*, with both forms possessing straight tubular borings with mean diameters of ~1 mm. However, major differences between *C. thomasi* and *C. clarkei* include branching patterns and perforation orientation/location. *Clionoides clarkei* possesses branches on 7.9 percent of tunnels while *C. thomasi* tunnels branch more frequently (~15%).

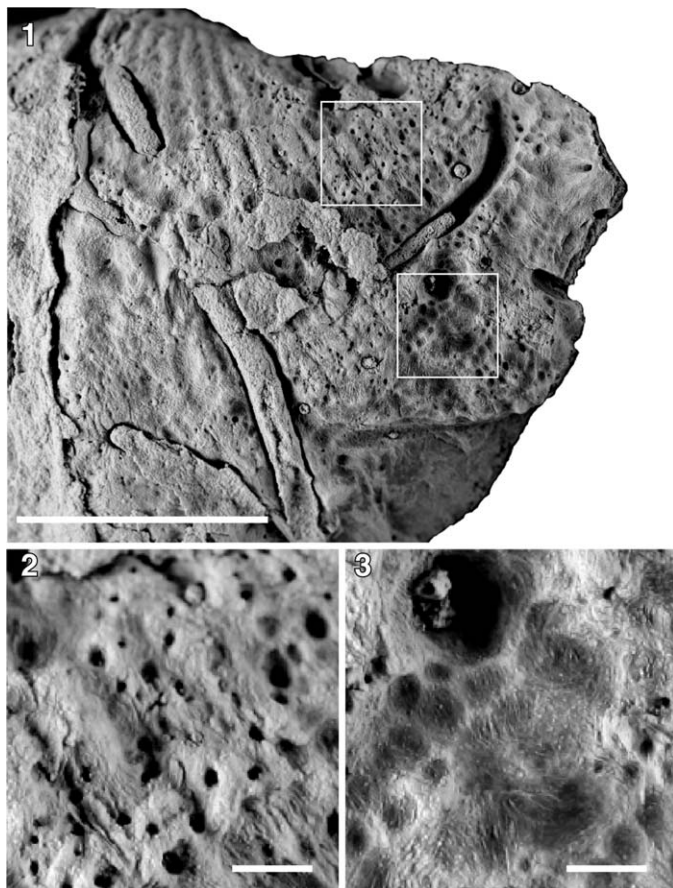


FIGURE 4—Shell surficial texture preserved within the shell. 1, pedicle valve of *Spinocyrtia granulosa*, shell with sediment filled and empty *Clionoides clarkei*, NYSM 18212, scale bar=1 cm; 2, magnified view of canals and shafts in the upper shell layer of same host, scale bar=1 mm; 3, magnified view of micro-terraced, bowl-shaped pitted textured area penetrating the lower shell layer of same host, scale bar=1 mm.

Additionally, the perforations present in *C. thomasi* are located within tunnels (analogous to cone extensions) possessing diameters ranging from 0.5–0.7 mm, which are larger than the perforations within *C. clarkei* (0.1–0.3 mm).

Clionoides clarkei has a similar structure and orientation to ?*Clionoides frimbriatus*, however, ?*C. frimbriatus* is questionably placed within the genus because the clavate forms described by Stephenson (1952) possess smooth walls with no indication of cone structures. Due to the large variability within the genus *Clionoides*, a larger sample size of ?*C. frimbriatus* from localities described by Stephenson (1952) may reveal is the form to possess cone extensions and thereby assigning *C. clarkei* or similar ichnospecies, or reveal characteristics more closely attributed to *Trypanites*.

Ichnogenus CLIONOLITHES Clarke, 1908

Type ichnospecies.—*Clionolithes radicans* Clarke, 1908 by subsequent designation (Fenton and Fenton, 1932). Upper Devonian, Pennsylvania.

Diagnosis.—Dendritic or rosette network; small tunnels radiate and branch outward from a central node. Tunnels unite, fuse coil, cross or anastomose somewhat irregularly; walls are smooth to highly ornamented. Branching network within uppermost shell substrate; central node shows deepest penetration of trace. Central node may be singular and pronounced or multiple and indistinct.

Remarks.—Clarke (1908) originally established *Clionolithes*

for trace networks that possess small tunnels radiating and branching outward from a central node, creating a root-like form in which tunnels often unite, fuse or anastomose producing somewhat irregularly reticulated morphologies. Clarke (1908, 1921) failed to establish a type ichnospecies and subsequently Fenton and Fenton (1932) designated *Clionolithes radicans* Clarke, 1908 as the type (re-illustrated in Fig. 5.1).

Clionolithes demonstrate the dendritic/rosette morphology described by Teichert (1945) and is accepted here as traces indicative of boring sponge activity. *Clionolithes* characteristically radiate from a small central cavity; the central node is below the shell surface, while the branching rosette forms at the surface of the shell substrate. *Clionolithes* is morphologically similar to *Cicatricula* Palmer and Palmer, 1977, but *Cicatricula* differs in that its central cavity is parallel to or at the substrate surface (Pickerill and Harland, 1984). *Clionolithes* also differs from *Pyrodendrina* Tapanila, 2008, which has the central cavity at the substrate surface (with a diameter of 0.3 mm) and “root”-like terminations penetrating deeper into the shell substrate.

Vogel et al. (1987) considered the types of *Clionolithes* to be *nomina dubia* based on their presumably poor preservation. However, our examination of Clarke’s specimens of *Clionolithes* shows the borings to be sufficiently well-preserved to adequately determine characteristic traits. We consider *Nododendrina* Vogel et al., 1987 and *Ramodendrina* Vogel et al., 1987 to be synonymous with *Clionolithes* based on the similar size and rosette-shaped radiating branches, which diverge from a central point.

Two ichnospecies belonging to *Clionolithes* were found within this study. Both forms have the dendritic/rosette morphology that is characteristic of the ichnogenus, but each possess different tunnel morphologies; *Clionolithes radicans* possess narrow branches with spiny outgrowths while, *Clionolithes cervicornis* possess more flattened palmate branches. Both ichnospecies frequently co-occur with one another, making it difficult to determine if *C. radicans* and *C. cervicornis* were produced by the same sponge endozoan species. Although we currently accept that the morphological differences between the two ichnospecies are significant (as did Vogel et al, 1987), larger sample sizes may show that these two co-occurring forms are indeed two morphologically different traces produced by the same sponge originator or that the forms are variants of the same ichnospecies.

