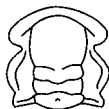


Palaeoecology and diversity of endosymbionts in Palaeozoic marine invertebrates: Trace fossil evidence

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LETHAIA



Tapanila, L. 2005 06 15: Palaeoecology and diversity of endosymbionts in Palaeozoic marine invertebrates: Trace fossil evidence. *Lethaia*, Vol. 38, pp. 89–99. Oslo. ISSN 0024-1164.

Endosymbionts are organisms that live within the growing skeleton of a live host organism, producing a cavity called a bioclastration. The endosymbiont lives inside the bioclastration, which it forms by locally inhibiting the normal skeletal growth of the host, a behaviour given the new ethological category, *impedichnia*. As trace fossils, bioclastrations are direct evidence of past symbioses and are first recognized from the Late Ordovician (Caradoc). Bioclastrations have a wide geographic distribution and occur in various skeletal marine invertebrates, including tabulate and rugose corals, calcareous sponges, bryozoans, brachiopods, and crinoids. Ten bioclastration ichnogenera are recognized and occur preferentially in particular host taxa, suggesting host-specificity among Palaeozoic endosymbionts. The diversity of bioclastrations increased during the Silurian and reached a climax by the late Middle Devonian (Givetian). A collapse in bioclastration diversity and abundance during the Late Devonian is most significant among endosymbionts of host coral and calcareous sponge taxa that were in decline leading up to the Frasnian–Famennian mass extinction. □ *Embedment, Frasnian–Famennian, impedichnia, symbiosis, trace fossil.*

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Understanding the interaction of organisms with each other and their environment is a primary goal in modern and ancient ecology. Direct study of inter-specific relationships (symbiosis *sensu stricto*: Hertig *et al.* 1937) in the fossil record requires that the relationship is preservable, and that it is not obscured by differential taphonomic histories of the interacting organisms. Endosymbiosis, a faunal relationship where an endosymbiont resides within the skeleton of a live host, is particularly well-suited for studying animal interactions. This relationship can produce a special group of trace fossils called bioclastrations (Palmer & Wilson 1988; Taylor 1990), which overcome many taphonomic limitations by providing fossil evidence that two organisms were interacting and in direct contact during life.

Bioclastrations are produced by the embedding of an endosymbiont within the growing skeleton of a living, host organism. As a result of this interaction, a cavity is produced within the host skeleton in which the endosymbiont lives. Bioclastration cavities are distinguished from borings in skeletal materials, which are produced by mechanical grinding or chemical dissolution (bioerosion) of the skeleton. Because bioclastration cavities are formed in skeletal material, they have a high potential for preservation in the fossil record.

Although bioclastrations provide direct evidence of symbiosis, the precise relationship of the infesting animal with its host may be open for interpretation (see Darrell & Taylor 1993). Invariably, bioclastrations provide a home for the endosymbiont; however, the impact of the relationship on the host may range from negligible (neutralism) to detrimental (parasitism, by which the endosymbiont derives food from the host). It is inherently difficult to recognize the precise relationship of the endosymbiont with its host in fossil examples (Fagerstrom 1996), so the neutral term endosymbiont (or endozoozoan: Taylor & Wilson 2002) is commonly preferable.

This paper reviews the literature on Palaeozoic endosymbiosis, primarily in corals, using modern examples as a guide to its interpretation and focussing on the record of bioclastrations.

Modern endosymbionts and their traces

The modern marine record of endosymbiosis is a critical starting point towards interpreting fossil bioclastrations. A high diversity of endosymbionts live in modern marine settings, especially in reefs, and

include polychaetes, crustaceans and bivalves as the most common taxa. The life habit of endosymbionts, which results in the formation of bioclaustrations, has received increasing attention from biologists. *Spirobranchus giganteus*, a calcareous tube-secreting serpulid polychaete that is commonly known as the Christmas tree worm, and pyrgomatid barnacles are among the best-studied endosymbionts of modern scleractinian corals (Utinomi 1943; Ross & Newman 1973; Smith 1984; Hunte *et al.* 1990a,b; Marsden & Meeuwig 1990; Nishi & Nishihira 1996, 1999).

Initiation

Bioclastration structures initiate by the settlement of the endosymbiont on the surface of the skeletal host. *Spirobranchus* larvae (10–14 days old) settle on dead portions of the host coral near living polyps, rapidly grow a calcareous tube toward the living tissue of the coral at a rate of 0.5–1.0 mm per day, and are eventually overgrown by the coral skeleton (Smith 1984). By contrast, the cyprid larvae of pyrgomatid barnacles apparently penetrate and briefly reside within the living tissues of a host polyp (Utinomi 1943; Moyse 1971). Following the secretion of its basal plate, the barnacle becomes entombed in the coral skeleton and grows rapidly in diameter.

Life

The site of initial endosymbiont settlement defines the base of an incipient bioclastration. As the host skeleton grows, a cavity with a direct connection to the water column (aperture) is produced around the endosymbiont. Within this cavity, the endosymbiont performs the routine functions of life. Most coral associates (sessile invertebrates living in or on live corals) are heterotrophic filter feeders (Risk *et al.* 2001). Endosymbiotic *Spirobranchus* and most pyrgomatid barnacles feed on suspended particles and may benefit from water currents generated by the host (i.e. a commensal relationship). Only one modern pyrgomatid species, *Hoekia monticulariae*, is known to feed parasitically on the living tissues of the host coral (Ross & Newman 1969).

