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SEDILICHNUS, OICHNUS, FOSSICHNUS, AND *TREMICHNUS*: 'SMALL ROUND HOLES IN SHELLS' REVISITED

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ABSTRACT—Small round pits and holes in fossil skeletal material are found in a wide variety of invertebrate substrates from diverse environmental settings. They are associated with parasitism, predation and commensal attachment. Four ichnogenera have been proposed for these trace fossils: *Sedilichnus* Müller, *Oichnus* Bromley, *Tremichnus* Brett and *Fossichnus* Nielsen, Nielsen and Bromley. Previous authors have established that *Tremichnus* is a junior synonym of *Oichnus*. Herein we show that *Oichnus* and *Fossichnus* are junior synonyms of *Sedilichnus*.

Sedilichnus, as defined herein, includes 10 ichnospecies. *Sedilichnus spongiophilus, S. simplex, S. paraboloides, S. ovalis, S. coronatus, S. gradatus, S. halo, S. asperus, S. excavatus* and *S. solus*. Consistent with previous work *Sedilichnus* ichnospecies are defined solely by morphological criteria and not by a priori assumptions regarding depositional environment or tracemaker. Thus, this ichnotaxon is recognized in both marine and continental settings on a wide variety of invertebrate skeletal tests. As is true with many ichnotaxa, *Sedilichnus* ichnospecies represent end-members in morphological spectra, however each ichnospecies is clearly differentiable from the others.

Sedilichnus spongiophilus are circular, non-penetrative pits in shells. *Sedilichnus paraboloides* are penetrative holes with spherical paraboloid forms and typically have larger external openings and smaller internal openings. *Sedilichnus simplex* are simple cylindrical borings that have both penetrative and non-penetrative forms. *Sedilichnus coronatus* differ from other forms by the presence of an etched or granular halo surrounding the boring. *Sedilichnus gradatus* have two concentric parts, an outer boring and an inner shelf of smaller diameter. *Sedilichnus ovalis* and *S. asperus* are both oval in outline differing in the presence of tapering paraboloid margins in *S. ovalis* and margins perpendicular to the substrate in *S. asperus*. *Sedilichnus excavatus* and *S. solus* are primarily non-penetrative and differ from other *Sedilichnus* by the presence of central, raised bosses or platforms. These two ichnospecies differ in the shapes of their external walls and the proportional thickness of the bounding groove.

INTRODUCTION

AMONG THE most common of boring or embedment structures in fossil and Recent skeletal material are diminutive circular to subcircular pits and holes (Figs. 1, 2). These traces are made by a variety of organisms within a range of host skeletal substrates (Kelley and Hansen, 2003; Kelley, 2008). Perhaps the most well known are the circular holes emplaced by naticid and muricid gastropods in fossil and Recent bivalve shells (Figs. 1.1–1.10, 2.8–2.11). These borings are emplaced for the purposes of predation (e.g., Ziegelmeier, 1954; Thomas, 1976; Carriker, 1981; Huebner and Edwards, 1981; Kitchell et al., 1981; Kabat, 1990; Peitso et al., 1994). The snails drill a hole in the umbo or center of a valve allowing the proboscis to be inserted into the shell, and consume the soft tissues within (Ziegelmeier, 1954; Carriker, 1981).

In addition to predation, circular borings also result from the activities of parasites and commensals. Gastropod parasites such as the eulimid gastropod genera *Pelseneeria* Koehler and Vaney 1908 and *Thyca* Adams and Adams 1854 attain sustenance without killing their echinoderm host taxa and in so doing excavate variably shallow pits in their host organism (Köhler and Vaney, 1908; Köhler, 1924; Bromley, 1981; Neumann and Wisshak, 2009). Circular borings resulting from predation are commonly penetrative (Fig. 1.1–1.6) although failed predation attempts may result in non-penetrative borings (Figs. 1.1, 2.9–2.11). Circular borings produced through commensalism are typically non-penetrative (Bromley, 2004).