CLIONOLITHES RADICANS (Clarke, 1908)

Figures 5.1–5.4, 5.6, 5.7, 6.1, 6.3, 6.4, 7.6

- 1908 *Clionolithes radicans* CLARKE, p. 168, pl. 9, fig. 2, pl. 10, pl. 11, figs. 1, 2.
- 1921 *Clionolithes radicans* CLARKE, p. 87, figs. 70–72.
- 1932 *Clionolithes radicans* FENTON AND FENTON, p. 43, pl. 6, fig. 7.
- 1987 *Nododendrina nodosa* VOGEL, GOLUBIC AND BRETT, p. 271, fig. 4.

Description.—Rosette-shaped branching network of small tunnels inhabiting up to 5 mm² area of the host shell; possesses primary, secondary and tertiary branches, which diverge from a common central node (75–270 μm wide); branches are straight to slightly curved with high and narrow cross sections, covered with small spiny outgrowths; branching varies in density with anastomoses; network of branches is parallel to the host substrate surface, with the central node representing the deepest penetration (<300 μm deep); rosette network located within uppermost preserved shell layer and rarely penetrating the middle layer of the shell substrate.

Types.—*Clionolithes radicans* Clarke, 1908 by subsequent

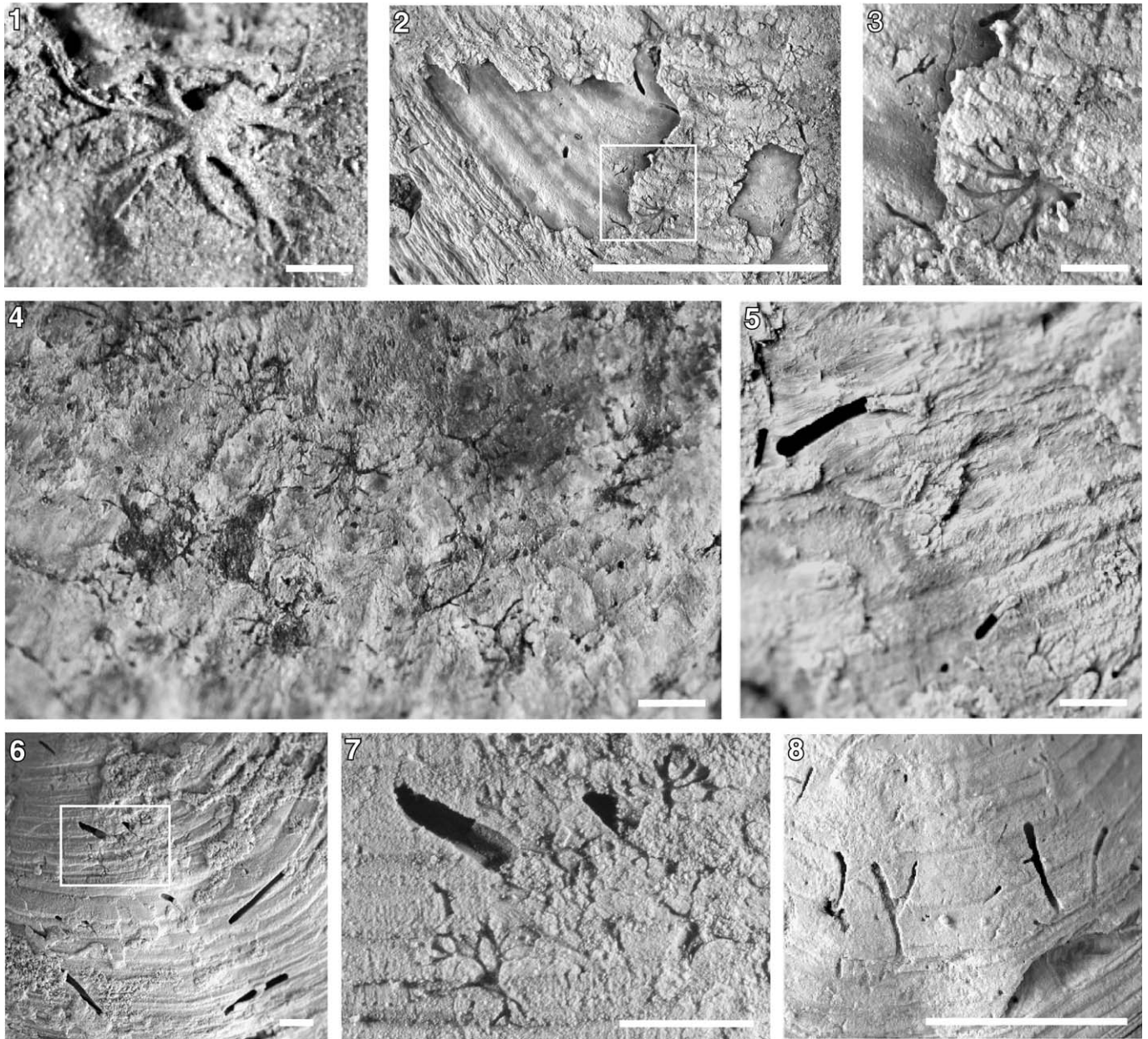


FIGURE 5—1, *Clionolithes radicans*, cast of borings in *Spinatrypa* from the Chemung Group of Mansfield, Pennsylvania, re-illustrated from Clarke (1908, pl. 11, fig. 1), NYSM 6702; 2, *Athyris* host containing *Canaliparva circularis*, NYSM 18214, in the lower shell layer and *Clionolithes radicans*, NYSM 18213, within the upper shell layer, scale bar=1 cm; 3, magnified view of 2 demonstrating one colony of *Clionolithes radicans*; 4, *Clionolithes radicans* within *Pseudoatrypa devoniana*, NYSM 18215; 5, *Canaliparva circularis* within *Athyris spiriferoides*, NYSM 18216; 6, *A. spiriferoides* host containing *Canaliparva circularis*, NYSM 18218, and *Clionolithes radicans*, NYSM 18217; 7, magnified image of 6, a single *Canaliparva circularis* tube is in close proximity to many *Clionolithes* ichnospecies; 8, *A. spiriferoides* host containing *Canaliparva circularis* located along specific growth line, NYSM 18219, scale bar=1 cm. All scale bars=1 mm unless otherwise noted.

designation (Fenton and Fenton, 1932). Upper Devonian, Pennsylvania.