The life activities performed by the endosymbiont deform the normal skeletal growth of the host. The response of the host to the endosymbiont may result in chimney-like projections around the infester or broad depressions in the skeletal surface (Weilgus *et al.* 2002). However, immediately adjacent to the cavity, the endosymbiont's activity appears to decrease the host's skeletal growth rate. Immediately below the endosymbiont is a surface of the host skeleton that does not grow (Ross & Newman 1973). The decrease

in skeletal accretion around the endosymbiont is preserved as a base-ward deflection of host skeletal elements surrounding the bioclastration (see Nishi & Nishihira 1999, fig. 1). The shape and size of the cavity is generally distinctive for certain endosymbionts, although Hunte *et al.* (1990b) observed that *Spirobranchus giganteus* size varied significantly within different host coral taxa.

Reproduction among endosymbionts ranges from broadcast spawning (e.g. *Spirobranchus*, as reported by Smith 1984) to internal fertilization (e.g. pyrgomatid barnacles, as reported by Mokady & Brickner 2001). Endosymbionts are generally gregarious, which facilitates reproduction. Free-swimming *Spirobranchus* larvae demonstrate a preference for settling on particular corals based on their recognition of host chemical emissions and the presence of settled *Spirobranchus* (Marsden & Meeuwig 1990; Hunte *et al.* 1990a).

Death

The lifespan of an endosymbiont is ultimately limited by the lifespan of the host. Modern *Spirobranchus giganteus* living in coral colonies of *Porites* are among the longest-lived annelids, some exceeding 20 years of age (Nishi & Nishihira 1996). A more typical lifespan of coral endosymbionts ranges between 1 and 5 years (Nishi & Nishihira 1999). Once a bioclastration is vacated, the host commonly will overgrow the structure. Therefore, the length of an overgrown cavity is directly related to the lifespan of the endosymbiont. An important caveat is that a bioclastration cavity may be occupied more than once throughout its formation. A prime example is a nestling organism, i.e. an animal that settles in a previously formed, vacant cavity. Multiple occupations of the cavity might be recorded in distinctive changes with depth in the shape, size and orientation of the bioclastration. Modern examples further demonstrate a positive correlation between bioclastration width and endosymbiont lifespan (Nishi & Nishihira 1999); however, this relationship has not yet been used to estimate longevity in fossil bioclaustrations.

The fossil record of bioclaustrations

Fossil preservation of interference behaviour

The fossil product of endosymbiosis is the formation of a bioclastration cavity, which is defined by the abnormal growth of a host skeleton. The bioclastration is likely to be preserved since it depends on the durability of the host skeletal material, which

commonly is calcareous and massive in form. By contrast, the endosymbiont typically is soft-bodied and is unlikely to be preserved in the fossil record. Bioclaustrations are *in situ* structures that reliably preserve the behavioural interaction of the endosymbiont with its host, and they provide fossil evidence of organisms with inherently low preservation potential. Bromley (1970) recognized this behavioural attribute of bioclaustrations and considered them as trace fossils, i.e. as fossil evidence of past behaviour.

The behavioural, or ethological, classification of trace fossils (Seilacher 1953) is among the most useful ways to organize trace fossils above the ichnogeneric level. Roughly a dozen ethological categories are in current usage (Bromley 1996), of which only five describe behaviours preserved by trace fossils in skeletal substrates (Gibert *et al.* 2004). These include *domichnia* (dwelling), *fixichnia* (anchoring), *prae-dichnia* (predation), *equilibrichnia* (gradual adjustment) and *pascichnia* (locomotion and feeding). *Domichnia*, an ethological category that includes many boring trace fossils (e.g. *Gastrochaenolites*, *Trypanites* and *Entobia*), currently is the most appropriate category to describe bioclaustrations. However, the *domichnia* category is deficient in describing the complexities of endosymbiotic behaviour required to produce a bioclaustration, and therefore a new category is required.

A bioclaustration records two distinct behaviours during the manufacturing of the cavity. First, the bioclaustration results from the activity of *both* the endosymbiont, which directly inhibits the skeletal accretion of the host at a localized site, and the host organism, which alters its own skeletal growth to accommodate the infesting organism. Second, the resultant bioclaustration serves as a dwelling structure for the endosymbiont. This combination of inhibition and dwelling behaviours on the part of the endosymbiont is uniquely recorded by bioclaustration trace fossils. A new ethological category '*impedichnia*' (*imped-* Latin, to hinder or prevent; *-ichnos* Greek, trace) is proposed here to address the dual behaviours of endosymbionts preserved as bioclaustrations.

The diversity of Palaeozoic bioclaustrations

Bioclaustrations have existed in a taxonomic grey area. Prior to Bromley's (1970) inclusion of embedment structures as trace fossils, bioclaustrations were described as body fossils and were classified most often as worms (e.g. Howell 1962). Following a review of the descriptive literature on bioclaustrations, ten formally named ichnogenera are recognized here (Table 1, Fig. 1). They occur primarily in corals and calcareous

sponges (stromatoporoids and chaetetids), but also in bryozoans, brachiopods and crinoids. Refer to the Appendix for details on the ichnotaxonomy used to compile and organize the trace fossil data.

Palaeoecology of endosymbiosis

The traces of endosymbionts reveal palaeoecological information about both the host and the infesting organism. Comparison of ancient endosymbionts to their modern counterparts reveals many similarities.

Palaeozoic bioclaustrations occur commonly in particular host taxa, yet are entirely absent from others. Such preference for particular hosts is commonly observed among modern endosymbionts of scleractinian corals. The observed preference could be explained by selective recruitment by endosymbiont larvae in particular coral taxa or it may reflect decreased larval survivorship in all but the few coral taxa with bioclaustrations. Recruitment preference, not merely survivorship, is the driving mechanism for the distribution of *Spirobranchus* in modern corals (Marsden & Meeuwig 1990). The mechanism for preferred substrate recruitment by larvae is largely behavioural (Marsden & Meeuwig 1990; Marsden *et al.* 1990). Larvae may be attracted by chemical emissions produced by the preferred host or by newly settled larvae of the infesting species. A gregarious lifestyle on the part of endosymbionts facilitates reproduction and increases the likelihood of successful settlement (Mokady & Brickner 2001).