Over the past several decades, several ichnogenera have been named for these trace fossils. These include *Sedilichnus* (Müller, 1977), *Oichnus* (Bromley, 1981) and *Tremichnus* (Brett, 1985). Although the holotypes of the type ichnospecies of each of these ichnogenera occur in the shells of a variety of marine invertebrates (sponges, crinoids, bivalves and snails) considerable overlap occurs in their diagnoses. It has been suggested that *Tremichnus* should be considered to be a junior synonym of *Oichnus* (Pickerill and Donovan, 1998). Subsequent authors have concurred (Nielsen and Nielsen, 2001; 2002; Donovan and Jagt, 2002; Donovan and Pickerill, 2002; Todd and Palmer, 2002; Bromley, 2004). Bromley (2004) followed this synonymy and further suggested that both *Oichnus* and *Tremichnus* should, in actuality, be considered junior synonyms of *Sedilichnus*. This suggestion is formalized herein and a new ichnotaxonomy of *Sedilichnus* is proposed.

SYSTEMATIC PALEONTOLOGY

The traces discussed herein occur on a broad variety of skeletal substrata. Following the protocol of previous workers (i.e., Bromley, 1981; Nielsen and Nielsen, 2001, 2002; Donovan and Jagt, 2002; Donovan and Pickerill, 2002; Todd and Palmer, 2002; Bromley, 2004; Bertling et al., 2006), we consider neither inferred environment of occurrence nor the choice of skeletal substrate to be ichnotaxonomically significant criteria.

Sedilichnus occur in two distinct end-members: those that penetrate fully through the shell (referred to as 'penetrative') and those that terminate within the skeletal substrate (referred to as 'non-penetrative). Following Nielsen and Nielsen (2001), the word 'hole' indicates a boring that penetrates through a skeletal substrate whereas 'pit' denotes a boring that does not fully penetrate the substrate. Skeletal substrates, particularly the shells of bivalves, gastropods, brachiopods and similar organisms, may have two distinct types of surfaces: those exposed to the external environment (referred to as 'outer' surfaces) and those that, during the life of the organisms, were protected from the external environment and typically served as the interface between the soft tissue and the shell (referred to as the 'inner' surface). 'Margin' is used for the boundary surface separating a boring from the surrounding, unaffected substrate (Goldring and Pollard, 1996).

Several examples included in *Sedilichnus* (such as material included in the original description of *Tremichnus*) exhibit evidence of a reaction by the host organism to activity of the epizoan taxon (Brett, 1985). These include galls, stereom swellings, bioclaustrations and embedment structures (Brett, 1985; Tapanila, 2005; Donovan et al., 2006). Following the precedence set by other workers, these deformities on the host taxon's skeletal test or shell are not considered to be viable ichnotaxobases (Nielsen and Nielsen, 2001; Bromley, 2004; Bertling et al., 2006). Thus, although these growths/deformities provide clear evidence of excavation of the borings on a living host taxon, they play no role in the ichnotaxonomy of small round holes in skeletal substrata.

Holotype material for ichnospecies included within *Sedilichnus* is housed in several different institutions. Institutional acronyms are as follows: PSSGBF, Paläontologische Sammlung der Sektion Geowissenschaften der Bergakademie Freiberg; MGUH, Geological Museum of the University of Copenhagen; NHMM, Natuurhistorisch Museum Maastricht, The Netherlands; and UAIC, University of Alberta Ichnology Collections.

Ichnogenus Sedilichnus Müller, 1977

Type ichnospecies.—*Sedilichnus spongiophilus* Müller, 1977.

Other ichnospecies.—*Sedilichnus simplex* (Bromley, 1981); *S. paraboloides* (Bromley, 1981); *S. ovalis* (Bromley, 1993); *S. coronatus* (Nielsen and Nielsen, 2001); *S. gradatus* (Nielsen and Nielsen, 2001); *S. asperus* (Nielsen and Nielsen, 2001); *S. excavatus* (Donovan and Jagt, 2002); *S. halo* (Neumann and Wisshak, 2009); *S. solus*.

