

Patterns and Processes in the Ordovician Bioerosion Revolution

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The Ordovician Bioerosion Revolution was a dramatic diversification of macroboring ichnotaxa during the Middle and Late Ordovician. This was also a time during which the intensity of carbonate substrate bioerosion greatly increased, reaching a peak in the Late Ordovician and Early Silurian that was not achieved again until the Jurassic. This burst of ichnological diversity was a function of the Ordovician Radiation of marine invertebrates, and it reflects the range and rate of niche differentiation on hard substrates at that time.

Keywords Ordovician, bioerosion, macroborings

INTRODUCTION

The Ordovician Period was a time of extraordinary evolutionary radiation among marine invertebrates, so much so that it has been termed “The Great Ordovician Biodiversification Event” (Webby et al., 2004). This increase in diversity was primarily driven by ecological innovations by benthic marine invertebrates, and many of these new life modes and behaviors are represented in the Ordovician trace fossil record (Mángano and Droser, 2004). Macroboring in shells, rocks, and hardgrounds show this same diversification (for example, in the early compilation of data by Kobluk et al., 1978, and in later more detailed reviews by Taylor and Wilson, 2003, and Bromley, 2004). Recently the record has grown robust enough to recognize the Ordovician Bioerosion Revolution (OBR; Wilson and Palmer, 2001a) and begin to plot a Phanerozoic diversity curve for macroborings (Fig. 1). Diversity is not the only result of the OBR: the increased intensity of boring on hard substrates is also evident (Fig. 2).

BORING ICHNOTAXA IN THE ORDOVICIAN

Few ichnological diversifications were as dramatic as those in the OBR, even though the number of ichnotaxa involved

is relatively small. We are currently studying the macroborings found in Ordovician hard substrates (hardgrounds, rockgrounds and shells) to sort out their ichnotaxonomy, their distributions in time and space, and the tracemaker behaviors they may represent. We have confined ourselves primarily to the dominichnia among the Ordovician macroborings because they more closely reflect the niche differentiation during the Ordovician. Effectively this means that we are not including the round holes known as *Oichnus* in shells which may (or may not, see Wilson and Palmer, 2001b) represent predatory borings in the Lower Paleozoic. So far we can say the following about these Ordovician dominichnial macroboring ichnogenera.

Trypanites Mägdefrau 1932

The ichnogenus *Trypanites* appears in the Lower Cambrian in some abundance (James et al., 1977), but it is very rare (if not actually absent) in the Middle and Upper Cambrian. It is the only pre-Ordovician macroboring known. *Trypanites* reappeared in the Early Ordovician and by the Late Ordovician was common enough to have been a significant bioeroder of calcium carbonate substrates (Fig. 2). *Trypanites* continues as a common boring throughout the rest of the Phanerozoic, but it did not reach again the densities it displays on Upper Ordovician and Lower Silurian carbonate hard substrates.

Palaeosabella Clarke 1921

The long, cylindroclavate macroboring *Palaeosabella* first appears in the Upper Ordovician (Fig. 3). It resembles *Trypanites* and may in fact be indistinguishable from it unless its slightly clavate terminus is observed. *Palaeosabella* and *Trypanites* are the first borings to provide secondary niche space for cryptic organisms (especially lingulid brachiopods) which settled in its expanded cavity (Tapanila and Copper, 2002).

Gastrochaenolites Leymerie 1842

The ichnogenus *Gastrochaenolites* is among the most common borings in carbonate hardgrounds and thick shells

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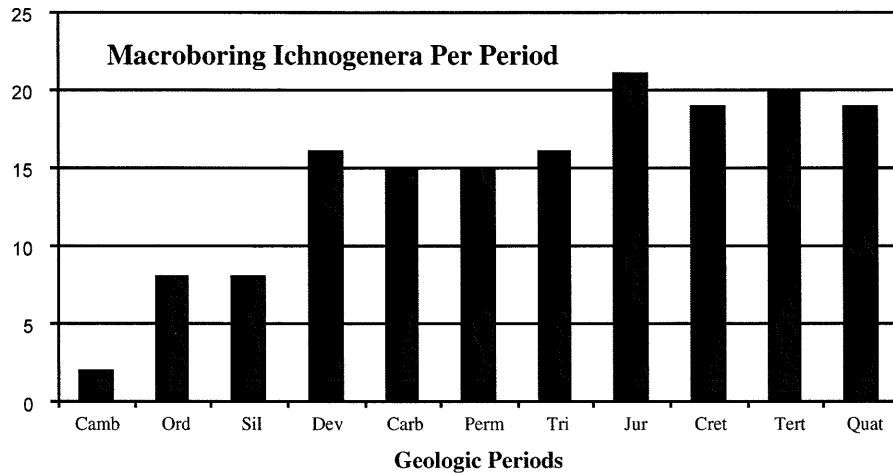