Modern endosymbionts favour hosts that were common in the habitat and that were among the more robust hosts capable of withstanding catastrophic storm events (Scott 1987). Indeed, ancient endosymbionts appear to have preferred these kinds of hosts. In Palaeozoic tabulate corals, bioclaustrations are preferentially found in common host taxa that span millions of years of geologic time, e.g. *Favosites*. In a Late Ordovician patch reef setting, Tapanila (2002) described abundant *Chaetosalpinx rex* found exclusively in the dominant reef-building skeletons of *Columnopora* tabulate corals. Many of these bioclaustrations extend through more than 4 years of growth in the host *Columnopora*, a longevity similar to many modern coral endosymbionts (Nishi & Nishihira 1999). Dai and Yang (1995) observed that modern endosymbionts preferred massive coral hosts over more fragile forms (foliated or branching), suggesting that the greater thickness for accommodating an endosymbiont and greater longevity of the host might account for this preference. Similarly, Palaeozoic endosymbionts appear to have preferred colonial corals having a massive, cerioid (e.g. favositids) to coenenchymal (e.g. heliolitids and sarcinulids)

Table 1. Listing of bioclaustration ichnotaxa reported in the literature. * *Parafavosites* and *Gephuropora* are likely species of *Favosites* (Hill 1981). Abbreviations. – Groups: R=rugose coral, T=tabulate coral, CS=calcareous sponge, Bz=bryozoan, Bc=brachiopod. Age: ?O/S erratic=erratic of unknown Ordovician or Silurian age.

Bioclaustration Taxon (Synonymy)	Age	Location	Reference
Host [Group]			
<i>Chaetosalpinx ferganensis</i> Sokolov 1948 (= <i>C. khatangaensis</i> , = <i>C. huismani</i> , = <i>C. groningae</i>)			
<i>Favosites antipertatus</i> [T]	Givetian	Spain	Oekentorp 1969
<i>Favosites</i> (Sq.) <i>divissimus</i> [T]	Givetian	Spain	Oekentorp 1969
<i>Eridophyllum seriale</i> [R]	Eifelian	New York	Oliver 1976, 1983
<i>Favosites gilsoni</i> [T]	Eifelian	Germany	Oekentorp & Brühl 1999
<i>Xystriphyllum varium impicatum</i> [R]	Eifelian	Germany	Birenheide 1979
<i>Breviphrentis</i> NYSM 7812 [R]	Mid. Devon.	New York	Clarke 1908
<i>Favosites regularissimus</i> [T]	Emsian	W Europe	Birenheide 1985
<i>Favosites</i> (<i>Squameofavosites</i>) <i>delicatus</i> [T]	Emsian	Spain	Stel 1976
<i>favositids</i> [T]	Ludlow	NE Russia	Oekentorp 1969
* <i>Parafavosites ferganensis</i> [T]	Wenlock	Uzbekistan	Sokolov 1948
<i>Favosites vicinalis</i> [T]	Llandovery	Gotland	Stel 1976
<i>Heliolites</i> [T]	Llandovery	Gotland	Stel 1978
<i>Favosites pseudoforbesei muratsiensis</i> [T]	?O/S erratic	Netherlands	Stel 1976
<i>Thecia swindereniana</i> [T]	?O/S erratic	Netherlands	Stel 1976
<i>Calapoecia</i> [T]	Ashgill	Quebec	Tapanila 2004
<i>Columnopora</i> [T]	Ashgill	Quebec	Tapanila 2004
<i>Grewinkia</i> [R]	Caradoc	Manitoba	Elias 1986
<i>Chaetosalpinx siberiensis</i> Sokolov 1948 (= <i>Camptosalpinx estonicus</i>)			
* <i>Parafavosites germana</i> [T]	Wenlock	NE Russia	Sokolov 1948
<i>Paleofavosites balticus</i> [T]	Llandovery	Estonia	Klaamann 1958
<i>Favosites pseudoforbesei muratsiensis</i> [T]	?O/S erratic	Netherlands	Stel 1976
<i>Chaetosalpinx rex</i> Tapanila 2002			
<i>Columnopora</i> [T]	Ashgill	Quebec	Tapanila 2002
<i>Phragmosalpinx australiensis</i> Sokolov 1948			
* <i>Gephuropora dumi</i> [T]	Mid. Devon.	SE Australia	Sokolov 1948
<i>favositids</i> [T]	Early Devon.	France	Plusquellec 1968a
<i>Torquaysalpinx sokolovi</i> Plusquellec 1968b			
<i>Alveolites</i> [T]	Givetian	NE Australia	Zhen 1996
<i>chaetetid</i> [CS]	Givetian	Great Britain	Plusquellec 1968b
<i>Actinostroma</i> [CS]	Eifelian	Spain	Stel 1976
<i>Helicosalpinx asturiana</i> Oekentorp 1969			
<i>Actinostroma filitextum</i> [CS]	Givetian	NE Australia	Cook 1999
<i>Alveolites</i> [T]	Givetian	NE Australia	Zhen 1996
<i>Favosites alpenensis</i> [T]	Givetian	Michigan	Swann 1947
<i>Gerronostroma hendersoni</i> [CS]	Givetian	NE Australia	Cook 1999
<i>Pachyfavosites polymorphus cronigerus</i> [T]	Givetian	Spain	Oekentorp 1969
<i>Scoliopora denticulata</i> [T]	Givetian	Germany	Birenheide 1985
<i>Squameoalveolites perporosus</i> [T]	Givetian	Germany	Birenheide 1985
<i>Favosites</i> [T]	Eifelian	E Russia	Oekentorp 1969
<i>Favosites</i> cf. <i>radiciformis</i> [T]	Eifelian	Austria	Hubmann 1991
<i>Alveolites tischnoffi</i> [T]	Emsian	Spain	Stel 1976
<i>Favosites goldfussi</i> [T]	M. Dev.	Germany	Birenheide 1985
<i>Xystriphyllum</i> [R]	E.-Mid. Dev.	N Russia	Kravtsov 1966
<i>favositid</i> [T]	Ludlow	Uzbekistan	Gekker & Ushakov 1962
<i>Thecia swindereniana</i> [T]	?O/S erratic	Netherlands	Stel 1976
<i>Columnopora</i> [T]	Ashgill	Ohio	Cox 1936
<i>Columnopora</i> [T]	Ashgill	Ontario	Horst 1978; Tapanila 2004
<i>Calapoecia</i> [T]	Ashgill	Ontario	Horst 1978; Tapanila 2004
<i>Helicosalpinx concoenatus</i> Clarke 1908 (= <i>Streptindytes concoenatus</i>)	Late Sil.	New York	Clarke 1908
<i>stromatoporoid</i> [CS]			
<i>Streptindytes acervulariae</i> Calvin 1888	Mid. Devon.	Iowa	Calvin 1888
<i>Acervularia davidsoni</i> [R]			
<i>Streptindytes compactus</i> Clarke 1908	Mid. Devon.	New York	Clarke 1908
<i>Stromatopora</i> [CS]			
<i>Streptindytes chaetetiae</i> Okulitch 1936	Carboniferous	Russia	Okulitch 1936
<i>Chaetetes radians</i> [CS]			