Diagnosis.—Circular to subcircular and oval holes bored into hard skeletal substrates. The hole may penetrate fully through the substrate or terminate within the substrate as a shallow, bowl-shaped pit or as a deeper shaft with a rounded, blunt or pointed terminus.

Occurrence.—Neoproterozoic to Holocene, cosmopolitan.

Remarks.—Müller (1977) interpreted *Sedilichnus* to have been formed while the host organism was alive and suggested that the boring taxon had its body partially embedded within the skeletal substrate during life. He also stated that the relationship between the two organisms to be one based on commensalism rather than parasitism (Müller, 1977) and originally included this as part of the diagnosis of the ichnogenus. These interpretations are not included in our amended diagnosis. Evidence suggests that commensal organisms may form some *Sedilichnus* but others are clearly produced by parasites or predators. Regardless, inferences of behavior in fossil material are inherently interpretative and thus are invalid ichnotaxobases.

The diagnosis of *Sedilichnus* is, in part, dependent upon its occurrence in a skeletal substrate of some sort. However the nature of this substrate (i.e., the taxonomy of the host organism) is irrelevant. *Sedilichnus* has been reported on a broad variety of invertebrate taxa, including echinoderms (crinoids and echinoids), brachiopods, mollusks (gastropods, bivalves, cephalopods and scaphopods), ostracods, bryozoans, sponges and foraminifera (e.g., Müller, 1977; Bromley, 1981; Brett, 1985; Nielsen and Nielsen, 2001; Donovan and Jagt, 2002; Donovan et al., 2006). The definition of *Sedilichnus* is amended herein to clarify the range of morphologies included in this ichnogenus with the goal of providing a simpler and more utilitarian ichnotaxonomy.

Sedilichnus spongiophilus Müller, 1977

1985 *Tremichnus paraboloides* Brett, p. 627, figs. 1, 2.
1985 *Tremichnus cysticus* Brett, p. 628, fig. 3.
1985 *Tremichnus minutus* Brett, p. 629, figs. 4, 5.
1985 *Tremichnus puteolus* Brett, p. 629, fig. 6.
1986 *Tremichnus cysticus* Harper, p. 16, fig. 3.
1988 *Tremichnus cysticus* Eckert, p. 281, figs. 1, 2.
1988 muricacean borehole Aitken and Risk, p. 345, fig. 1D.
1994 abortive predatory borehole Morris and Bengtson, p. 18, fig. 14/16.
1998 incomplete borings Hagan, Coniglio and Edwards, p. 121, fig. 2A, 2D.
2000 predatory boreholes Harper and Wharton, p. 19, fig. 1A, 1C.
2002 Taddei Ruggeiro and Annunziata, p. 46, pl. 1, fig. 3.
2006 *Oichnus paraboloides* Donovan et al., p. 44, fig. 1.
2006 failed drill hole, Baumiller et al., p. 315, fig. 2G, 2I.
2008 borehole Deline, p. 740, fig. 1.
2010 incomplete drill hole Martinell et al., p. 223, fig. 3a.
2010 *Oichnus paraboloides* Wilson et al., p. 97, fig. 3D, 3E.
2011 *Oichnus paraboloides* Chattopadhay, p. 41, fig. 4.

Diagnosis.—*Sedilichnus* that consist of smooth-walled, bowl-shaped pits with a circular outline and rounded edge.

Description.—The holotype and associated material occur on the external surface of the siliceous demosponges *Prokaliapsis janus* (Roemer). The borings range in size from 6 to 11 mm in diameter. They range from shallow pits (1–2 mm in depth) to deeper pits (several mm in depth) but do not penetrate through the skeletal substrate.

Holotype.—PSSGBF 210/284, Upper Cretaceous (Campanian) strata at Ilsenberg-Entwicklung, Germany.

Occurrence.—Cambrian to Pleistocene, cosmopolitan.