FIG. 1. Graph showing the diversity of macroboring ichnogenera through the Phanerozoic. Data is from Taylor and Wilson (2003) and Bromley (2004).

in Jurassic and later deposits. It is a broad, clavate boring constructed by gastrochaenid and lithophagid bivalves today. The earliest occurrence of *Gastrochaenolites* was thought to be Upper Carboniferous (Wilson and Palmer, 1998), but shortly afterwards Ekdale and Bromley (2001) described *G. oelandicus* from the Lower Ordovician of Sweden, and then Benner et al. (2004) documented additional *Gastrochaenolites* in the Lower Ordovician of Utah. We have some concerns about whether these Ordovician *Gastrochaenolites* specimens are true borings or instead some type of burrow system. Our reservations are that (a) there is a diagenetic halo around the Swedish *G. oelandicus* specimens which is identical to that surrounding a *Thalassinoides*-like soft-sediment burrow system in the same bed; (b) this halo is cut by undoubted borings (*Trypanites*); (c) the bioclasts "cut" by these *Gastrochaenolites* could have been truncated by other means such as early diagenetic weakening (as with the crystallites in trilobite cuticle), early diagenetic dissolution (as with nautiloid conchs), or later erosion in an exposed, cemented burrow system; and (d) the shape of *G.*

oelandicus, especially its very narrow neck and irregular walls, is inconsistent with any known boring tracemaker. The Utah *Gastrochaenolites* are more compelling as borings than the Swedish examples, but further study of the material is necessary to sort out these issues. We tentatively consider them here to be borings. We can at least all agree that whatever formed the Ordovician versions of *Gastrochaenolites*, it was not a bivalve.

***Petroxestes* Wilson and Palmer 1988**

The mytilacean bivalve *Corallidomus* has been found in shallow, elongate borings excavated in bryozoan and stromatoporoid skeletons and hardgrounds of the Upper Ordovician of North America (Whitfield, 1893; Pojeta and Palmer, 1976). This boring was later described from the Lower Silurian of Anticosti Island, Canada, by Tapanila and Copper (2002). These are the earliest known bivalve borings (Fig. 4).

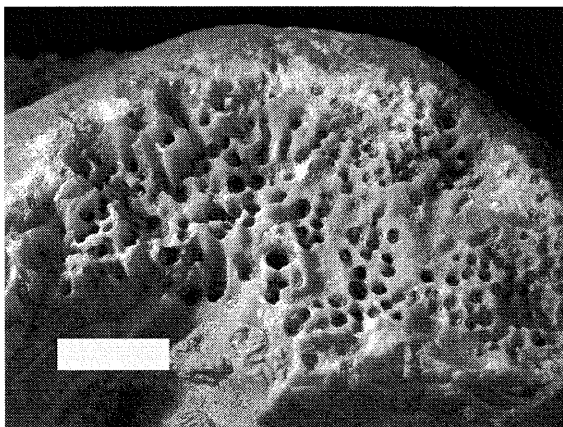


FIG. 2. Trepostome bryozoan heavily bored by *Trypanites*; Kentucky, Upper Ordovician; scale bar equals 10 millimeters.

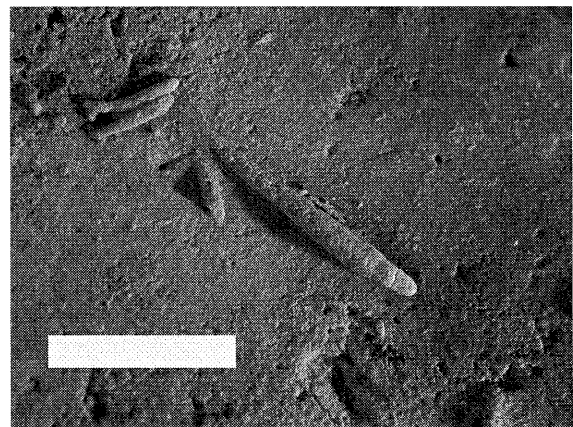


FIG. 3. Natural cast of *Palaeosabella* borings in what was the aragonite of a bivalve shell; Indiana, Upper Ordovician; scale bar equals 5 millimeters.

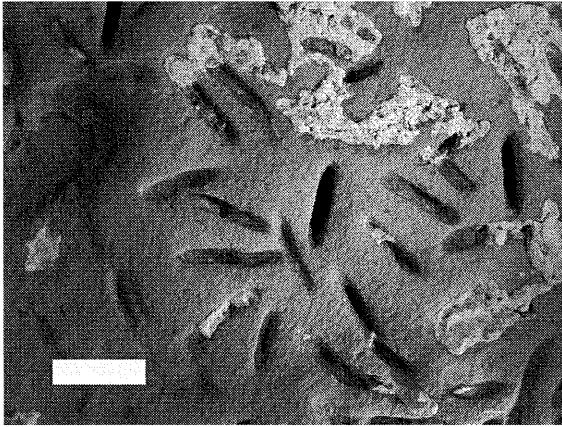


FIG. 4. *Petroxestes pera* in a carbonate hardground; Ohio, Upper Ordovician; scale bar equals 10 millimeters.