Table 1. Continued.

Bioclaustration Taxon (Synonymy) Host [Group]	Age	Location	Reference
<i>Hicetes innexus</i> Clarke 1908	Prag.-Emsian	Germany	Clarke 1908
<i>Pleurodictyum</i> [T]			
<i>Pleurodictyum americanum</i> [T]	Mid. Devon.	New York	Brett & Cottrell 1982
<i>Burrinjuckia spiriferidophila</i> Chatterton 1975	Emsian	SE Australia	Chatterton 1975
<i>Howellella</i> [Bc]			
<i>Spinella buechanensis</i> [Bc]	Emsian	SE Australia	Chatterton 1975
<i>Spinella yassensis</i> [Bc]	Emsian	SE Australia	Chatterton 1975
<i>Diorygma atrypophila</i> Biernat 1961	Givetian	Poland	Mackinnon & Biernat 1970
<i>Desquamatia subzonata</i> (= <i>Atrypa zonata</i>) [Bc]			
<i>Catellocaula vallata</i> Palmer & Wilson, 1988	Caradoc	Ohio	Palmer & Wilson 1988
<i>Amplexopora persimilis</i> [Bz]			
<i>Tremichnus paraboloides</i> Brett 1985 various crinoids	Caradoc to Mississippian		Brett 1985
<i>Tremichnus cysticus</i> Brett 1985 (= <i>Myzostomites clarkei</i>) various crinoids	Wenlock to Carbonif., ?Jura		Feldman & Brett 1998
<i>Tremichnus minutus</i> Brett 1985 various <i>Eucalyptocrinitidae</i> crinoids	Wenlock to Givetian		Brett 1985
<i>Tremichnus puteolus</i> Brett 1985 various crinoids and possible blastoids	Wenlock to? Carboniferous		Brett 1985
Unnamed traces:			
Paired aperture cavity in side of rugose coral charactophylloid NYSM 7813 [R]	Mid. Devon.	New York	Clarke 1908; Oliver 1983
<i>Lingulid endosymbionts</i> (= Type 2 cavities of Tapanila & Copper 2002)	Ludlow	Gotland	Richards & Dyson-Cobb 1976
<i>Densastroma podolicum</i> [CS]			
<i>Heliolites interstinctus</i> [T]	Ludlow	Wales	Newall 1970
<i>Heliolites interstinctus</i> [T]	Ludlow	Gotland	Richards & Dyson-Cobb 1976
<i>Clathrodictyum</i> [CS]	Llandovery	Quebec	Tapanila & Copper 2002
heliolitid [T]	Llandovery	Quebec	Tapanila & Copper 2002

structure, and more rarely they are found in solitary rugosans. To date, Palaeozoic bioclaustrations are unknown in cateniform, fasciculate and auloporoid tabulate corals.

Ancient endosymbionts, with some exceptions, occur in corals with small corallite diameter (i.e. small polyp size, <4 mm), as do modern endosymbionts (Scott 1987). Figure 2 shows the diameters of some

infested tabulate and rugose coral hosts and the diameter of bioclaustrations found in these hosts. In addition to preferring corals with small polyps, the ancient endosymbionts almost always were smaller in diameter than their host's polyps. The diameter of fossil bioclaustrations is within the size ranges of those produced by modern endosymbionts (e.g. *Spirobranchus corniculatus* = 3–10 mm, *Idanthyrus*