Remarks.—*Sedilichnus spongiophilus* are among the simplest of *Sedilichnus*, consisting of variably shallow hemispherical pits (Figs. 1.1, 3.1, 3.2), typically emplaced on the external surface of a skeletal test. Müller (1977) identified two types of *S. spongiophilus*. Type I includes the holotype and consist of the smooth-walled hemispherical pits that typify *S. spongiophilus*. Type II are oblong, almond-shaped traces which may be referable to *S. ovalis* although they differ in being non-penetrative. Müller (1977) suggested cirripedes (barnacles) as a possible tracemaker.

Sedilichnus spongiophilus occur on a broad variety of invertebrate skeletal substrata including sponges, bivalves, brachiopods and crinoids. Failed predatory boreholes drilled by the naticid gastropod *Lunatia* Gray 1847 and the muricid gastropod *Nucella* Röding 1798 are consistent in morphology with *S. spongiophilus* (Fretter and Graham, 1962; Figs. 1.1, 4.2).

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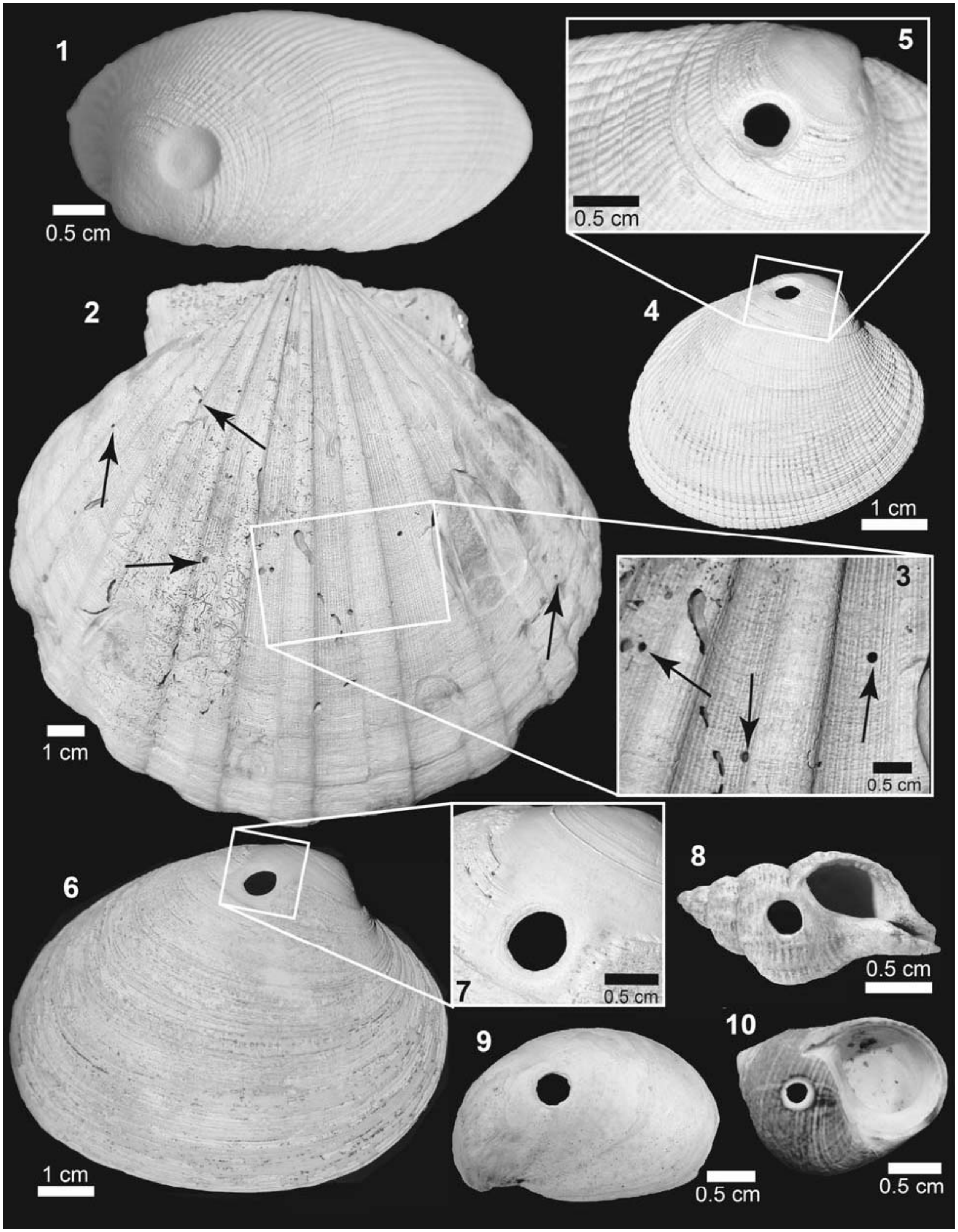
Figure *1*—*Sedilichnus* in a variety of fossil and extant skeletal tests. *1*, boring consistent with *Sedilichnus spongiophilus* in the umbo region of *Leukoma staminea* (Conrad, 1857) valve, Craig Bay, Vancouver Island, British Columbia; *2*, extensively bored *Chesapecten* Ward and Blackwelder 1975, Pliocene of North Carolina; arrows indicate *S. simplex* borings; *3*, close-up of three *S. simplex* from *1*; note that the boring at right penetrates fully through the shell whereas the other two borings indicated terminate within the shell; note the larger external opening and smaller internal opening; *4*, circular boring, consistent with *Sedilichnus paraboloides* likely emplaced by the moon snail *Lunatia lewisii* (Gould, 1847) in bivalve shells; *Sedilichnus paraboloides* in *Leukoma staminea*