Occurrence.—Moderately rare from Rose Hill Quarry (Otisco Member, Ludlowville Formation) and Swamp Road (Pecksport Member, Oatka Creek Formation), Hamilton Group, New York. Additionally, Vogel et al. (1987) described this ichnotaxon from several additional Middle Devonian Hamilton localities in western and central New York.

Remarks.—The ichnospecies was originally introduced by Clarke (1908), as a small rosette-shaped form, whose radially branching network of small tunnels diverges from a central node. Vogel et al. (1987) described *Nododendrina nodosa* as displaying similar morphological features to *Clionolithes* Clarke, 1908, but

suggested that the names given by Clarke were invalid based on poor preservation. *Clionolithes radicans* and *Nododendrina nodosa* both possess a small rosette-shaped form covered with small spiny outgrowths, but differ in size; *Clionolithes radicans* covers 4–5 mm² of the host shell by a single trace and *Nododendrina nodosa* covers 1–3 mm². This size difference is insignificant and is an invalid ichnotaxobase to solely differentiate the two forms; therefore they are considered synonyms here, with *Clionolithes radicans* as the senior synonym.

Clarke (1908, 1921) described various ichnospecies belonging to *Clionolithes* and distinguished them based on morphology. *Clionolithes reptans* Clarke, 1908 has sparse, diffused tunnels that

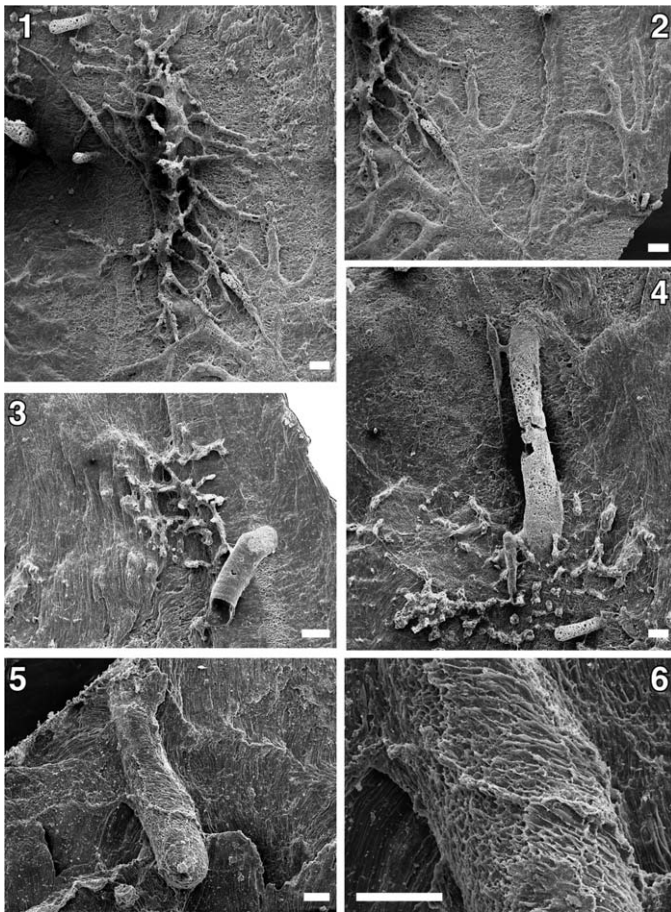


FIGURE 6—Scanning electron micrographs of *Clionolithes* and *Canaliparva*. 1, *Clionolithes radicans* network with both *Clionolithes radicans*, NYSM 18220, and *Clionolithes cervicornis*, NYSM 18221, scale bar=159 μ m; 2, co-occurring of *Clionolithes radicans* and *Clionolithes cervicornis* showing an overlapping pattern, same individuals as in 1, scale bar=156 μ m; 3, *Clionolithes radicans* NYSM 18222, and *Canaliparva circularis* n. ichnogen. n. ichnosp., NYSM 18241, scale bar=159 μ m; 4, *Clionolithes radicans*, NYSM 18224, and holotype of *Canaliparva circularis* NYSM 18223, scale bar=161 μ m; 5, *Canaliparva circularis* with club-shaped terminus, NYSM 18225, scale bar=115 μ m; 6, enlarged image of 5, scale bar=34.5 μ m.

lack a central node and covers an area of the host shell that is more than 15 times larger than *C. radicans*. *Clionolithes palmatus* Clarke, 1908 possess non-anastomose, dendritic forms with decrease in diameter from primary to tertiary branches; individual borings cover ~ 4 mm² of the host shell. *Clionolithes hackberryensis* (Fenton and Fenton, 1932) is almost ten times larger than *C. radicans*, and has more widespread branches, which less frequently anastomose. *Clionolithes irregularis* Fenton and Fenton, 1932 possesses long (10 mm in length), slender (0.3–0.5 mm in diameter), thread-like tunnels that radiate from a central node. *Clionolithes fossiger* Fenton and Fenton, 1932 are straight to curved borings, which branch and have only a slight overall rosette shape that infrequently anastomoses.

CLIONOLITHES CERVICORNIS (Vogel et al., 1987)

Figure 6.2

1987 *Ramodendrina cervicornis* VOGEL, GOLUBIC AND BRETT, p. 271, fig. 5.

Description.—Rosette-shaped, branching network of small tunnels inhabiting up to 3 mm² area of the host shell; possesses

primary and secondary branches, diverge from a common central node (35–150 μ m wide); tube termini are tapered or rounded. Smooth walled, palmate, branching tunnels spread radially in straight to slightly curved lines; flattened cross-sectional branches (70–125 μ m wide) that decrease slightly in size distally, and remain constant between branching points; branching varies in density, without anastomose. Rosette network located at the surface and within the uppermost preserved shell substrate; central node represents deepest penetration into the shell's upper substrate.

Types.—Original specimens of Vogel et al. (1987): holotype: SEM 004.02885, GPIF Bo 1/4; paratypes: SEM 85.3302, GPIF Bo 1/5; SEM 85.5205, GPIF Bo 1/6; Middle Devonian, New York.