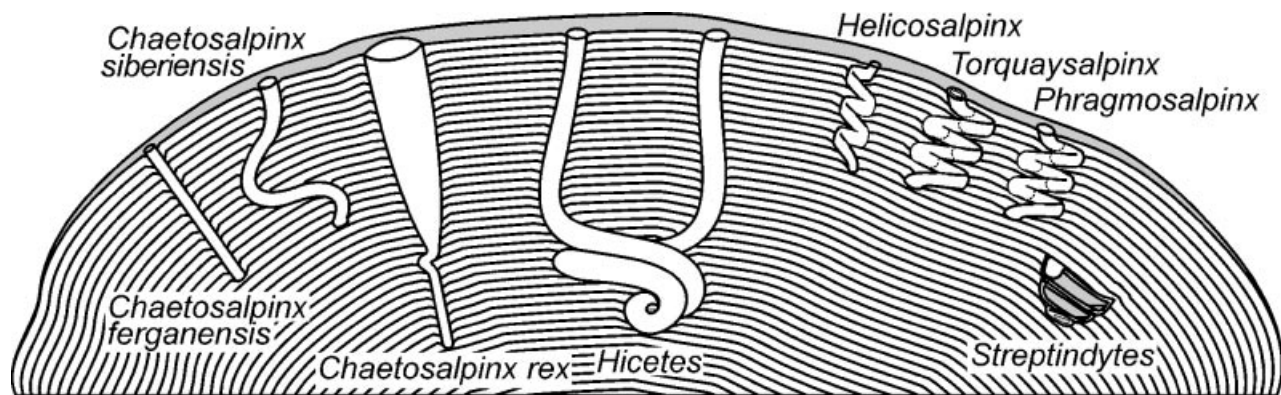


Fig. 1. Schematic diagram of bioclaustration ichnotaxa found in Palaeozoic corals and calcareous sponges. Note downward deflection of host skeletal laminae adjacent to the bioclaustrations. Scale exaggerated.

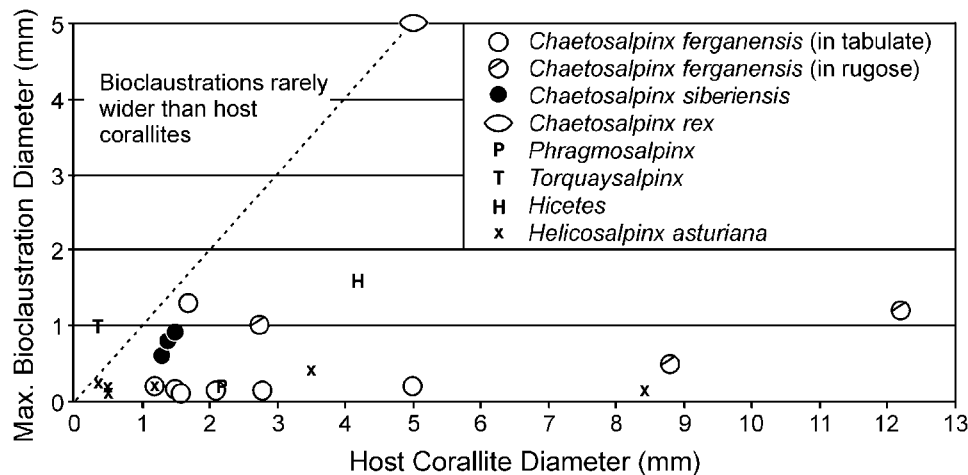


Fig. 2. Comparison of the diameter of several bioclaustration ichnotaxa with their host's corallite diameter. Dashed line indicates equal diameter of both bioclaustration and host corallites.

polychaete = 0.3–1.2 mm, vermetid gastropod <10 mm, *Cantellius* barnacle = 4–7 mm: Nishi & Nishihira 1999). Modern coral associates also tend to occur in the least aggressive coral taxa (Scott 1987; Dai & Yang 1995), i.e. corals which are less capable of actively damaging neighbouring corals (Lang 1973). Dai and Yang (1995) suggest that non-aggressive corals favour increased survivorship of the endosymbiont larvae. Similarly in Palaeozoic endosymbiosis, it is possible that the particular tabulate coral taxa which tend to contain bioclaustrations may have been among the community's least aggressive or toxic corals.

Despite the diversity of bioclaustration morphologies, infested host skeletons in almost all instances contain only one bioclaustration ichnotaxon. Further, where they are present, bioclaustrations tend to be abundant. This likely reflects the gregarious settlement of host substrates by endosymbiotic larvae, as observed in modern *Spirobranchus* and pyrgomatid barnacles (Ross & Newman 1973; Hunte *et al.* 1990a, b). The spatial arrangement of bioclaustrations in densely colonized host skeletons appears to be non-random. Individual bioclaustration cavities commonly are evenly spaced across the host skeletal surface and rarely overlap (Brett 1985; Stel 1976; Tapanila 2002, 2004). The even spacing of bioclaustrations is likely a display of territoriality by neighbouring endosymbionts competing for ambient resources (e.g. nutrients and water currents).

The endosymbiotic lifestyle requires increased specialization in behaviour, morphology and physiology, compared to closely related, non-symbiotic species (Patton 1967; Ross & Newman 1969; Morton & Scott 1980; Mokady & Brickner 2001; Savazzi 2001). The bodies of endosymbionts rarely

fossilize, therefore the primary record of behavioural specialization from the Palaeozoic is preserved by bioclaustrations. These behaviours, including the active selection of a host and gregarious recruitment, strongly resemble those observed in modern endosymbionts, suggesting that these are fundamental mechanisms for endosymbiotic survivorship that have remained essentially unchanged since the early Palaeozoic.

Palaeozoic evolution of endosymbiosis

Bioclaustrations are first recognized in the Late Ordovician of North America, where they occur in tabulate and rugose corals, bryozoans and crinoids (Fig. 3). These earliest cavities exhibit varied shapes, ranging from simple straight *Chaetosalpinx ferganensis*, to helical tubes (*Helicosalpinx*), to radial cavities (*Catellocaula*). A gradual increase in bioclaustration types and geographic occurrence is observed through the Silurian, and maximum diversity of bioclaustration forms occurred in the Middle Devonian. The apparent acme of bioclaustration diversity occurs in a broad range of skeletal fauna (tabulate and rugose corals, stromatoporoids, chaetetids, brachiopods, and crinoids) and has a global distribution (see Table 1). Traces of crinoid infesters (*Tremichmus*) continue through the Late Devonian, but all other known traces are absent. A single occurrence of *Streptindytes* is recorded from the Carboniferous. No other Palaeozoic occurrences of bioclaustrations in corals or calcareous sponges are currently known following the Givetian.