valve, Craig Bay, Vancouver Island, British Columbia; *5*, close-up of the *trace* from *1*; note the larger external opening and smaller internal opening; *6*, boring consistent with *S. paraboloides* in *Mya arenaria* Linnaeus 1758 valve, Craig Bay, Vancouver Island, British Columbia; *7*, close-up of the *S. paraboloides* from *1*; note the post mortem weathering on the shell in the area of the boring which has significantly modified the shape of the boring; *8*, modern trace identical to *Sedilichnus paraboloides* in the shell of the mud snail *Littorina saxatilis* (Olivi, 1792)*,* Economy Point, Nova Scotia; scale bar=5 mm; *9*, modern trace identical to *Sedilichnus paraboloides* in the shell of the slipper shell *Crepidula fornicata* (Linnaeus, 1758)*,* Economy Point, Nova Scotia; scale bar=5 mm; *10*, modern trace identical to *Sedilichnus paraboloides* in the shell of the oyster drill *Urosalpinx cinerea* (Say, 1822)*,* Economy Point, Nova Scotia; scale bar=5 mm.

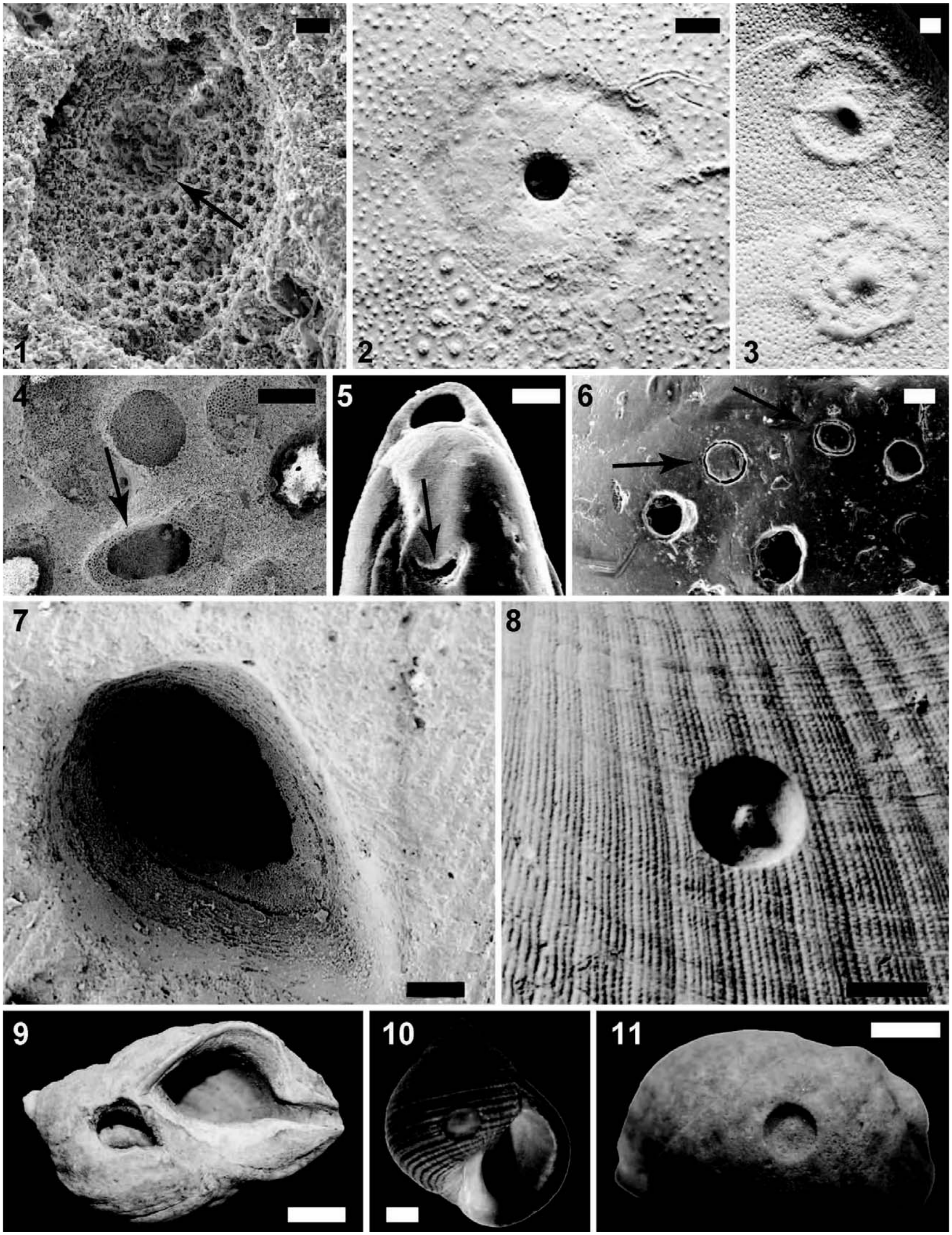