Occurrence.—Moderately rare from Rose Hill Quarry (Otisco Member, Ludlowville Formation) and Swamp Road (Pecksport Member, Oatka Creek Formation), Hamilton Group, New York. Vogel et al. (1987) described this ichnotaxon from several Middle Devonian Hamilton localities in western and central New York.

Remarks.—This form is similar to *Clionolithes radicans* but lacks branches with high and narrow cross sections and spiny growths. *Clionolithes cervicornis* possesses smooth walled, palmate rosette tunnels. *Clionolithes cervicornis* is similar to *C. radicans* in regards to the overall inhabiting area on the host and tube size diameter, but both are much smaller and morphologically different than those characteristics of other *Clionolithes* ichnospecies described above. *Clionolithes cervicornis* also differs from *C. palmatus* Clarke, 1908 which inhabits a larger area of the host shell (~ 6 mm²) and has palmate tunnels with wider diameters (0.5–3 mm).

Ichnotaxon CANALIPARVA new ichnotaxon

Type ichnospecies.—*Canaliparva circularis* n. ichnosp. (Otisco Member, Ludlowville Formation) Middle Devonian Hamilton Group, central New York, by monotypy.

Diagnosis.—Cylindrical tunnels, straight to moderately curved, circular in cross section with very small diameters (~ 0.2 mm), variable in length; branching/forking infrequently; walls smooth. Fully developed tunnels vertically U-shaped, entering and exiting at very low angles to the shell surface; tunnel entrances and exits vary from circular to elliptical. Tunnels that are not fully U-shaped may terminate with a tapering or swollen chamber or maintain a uniform diameter along the length of the tunnel. All borings are located within the upper and middle shell substrate of the host.

Etymology.—*Canali*=tubular; *parva*=small.

Occurrence.—Common from Rose Hill Quarry (Otisco Member, Ludlowville Formation) and Swamp Road (Pecksport Member, Oatka Creek Formation), Hamilton Group, New York. Similar forms are known from additional Ludlowville and Moscow Formation localities within central and western New York (Vogel et al., 1987).

Remarks.—*Canaliparva* n. ichnotaxon. exhibits the tubular, U-shaped morphology that is typical of worm activity as described by Teichert (1945). *Canaliparva* is characterized by cylindrical tunnels with small circular cross sections that are slightly, vertically oriented within the upper and middle shell substrate. Tunnel entrances vary from circular to elliptical, but are not typically observable due to the thin overlying shell substrate being removed during diagenesis. We suggest that the simple U-shaped forms were excavated by boring worms.

Unlike many U-shaped trace fossils, *Canaliparva* is slightly, vertically U-shaped with maximum depth within the shell substrate being ~ 1 mm. *Canaliparva* is dissimilar to other U-shaped forms described by Clarke (1908) from the Devonian. The horizontally oriented, U-shaped pouches of *Caulostrepsis* Clarke, 1908, are larger in tunnel size (length and diameter), possess an

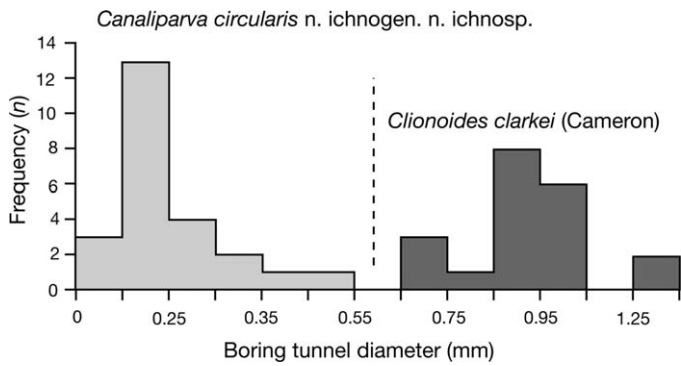


FIGURE 7—Frequency histogram of boring diameter of cylindrical tunnels of *Clionoides clarkei* and *Canaliparva circularis*. The bimodal distribution suggests that two different tubular ichnospecies are present within this study. *Canaliparva circularis* possesses a smaller diameter averaging 0.2 mm, while *Clionoides clarkei* possesses a larger diameter averaging 1.0 mm (N=44).

elevated edge around the narrow loop-shaped tubes and are oriented along the host shell margin. *Canaliparva* is also unlike the bioclastration form *Hicetes* (Clarke, 1908), which is a U-shaped trace that has a tightly coiled base that leads to two straight, vertical shafts and is host-specific with tabulate corals (Brett and Cottrell, 1982; Tapanila, 2005). *Canaliparva* may be confused with U-shaped parts of *Maeandropolydora* Voigt, 1965 and *Talpina* von Hagenow, 1840. *Maeandropolydora* are long, sinuous to contorted galleries with pouches that have two or more apertures, while *Talpina* are narrow, curved, branching tunnels with numerous apertures (Taylor and Wilson, 2003; Wilson, 2007). U-shaped parts of *Maeandropolydora* and *Talpina* frequently occur in higher densities within hosts than *Canaliparva*, may change in diameter width throughout the length of the tunnel and may be oriented horizontally and vertically within a small area within the host shell. *Canaliparva* is also different from the previously described ichnogenus *Clionoides*, with *Canaliparva* being much smaller in diameter (Fig. 7) and having only a simple morphologic tunnel associated with no complex three dimensional network of multi-diameter canals, shafts, cone extensions or microterraced bowl-shaped structures.

Vogel et al. (1987) provisionally used the name *Specus* Stephenson, 1952 for their Devonian borings but described their forms as being smaller than the types described by Stephenson (1952). We suggest that Vogel et al. (1987) correctly interpreted the bimodal histogram of endolith tube diameters illustrated by Cameron (1969b, fig. 5b) as representing two distinct ichnospecies attributed to worms, but misidentified the two ichnospecies involved. They deemed *Specus* as being smaller in size (0.2–0.3 mm in diameter) and *Vermiforichnus* Cameron, 1969a (here considered a junior synonym of *Clionoides* Fenton and Fenton, 1932) as being larger in size with tunnels ~1.2 mm in diameter (Vogel et al., 1987). Since we propose that *Specus* (as described by Stephenson, 1952; with tunnels diameters of ~1 mm) should be considered a probable junior synonym of *Clionoides*, a new name must be established for borings described under *Specus* by Vogel et al. (1987) that possess simple morphologic tunnels with significantly smaller diameters.