The Frasnian collapse in bioclaustration diversity and abundance following the peak of the Givetian may have resulted either from a decline in endosymbiont

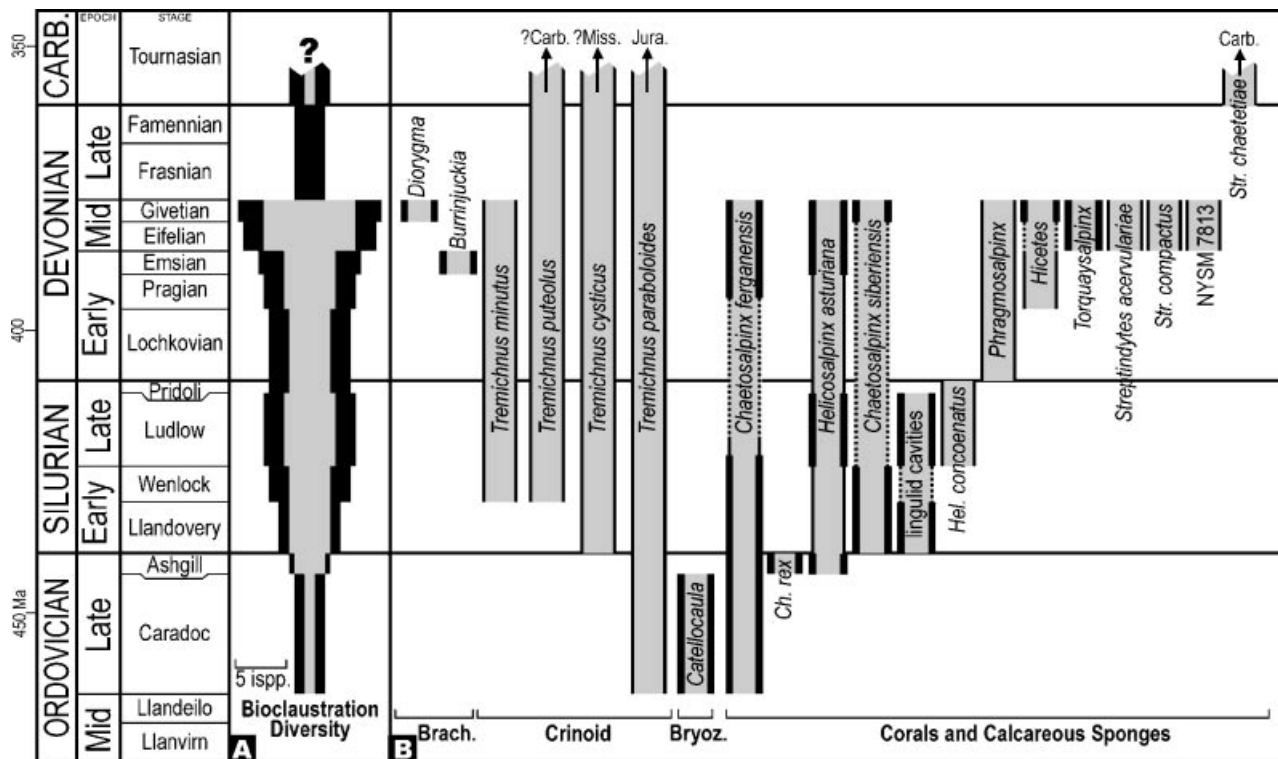


Fig. 3. Diversity of bioclaustration ichnotaxa during the Early to Middle Palaeozoic. □ A. Total number of bioclaustration ichnospecies in all host taxa (black) and for only coral and calcareous sponge host taxa (grey). Stage-scale resolution. □ B. Geologic ranges of ichnotaxa categorized by host invertebrates. Thick lines indicate stage-scale resolution, thin lines indicate epoch-scale resolution, and dotted lines connect known occurrences, though no record of the bioclaustration is known from this interval.

taxa following the Givetian, a decline in specific eligible host taxa following the Givetian, or it may have been related to the general decline in faunal diversity observed among all skeletal reef builders and dwellers in the Frasnian (Copper 2002).

The most commonly infested Palaeozoic tabulate corals belong to the superfamily Favositidae (e.g. the favositids: *Favosites*, *Paleofavosites*, *Pachyfavosites*, *Parafavosites* and *Gephyropora*). The Favositidae range from the mid-Ordovician to the end-Permian, but they suffered a significant decline in diversity following the Givetian (Copper 2002). Heliolitid corals, another frequently infested host group, originated in the Middle Ordovician and collapsed following the Givetian. The link between the disappearance of commonly infested host taxa and the disappearance of bioclaustrations appears to be real, although there is some evidence to suggest some flexibility among endosymbionts in choosing host substrates. The first *Helicosalpinx* are observed in the Late Ordovician sarcinulid corals, *Calapoecia* and *Columnopora*, which are host taxa that do not survive into the Silurian (Tapanila 2004). Yet *Helicosalpinx* very similar to the Late Ordovician examples occur repeatedly in other Silurian and Devonian host corals. If the endosymbionts that produced *Helicosalpinx* were derived

from the same lineage, they were able to exploit several host taxa and avoid the extinction that eliminated their early hosts, *Calapoecia* and *Columnopora*.

The sudden decline in bioclaustrations in coral and calcareous sponge hosts following the Givetian apparently did not affect the infesters of crinoids, preserved as *Tremichnus* bioclaustrations. *Tremichnus* is the longest ranging bioclaustration type known, spanning the Ordovician to Jurassic Periods. Most ichnospecies of *Tremichnus* are not specific to particular crinoid species, which may explain the longevity of this ichnotaxon.