***Cicatricula* Palmer and Palmer 1977**

Cicatricula is a shallow, ramifying boring found on Middle Ordovician hardground surfaces in Iowa (Palmer and Palmer, 1977). Although Elias (1980) regarded this ichnogenus as a junior synonym of *Dictyoporus*, we believe that its substantially larger size and more elaborate branching justifies its inclusion in an ichnogenus of its own. *Cicatricula* may be the earliest known sponge boring.

***Ropalonaria* Ulrich 1879**

Ropalonaria is a well known boring produced by runner-type ctenostome bryozoans; it is represented by many ichnospecies in the Ordovician (Pohowsky, 1978). The earliest ctenostome bryozoan borings yet known (and formally undescribed) are found in the Volkovian (Arenigian; Lower Ordovician) of the St. Petersburg area, Russia. Ctenostome bryozoan borings continue through the fossil record to the present. There is some ichnotaxonomic confusion regarding ctenostome borings, especially since some literature has treated them as body fossils (see Taylor and Wilson, 2003, for discussion). The relationship of *Ropalonaria* to a Middle Ordovician variety of *Pinaceocladichnus*, for example, is unclear (see Mayoral et al., 1994). We are here considering these ichnogenera synonymous, but further work may definitively separate them.

***Sanctum* Erickson and Bouchard 2003**

Sanctum laurentiensis is the latest addition to the list of Ordovician macroborings. It consists of excavations in the endozones of thick trepostome bryozoans, apparently as domichnia. *Sanctum* may be easily overlooked in collections and in the field because the endozones of trepostome skeletons are usually either not exposed or their thin walls have been preferentially eroded away. *Sanctum* is presently known only from the Cincinnati of North America.

BORING ICHNODIVERSITY IN THE ORDOVICIAN

If we measure the diversity of Ordovician macroborings simply by the number of ichnotaxa, then they show a dramatic diversification from the Cambrian (essentially one macroboring ichnogenus in the Lower Cambrian and at least eight in the Ordovician; see Fig. 1). This matches the diversity trends noted by Mángano and Droser (2004) for all Ordovician trace fossils, although with far fewer numbers. We suspect that the diversity of Ordovician macroborings will be increased with better ichnosystematics of *Trypanites*. This ichnogenus may be overused for a variety of cylindrical holes that may represent significantly different boring behaviors. Some excavations which are traditionally called *Trypanites* twist and turn, for example, in ways which suggest that filter-feeding alone may not be the primary motivation for boring. Other *Trypanites* borings can be found in populations with distinct size and shape differences which indicate many excavating “worm-like” organisms. Finding a realistic way to break through the present conservative definition of *Trypanites* may give us a more complete image of bioeroder diversity in the Ordovician.

BIOEROSION INTENSITY IN THE ORDOVICIAN

It is clear, though, that ichnotaxonomic diversity is only part of the Ordovician Bioerosion Revolution story. The intensity of boring, at least as measured by the number of borings per unit of hard substrate area, dramatically increases through the Ordovician, peaking in the Late Ordovician into the Early Silurian. Thick carbonate substrates such as hardgrounds, corals, and stromatoporoids are commonly found deeply bioeroded during this interval, especially by *Trypanites* and *Palaeosabella* (Fig. 2). Our procedural difficulty now is finding a way to measure boring intensity in the fossil record without a way to compensate for the amount of time a bored substrate has been exposed on the seafloor. We may only be able to measure the effects of bioerosion in terms of substrate removed and not the temporal intensity. Nevertheless, it is clear that the most significant bioerosion in the Paleozoic occurred during the Late Ordovician.

ORDOVICIAN BIOEROSION SETS THE PATTERN

The patterns of macroboring behavior established in the Ordovician Bioerosion Revolution remain dominant throughout the rest of the Paleozoic. The only significant Paleozoic additions are acrothoracican barnacle borings in the Devonian (*Rogerella*; we note, though, that there are hints of a similar undescribed boring in Ordovician gastropods of the Cincinnati in North America), the “worm” borings *Caulostrepsis* and *Talpina*, also first in the Devonian, and an apparently bivalve-produced *Gastrochaenolites* in the Carboniferous. Macroboring communities diversify again in the Devonian, but the general boring behavior does not significantly change until the Mesozoic Marine Revolution brings large increases in the diversity and abundance of bivalve, sponge and polychaete borings (Fig. 1).

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