CANALIPARVA CIRCULARIS new ichnospecies
 Figures 5.2, 5.5–5.8, 6.3–6.6

- non1952 *Specus fimbriatus* STEPHENSON, p. 51, pl. 8, figs. 4–6.
- 1987 *Specus fimbriatus* VOGEL, GOLUBIC AND BRETT, p. 279, fig. 11a–11c.

Diagnosis.—Cylindrical tunnels, straight to moderately curved,

circular in cross section with an average diameter of 0.2 mm, variable in length; branching/forking infrequently; walls smooth. Fully developed tunnels are vertically U-shaped, entering and exiting at very low angles to shell surface; tunnel entrances and exits vary from circular to elliptical. Tunnels that are not U-shaped may terminate with a tapering or swollen end, or maintain a uniform diameter along the length of the tube. All are located within the upper and middle shell substrate of the host.

Description.—Simple, shallowly vertical U-shaped tunnels, with apertures at low angles to shell surface (Fig. 5.4). Tunnels are straight to moderately curved, with uniform diameters, infrequently possess swollen or tapering chambers (when a U-shape was not fully developed), oriented upright, inclined or parallel to the substrate surface; clavate chambers only slightly larger than neck and aperture. Tunnels have smooth walls, are circular in cross section (mean diameter of 0.2 mm) and are variable in length; branching/forking is infrequent (7.2%) and tunnels possess no indicators of a significant lining. Tunnel entrances are circular to elliptical but are not typically preserved. Tunnels are located within primary and secondary shell substrate; oriented parallel, perpendicular or at various angles to host growth lines with no specific preference.

Etymology.—From *circularis*, in reference to the circular cross-section of tunnels.

Types.—Holotype, SEM stub, (Fig. 6.4; NYSM 18223); Rose Hill Quarry (Otisco Member, Ludlowville Formation) Middle Devonian, central New York. Paratypes, (Fig. 5.2; NYSM 18214), (Fig. 5.5–5.8; NYSM 18216, NYSM 18218, NYSM 18219), (Fig. 6.3; NYSM 18221), and (Fig. 6.5, 6.6; NYSM 18225); Rose Hill Quarry (Otisco Member, Ludlowville Formation) Middle Devonian, central New York. Additional specimens illustrated by Vogel et al. (1987; fig. 11A, SEM 014.12144, GPIF BO 1/18) from the Middle Devonian of New York contributed to the description and discussion.

Occurrence.—Common from Rose Hill Quarry (Otisco Member, Ludlowville Formation) and Swamp Road (Pecksport Member, Oatka Creek Formation), Hamilton Group, New York. Similar forms are known from additional Ludlowville and Moscow Formation localities within central and western New York (Vogel et al., 1987).

Remarks.—*Canaliparva circularis* is distinguished from other U-shaped smooth-walled borings by their simple and small sized tunnels (diameters ~0.2 mm) with circular cross sections. Apertures of vertical U-shaped cylinders are oriented at a low angle to the shell surface, which is dissimilar to many U-shaped forms described above. Some tunnels are straight or curved with only one apparent entrance. Vogel et al. (1987) used the name *Specus fimbriatus* Stephenson, 1952 to describe Devonian borings with similar morphologies and sizes as *Canaliparva circularis*. Tunnel sizes for these Devonian borings are significantly smaller than the type *S. fimbriatus* and are here placed within the newly established *Canaliparva circularis*. Although *Canaliparva circularis* has a similar tubular form as *Clionoides clarkei*, *Canaliparva circularis* has a simpler morphology with no associated shafts, canals, cone extensions or microterraced structures. Although the use of size has been rejected as a valid ichnotaxobase (Bertling et al., 2006; Bertling, 2007), size paired with morphological features (shape, orientation, etc.) allow for the differentiation between these two ichnotaxa.

BRYOZOAN FORMS

The collection of hosts within this study also contained several encrusting bryozoans and bryozoan boring traces. Much confusion has been introduced within bryozoan nomenclature as a result of the failure to make distinctions between the trace fossils produced by bryozoans and their body fossils. Consequently, many forms have been attributed to both trace and body fossils causing a dual nomenclature to exist (Rosso, 2008).