The general decline in the diversity of many marine fauna leading up to the Frasnian–Famennian (Late Devonian) extinction may also help to explain the decline in bioclaustrations following the Middle Devonian. Reefs, for example, show increasing abundance and faunal diversity in the Early Devonian, peak in the Givetian, and start a slow decline in the Frasnian before collapsing in the Famennian with a loss of 60–85% of all skeletal reef-building organisms (Copper 2002). McGhee (1996) noted that the survivors of the stressed marine ecosystems during the Late Devonian typically were the more simple and primitive members of faunal lineages (e.g. primitive labechiid stromatoporphoids). It is most likely that a combination of the

specialization of endosymbionts with the loss of their preferred hosts ultimately resulted in the rapid decline of bioclaustrations following the Givetian. The absence of coral-hosted bioclaustrations following the Givetian cannot by itself prove a diversity collapse among endosymbiont taxa, although obligate endosymbionts almost certainly disappeared. Late Palaeozoic recovery of bioclaustrations following the Late Devonian mass extinctions is unknown, suggesting that the impact on endosymbionts was severe. Following the Frasnian–Famennian mass extinction, the Favositidae recovered half of their Middle Devonian diversity and continued into the Permian, yet no record exists of bioclaustrations in these seemingly eligible host corals. For the remainder of the Palaeozoic, the only known post-Givetian bioclaustration (except for *Tremichnus* in crinoids) occurs in a chaetetid sponge during the Carboniferous (Okulitch 1936).

In addition to bioclaustrations, other types of symbiotic associations with corals, including caunopores and rugosan-stromatoporoid intergrowths, show a similar decline in the Late Devonian. Caunopores, an intergrowth of stromatoporoids and obligate syringoporoid-like organisms, are common during Silurian to Middle Devonian time (Mistiaen 1984). Occurrences of caunopores in the Frasnian are less common and restricted to North America, and, by Famennian time, caunopores are unknown. Similar to caunopores, rugosan-stromatoporoid intergrowths are well known during the Silurian to Middle Devonian time interval, but they are unknown following the Givetian (Darrell & Taylor 1993).

In contrast, bioeroding endoliths appear to be less affected by Palaeozoic mass-extinction events, as evidenced by similar fossil boring types and abundances above and below extinction boundaries (e.g. Ordovician–Silurian boundary: Tapanila & Copper 2002; Tapanila *et al.* 2004; see also bioerosion trends in Kiessling *et al.* 1999). Here it is likely that the flexibility in choosing a lithified substrate (whether biotic or abiotic) to excavate a home allows boring endoliths to overcome stressed environments better than the more substrate-dependent endosymbionts.

In spite of a restricted lifestyle of interdependence, endosymbionts were successful during the Early to Middle Palaeozoic, as they are in oceans today. Endosymbionts must overcome high larval mortality in search for a proper host. They must avoid being killed or overgrown by the host, and they must avoid predation by other animals (Zann 1987). The rewards for endosymbionts apparently outweigh the challenges. In addition to acquiring a place to live, the endosymbiont is able to exploit the secure habitat of a live host that is unavailable to most fauna, including

most macroborers. With this decrease in interspecific competition for space and resources, the endosymbiont can move away from cryptic niches (e.g. *Spirobranchus giganteus* compared to other serpulids in reef ecosystems: Smith 1984).

The host-selective and gregarious endosymbiotic lifestyle also favours reproduction by maintaining proximity of the embedded population, including both sexes, with their preferred host. This ‘rendezvous host’ hypothesis originally was proposed for aphids (Ward 1991) and later was applied to pyrgomatid barnacles (Mokady & Brickner 2001). It is an ideal strategy for sexually reproducing sessile organisms with clumped distributions.

Bioclaustrations offer much palaeontologic information that often has been overlooked or only reported anecdotally. With increased reporting of bioclaustrations (e.g. unnamed Late Ordovician coral bioclaustrations reported by Lee & Elias 2003), application of these unique trace fossils will contribute further to our understanding of the complex ecosystems of the past. For example, modern applications use the abundance of coral associates, including heterotrophic endosymbionts, as proxies for reef ecosystem health, which can be related to nutrient enrichment of surface waters (Risk *et al.* 2001). Translation of this application to the fossil record might be useful in characterizing ancient reef health in terms of reef ecosystem diversity and secular changes in nutrient content of surface waters.

On a broader scale, bioclaustration trace fossils might provide new insight into early metazoan development. Recent discovery of bioclaustrations in Cenozoic lacustrine stromatolites (Lamond & Tapanila 2003) suggests a possible mechanism for early Palaeozoic marine invertebrates to invade the endolithic habitat without boring.

Conclusions

- (1) Bioclaustrations are trace fossils that preserve dual behaviours of an endosymbiont that inhibits the skeletal growth of its host and produces a cavity which it uses as a dwelling structure. The new ethological category, *impedichnia*, is proposed to describe this complex behaviour.
- (2) Ten bioclaustration ichnogenera are recognized from the Palaeozoic. At times during the Palaeozoic, these bioclaustrations had a global distribution. They occur most commonly in the skeletons of tabulate and rugose corals, calcareous sponges (stromatoporoids and chaetetids) and crinoids.
- (3) Bioclaustrations in corals and calcareous sponges occur preferentially in certain host taxa and show

- a gregarious distribution, similar to that of modern endosymbionts.
- (4) Diversity of bioclustrations expanded during the Late Ordovician and peaked in the Middle Devonian. Bioclustrations in Palaeozoic corals and calcareous sponges are almost unknown following the Givetian.
 - (5) Fossil bioclustrations preserve rare direct evidence of animal interactions. These fossils are particularly well-suited for studies on the palaeoecology and evolution of animal interdependence, including the development of ancient reef ecosystems.

Acknowledgements. – I thank A.A. Ekdale and J.M. de Gibert for providing critical reviews on an early version of this manuscript. Thorough and constructive reviews by R. MacNaughton and an anonymous reviewer greatly helped to improve the clarity of the final text. This work also has benefited from insightful conversations on ichnotaxonomy with M. Bertling and R. Bromley.