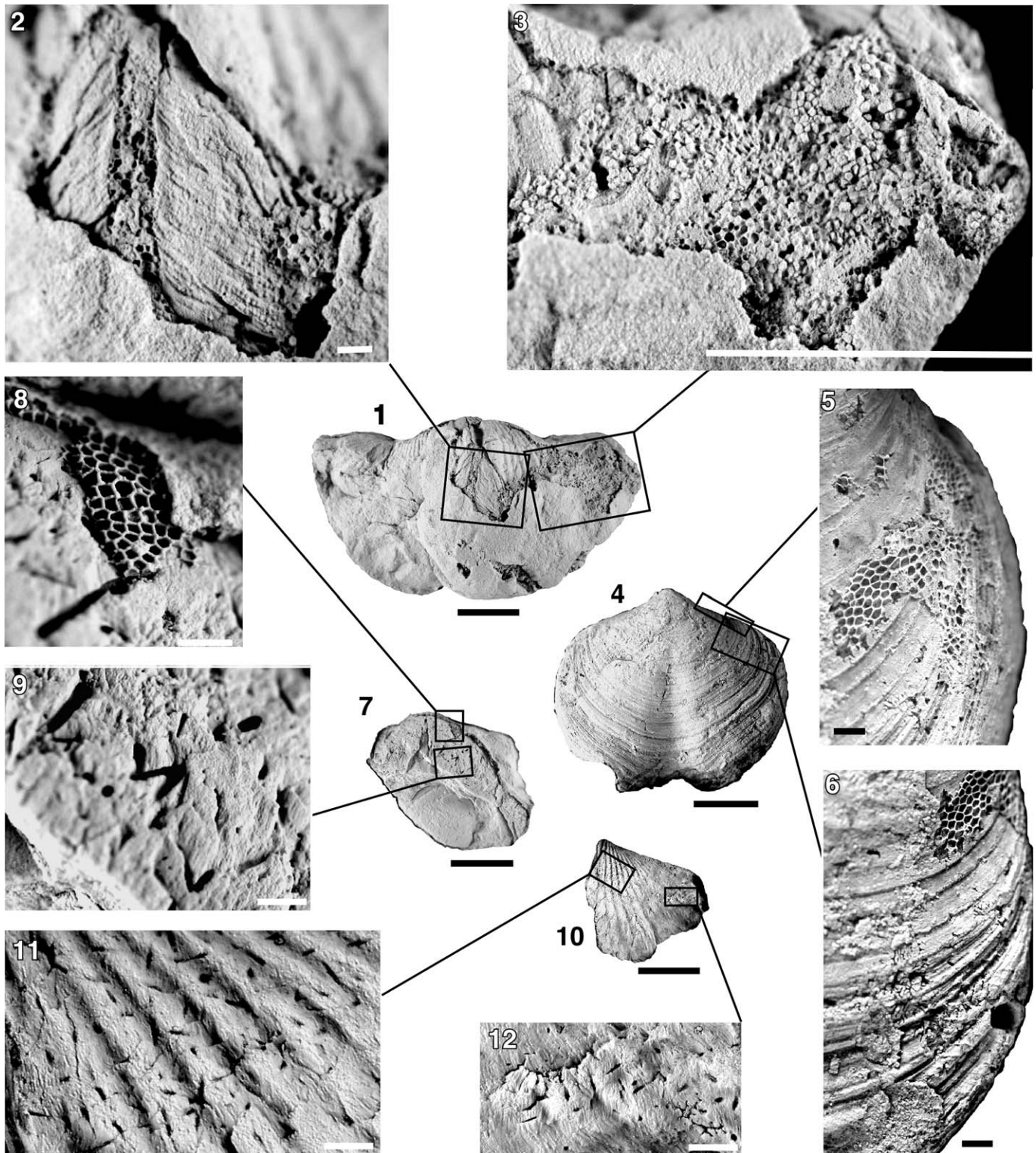


FIGURE 8—1, *Spinocyrtia granulosa* hosting encrusting bryozoan *Palaeschara incrustans*, NYSM 18227, and *Clionoides clarkei*, NYSM 18226, scale bar=1 cm; 2, enlarged image of 1, *P. incrustans* preserved within *Clionoides clarkei*, scale bar=1 mm; 3, enlarged image of 1 showing encrusting *P. incrustans*, scale bar=1 cm; 4, *Athyris spiriferoides* hosting well preserved *P. incrustans*, NYSM 18228, scale bar=1 cm; 5, enlarged image of 4, scale bar=1 mm; 6, enlarged image of 4, encrusting *P. incrustans* near *Clionolithes* ichnospecies, scale bar=1 mm; 7, *A. spiriferoides* hosting well preserved *P. incrustans*, NYSM 18229 and bryozoan endoliths, NYSM 18230, scale bar=1 cm; 8, enlarged view of 7, *P. incrustans* encrusting over bryozoan endoliths, scale bar=1 mm; 9, enlarged view of 7, bryozoan endoliths; 10, *Mucrospirifer mucronatus* hosting bryozoan endoliths, NYSM 18231, scale bar=1 cm; 11, enlarged view of 10, scale bar=1 mm; 12, enlarged view of 10, scale bar=1 mm.

TABLE 2—Frequencies of borings individuals based on location on host shells. Host species include *Athyris spiriferoides* (ATH), *Spinocyrtia granulosa* (SPIN) and *Mucrospirifer mucronatus* (MUC). Locations based on data in Figure 2. Abbreviations: PV=pedicle valve; BV=brachial valve; FS=area within the fold and sulcus; Flank=side areas around the fold and sulcus; Marg=margin; Inside=area consisting of the beak and interarea.

Host	<i>Clionoides Clarkei</i>			<i>Clionolithes</i> ichnospecies			<i>Canaliparva circularis</i>			Total		
	PV	BV	Sig (p)	PV	BV	Sig (p)	PV	BV	Sig (p)	PV	BV	Sig (p)
ATH	20	41	0.998	45	38	0.779	235	133	0.999	300	21	0.999
SPIN	39	16	0.999	11	20	0.954	30	13	0.998	81	49	0.998
MUC	5	1	0.986	7	2	0.977	25	48	0.997	37	51	0.875
Total	64	58	0.705	63	60	0.610	291	194	0.999			
	FS	Flank	Sig (p)	FS	Flank	Sig (p)	FS	Flank	Sig (p)	FS	Flank	Sig (p)
	ATH	26	35	0.929	19	64	0.988	137	231	0.939	182	330
SPIN	16	39	0.726	4	27	0.999	9	35	0.983	29	101	0.999
MUC	1	5	0.964	0	9	0.000	22	51	0.637	23	65	0.938
Total	43	79	0.670	23	100	0.999	168	317	0.622			
	Marg	Inside	Sig (p)	Marg	Inside	Sig (p)	Marg	Inside	Sig (p)	Marg	Inside	Sig (p)
	ATH	13	48	0.989	12	71	0.999	60	308	0.999	85	427
SPIN	19	36	0.575	9	22	0.702	11	33	0.899	39	91	0.797
MUC	4	2	0.958	4	5	0.749	47	26	0.999	55	33	0.999
Total	36	86	0.824	25	98	0.999	118	367	0.999			

Within this study, an encrusting bryozoan, *Palaeschara incrustans* Hall, 1874 (Fig. 8.1–8.8) and a bryozoan boring (Fig. 8.7–8.12) were observed within seven host brachiopods. It is likely that if *P. incrustans* was endolithic, the etchings would be more similar to those of the ichnogenus *Finichnus* (Taylor et al., 2012) (previously described as *Leptichnus* by Taylor et al., 1999 and Rosso, 2008), suggesting that *P. incrustans* did not produce the borings and that the forms were produced by a different bryozoan species. The preserved bryozoan traces likely belong to an ichnospecies similar to those attributed to *Orbignyopora* sp. Pohowsky, 1978, also from Hamilton Group strata, which was originally described as a bryozoan body fossil (Pohowsky, 1978) but was subsequently described as a trace fossil (Vogel et al., 1987; Vogel and Brett, 2009). More research and a larger sample size are needed to provide an adequate description of a new ichnogenus for these and similar forms to avoid and remove a dual nomenclature.

BORING DISTRIBUTIONS AND BIOTIC INTERACTIONS

Boring orientation and site preference.—Boring orientations and their spatial distribution permit interpretations to be made about biotic interactions between trace-makers and their hosts. The orientations of borings within this study are predominantly parallel to shell surfaces and occur within the upper and middle shell layers of hosts’ skeletons (Figs. 3.2, 5.2, 5.3). *Canaliparva circularis* n. ichnogen. n. ichnosp. tunnels are shallowly U-shaped with the boring tunnels entering and exiting at low angles to the shell surface (Fig. 6.4). No endolithic traces were observed on the interior of host shells suggesting that the endoliths did not colonize on any disarticulated hosts.

The spatial distribution of borings on host shells is dependent both on the ichnotaxon itself and the host species. All four ichnotaxa were concentrated in brachiopod host *Athyris spiriferoides* and to a lesser extent *Spinocyrtia granulosa* and *Mucrospirifer mucronatus* (Table 2). Most brachiopods did not host a high frequency of borings, with the majority of hosts being infested by less than 10 individual borings (Fig. 9). Some articulated hosts (36 out of 88) possess traces on both brachial and pedical valves, yet there is a strong preference ($p < 0.01$) for infestation of the pedicle valves of *A. spiriferoides* and *S. granulosa*, with slight variability for individual ichnospecies. Both of these host taxa were likely low-level, pedically attached and oriented with their commissure slightly inclined from vertical with the brachial valve down during life (Brower and Nye, 1991). Borings rarely occurred in the brachial valves of *M. mucronatus*, which presumably was oriented vertically with its beak and

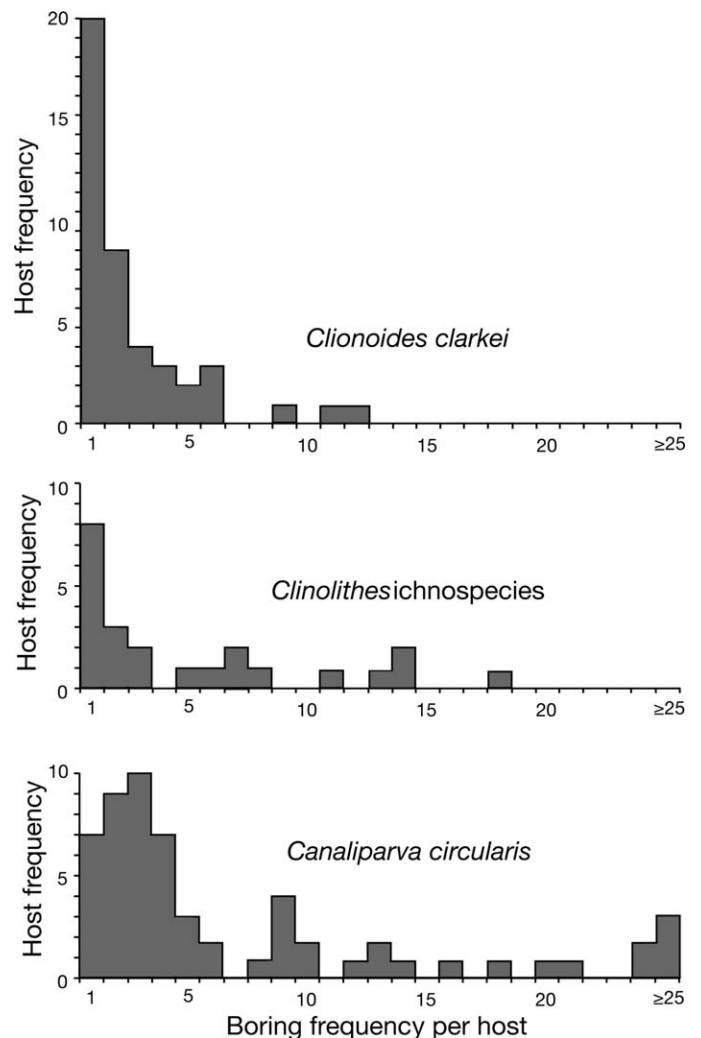


FIGURE 9—Boring frequency histograms for each ichnospecies per brachiopod hosts. Total hosts=88. Total borings=730. Total *Clionoides clarkei*=122 within 44 hosts. Total *Clionolithes* ichnospecies=123 within 23 hosts. Total *Canaliparva circularis*=485 within 56 hosts.

interarea embedded in the substrate during life (Brower and Nye, 1991). Host valve preferences for most ichnotaxa support the notion that infestation occurred on the valve that was more exposed towards open water flow and away from the sediment substrate.

Specific site preferences of each ichnotaxa are depicted in Figure 2 and Table 2. *Clionoides clarkei*, *Clionolithes* ichnospecies, and *Canaliparva circularis* more commonly infested the host valve flanks ($p < 0.05$) rather than the fold and sulcus regions (Table 2). Ager (1961) and Kesling et al. (1980) suggested that endozoans may have been able to benefit from the inhalant and exhalant currents produced by the brachiopod host and that the inhalant stream would have food in it that would seem most beneficial for the endozoan. Borers of *Mucrospirifer mucronatus* hosts preferred the margin suggesting that they used the feeding currents, or more likely, that this was the area of the host shell not covered by the sediment substrate. However, borers of *Athyris spiriferoides* and *Spinocyrtia granulosa* significantly favored the beak and interarea of the shell surface rather than the margin, suggesting that the endozoans did not utilize the inhalant stream produced by the brachiopod host. The preference of the beak and interarea may be due to a higher accommodation space provided by the slightly thicker shell of the areas (Tapanila et al., 2004; Tapanila, 2008).

Although the producer of *Clionoides clarkei* does not significantly favor the margin of host valves, the large tunnels do appear to commence near the hinge/umbo with growth extending and radiating towards the anterior margins of host valves (Figs. 3.1, 3.2, 4.1). It is likely that the radiating pattern was due to the endozoan attempting to maintain feeding position near the commissure and utilizing the feeding currents of the host. By maintaining maximum feeding efficiency near the edge of the host shell, the endozoan may have conserved energy by boring the most direct path towards the commissure which over the lifespan of the host and endozoan created the radiating pattern originating from the beak (Ager, 1961; Thayer, 1974). Although this is a logical explanation of the orientation, it is by no means an exclusive explanation.