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Appendix: remarks on ichnotaxonomy of Palaeozoic bioclaustrations

A total of ten formalized ichnogenera are regarded here as bioclaustrations, with an additional two bioclaustrations that are currently in open nomenclature. This review omits traces that originally were described as bioclaustrations (e.g. *Actinosalpinx*, *Antherosalpinx* and *Asterosalpinx*; Sokolov 1948, 1962), but since have been shown convincingly to be diagenetic features (Flügel 1973). Features typically considered invalid for the purposes of establishing trace fossil ichnotaxobases were avoided (e.g. Magwood 1992; Goldring *et al.* 1997). These include the presence or absence of deflected host laminae (a feature of the substrate, not the trace fossil), absolute size parameters, stratigraphic age, geographic location and the composition (or biotaxonomy) of the host substrate.

Chaetosalpinx includes dominantly straight cavities that are parallel to the host's axis of growth. The cavity is circular to oval in cross-section and it lacks a wall lining or floor-like tabulae. The type ichnospecies, *C. ferganensis*, is a straight, isodiametric *Chaetosalpinx* with a circular aperture and has been formally described only from tabulate corals. Several bioclaustrations described from rugose corals fit the description of this ichnospecies and are here included within it. *Chaetosalpinx siberiensis* also has a circular aperture and is isodiametric, but it is irregularly sinuous along its length. This trace has been observed only in tabulate corals and tends to be three times wider than most *C. ferganensis*. *Chaetosalpinx rex*, toward its base, resembles *C. ferganensis*, but it displays aperture-ward increase in size and a change in cross-sectional shape, from circular to biconvex. It is known only in tabulate corals.

Four helical bioclaustration ichnogenera are known from the Palaeozoic. The width of coiling is roughly constant in *Helicosalpinx*, *Phragmosalpinx* and *Torquaysalpinx*, but the *Streptindytes* helix tapers towards the base to form an inverted conical spiral. Two ichnospecies of *Helicosalpinx* are recognized by their lack of a lining and tabulae. *H. asturiana* is the most common ichnospecies of the helical traces, occurring in tabulates, rugosans and calcareous sponges. The trace forms a tight helical to sinuous cylinder throughout its length and tends to be sinistrally coiled (Tapanila 2004). *H. concoenatus* differs by having a radius of coiling wider than the tube diameter, resulting in a loosely coiled helix (Clarke 1908). Only one ichnospecies of the ichnogenera *Phragmosalpinx* and *Torquaysalpinx* have been described. *Phragmosalpinx australiensis* (possessing tabulae, but no lining) and *Torquaysalpinx sokolovi* (possessing tabulae and lining) tend to have a wider diameter than *Helicosalpinx*. Three ichnospecies are assigned to the inverted cone-shaped *Streptindytes*, all possessing a wall lining. The form of *S. acervulariae* is characterized by constrictions between

each whorl of the conical helix, whereas no constrictions between whorls are evident in *S. compactus* (Clarke 1908). Okulitch (1936) described *S. chaetetiae* as resembling *S. compactus*, but having a more circular cross-section and rounder outer margins than the angular outline of *S. compactus*.

Hicetes are bioclaustrations with two apertures and have no lining or tabulae. The sole ichnospecies, *Hicetes innexus*, appears to be a host-specific trace found only in the tabulate coral, *Pleurodictyum* (Clarke 1908; Plusquellec 1965; Brett & Cottrell 1982; Oliver 1983). This bioclaustration is U-shaped, having a tightly-coiled base that leads to two straight, vertical shafts that form a pair of apertures among the corallites of the host's upper surface.

Two currently unnamed types of bioclaustrations are added in this review. The first cavity occurs in a solitary rugose coral specimen originally described by Clarke (1908, pl. 2, fig. 2: New York State Museum, specimen NYSM 7813) as *Gitionia*, an ichnogenus synonymized by Cameron (1969) with the boring *Vermiforichnus*. In his review on rugosan symbioses, Oliver (1983) re-examined specimen NYSM 7813 and determined that the cavity was a bioclaustration having a pair of lined apertures that formed depressions in the side of the charactophylloid rugose coral. Oliver (1983) did not attempt to revise the ichnotaxonomy of this trace fossil, but his clear description and illustration of the specimen suggest that it is an important and distinct bioclaustration.

The second unnamed bioclaustration considered in this review is made by lingulids in tabulate corals and stromatoporoids, and it is known from three locations (Newall 1970; Richards & Dyson-Cobb 1976; Tapanila & Copper 2002). *Trypanites* borings in corals and stromatoporoids that were later occupied by nestling lingulids (i.e. not excavated by the lingulids) form the site of bioclaustration initiation. Deflected growth of the host coral or stromatoporoid resulted in a straight cylinder with a lenticular cross-section atop the *Trypanites* boring resembling the lenticular cross-section of the infesting lingulid, which is commonly preserved in the cavities.

Corals and calcareous sponges appear to have been the most common hosts for endosymbionts, but other skeletonized animals hosted endosymbionts during the Palaeozoic. Palmer and Wilson (1988) described a large bioclaustration (*Catellocaula vallata*) consisting of an array of radially disposed pits on the surface of bryozoans, presumed to have been formed around a tunicate or hydroid endosymbiont. Two bioclaustrations, *Diorygma* and *Burrinjuckia*, are hosted by brachiopods (Biernat 1961; MacKinnon & Biernat 1970; Chatterton 1975). *Diorygma atrypophilia* is a bifurcating tunnel having paired apertures and occurs only in the pedicle valves of atrypids. *Burrinjuckia spiriferidophilia* is a stout tunnel with an irregular aperture opening on the internal surface of the brachial valve of some spiriferids. Endosymbionts of echinoderms produced the ichnogenus *Tremichnus*, which includes four ichnospecies occurring particularly in crinoid ossicles and calices. Brett (1985) provided a comprehensive review of these pit-like traces, including systematic descriptions.