Host-endozoan relationships.—Based on the specific site preference of each ichnospecies, a commensal relationship is suggested to have existed between the endoliths and their hosts. Borings did not show any characteristics of bioclastration, but a few hosts show slight signs of repair structures around the borings. Boring assemblages on select hosts stopped at a specific growth lines suggesting that the host continued living as the endoliths ceased to grow or died. No borings penetrated the living chamber of the hosts suggesting that the endozoans did not kill their host in a predatory or parasitic manner. Due to the unlikelihood of host benefitting from the endoliths, there is little support of a mutualistic relationship between the host and the endoliths. The hosts may have fed off the excrement of the endoliths, but this is unlikely due to the majority of borings were not located at the margin. The endoliths mainly benefitted from the hosts providing a silt free, hard substrate, while the host neither benefited nor was harmed. Although it cannot be determined with certainty that all endozoans preferred live hosts, the specimens collected at Swamp Road were collected within life position, along with the boring locations suggest endozoans preferred to colonize on hosts that were living.

Intra-specific co-occurrence.—Previous research has suggested that the settlement of multiple endozoan species within the same host specimen is rare and that the preference to avoid other species' borings was common in marine invertebrates (Thayer, 1974; Sparks et al., 1980). However, within this study, five unique intra-specific co-occurrences were observed:

A co-occurrence was observed between *Clionolithes radicans* and *Clionolithes cervicornis* (Fig. 6.1, 6.2). Although it is unknown if a single sponge created the two forms, it is likely that the two forms were not excavated at the same time. Chronologies of boring co-occurrences, determined by cross cutting relationships, vary between hosts suggesting that one ichnospecies was not always formed prior to the other ichnospecies.

A second intra-specific co-occurrence is observed between *Canaliparva circularis* and *Clionolithes* ichnospecies (Figs. 5.2, 5.3, 5.6, 5.7, 6.3, 6.4). One specific example (Fig. 6.3, 6.4) shows the difficulty in determining which endozoan settled first, but since the two forms overlap, it is most likely that the two did not live simultaneously. The latter boring organism may have benefited from the preexisting endoliths void space created by the former organism. However, not all endoliths favor weakened substrates and prefer substrates that are most dense in order to better control trace morphology or increase structural integrity (Tapanila et al., 2004).

Clionoides clarkei is isolated from other sponge and worm traces; however, the bryozoan *Palaeschara incrustans* (Fig. 8.1–8.3) occasionally encrusted into the vacant tunnels of *Clionoides clarkei*, providing a third intra-specific co-occurrence. These bryozoan colonies occurred within preexisting *Clionoides clarkei* tunnels (Fig. 8.2) but also encrusted larger portions of host valves (Fig. 8.1, 8.3). The co-occurrence of bryozoans with the boring sponge may have allowed the latter to prevent the extension of the bryozoan colonies until the sponge died, was killed, or was eliminated in some manner (Hoare and Steller, 1967). We hypothesize that within this specific host, the sponge endolith bored prior to *P. incrustans* encrusting the majority of the host shell (Fig. 8.1–8.3).

A fourth and similar co-occurrence is observed between *Palaeschara incrustans* and *Clionolithes* ichnospecies (Fig. 8.4–8.6). However, unlike the co-occurrence of *P. incrustans* with *Clionoides clarkei*, *P. incrustans* appears to be separated from *Clionolithes* ichnospecies and did not invade the borings, which suggests that the two may have lived simultaneously on the host shell. Since the co-occurrence is present on only one host, a larger sample may reveal more insight into this issue.

A fifth co-occurrence is observed between *Palaeschara incrustans* and a bryozoan boring. As stated above, the endoliths were most likely formed by a different bryozoan species than *P. incrustans*. *Palaeschara incrustans* infills the borings suggesting that the boring bryozoan lived and produced traces before to *P. incrustans* encrusted over the shell surface.

CONCLUSIONS

This study of brachiopod hosts from the Middle Devonian of central New York State demonstrates that the simple morphologic differentiation between sponge and worm borings suggested by Teichert (1945) is not valid for all ichnotaxa. The new combination of *Clionoides clarkei* is needed to describe tubular borings (~1 mm in diameter) with multi-diameter canals, shafts, cone extensions and microterraced bowl-shaped structures. Although many authors have attributed the ichnospecies to both sponge and worm activity, we suggest that the forms are more likely produced by an ancient boring sponge because of its complex three dimensional morphology. Through the use of this new interpretation, the ichnogenus *Clionoides* Fenton and Fenton, 1932 should include *Palaeosabella* Clarke, 1921, *Vermiforichnus* Cameron 1969a and perhaps *Specus* Stephenson, 1952.

Two other ichnospecies, *Clionolithes radicans* and *Clionolithes cervicornis* are also attributed to the activity of ancient

boring sponges. Both possess the dendritic/rosette morphologies that Teichert (1945) attributed to sponges. The branching network of *Clionolithes radicans* has spiny outgrowths on the tunnels and the branching network of *Clionolithes cervicornis* has a smoother, palmate morphology. The new ichnogenus and ichnospecies *Canaliparva circularis* are needed to describe small and simple tubular borings (~0.2 mm in diameter) that are attributed to worm activity. This form also follows Teichert's (1945) simple morphologic differentiation between boring produced by sponges and worms.

Paleoecologic evidence supports a commensal relationship between the endoliths and hosts and reveals boring site frequencies in the hosts and boring patterns. Primary evidence for a commensal associations in our collection include the observations that no borings penetrated to the interior of host valves, several boring tunnel termini correspond to mid-valve growth lines, and that the host brachiopods were equally infested on pedicle and brachial valves which would be expected for vertical or slightly inclined life orientations of the host brachiopods. Five unique intra-specific co-occurrences were preserved between *Clionoides clarkei*, *Clionolithes radicans*, *Clionolithes cervicornis*, *Canaliparva circularis*, a bryozoan endolith and the encrusting bryozoan *Palaeschara incrustans*. The documentation of these relationships suggests that co-occurrence of endoliths within hosts is more common within ancient marine ecosystems.

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