FIGURE 2—*Sedilichnus* in a variety of fossil and extant skeletal tests. *1*, *Sedilichnus gradatus* on a foraminiferal test from the Cenozoic White Mountain Group, Jamaica; from Blissett and Pickerill (2007); arrow shows the inner depression or pit that characterizes *S. gradates*; scale bar=10 µm; *2*, *3*, *Sedilichnus halo* on an echinoid test (*Echinocorys conica* Agassiz 1847) from the Cretaceous (Campanian) of Germany; from Neumann and Wisshak (2009); scale bars=1 mm; *4*, *Sedilichnus asperus* (arrow) on a foraminifera test from the Cenozoic White Mountain Group, Jamaica; from Blissett and Pickerill (2007); *5*, *Sedilichnus asperus* in Pleistocene foraminiferal test from Rhodes, Greece; from Nielsen et al. (2003); scale bar=40 µm; *6*, *Sedilichnus solus* (arrows) in Pleistocene foraminiferal test from Rhodes, Greece; from Nielsen et al. (2003); scale bar=10 µm; *7*, *Sedilichnus ovalis* in Plio–Pleistocene scallop from Florida; from Harper (2002); scale bar=100 µm; *8*, *Sedilichnus excavatus* in shell of *Glycymeris americana*, Pliocene Waccamaw Formation, Columbus County, North Carolina; from Thomas

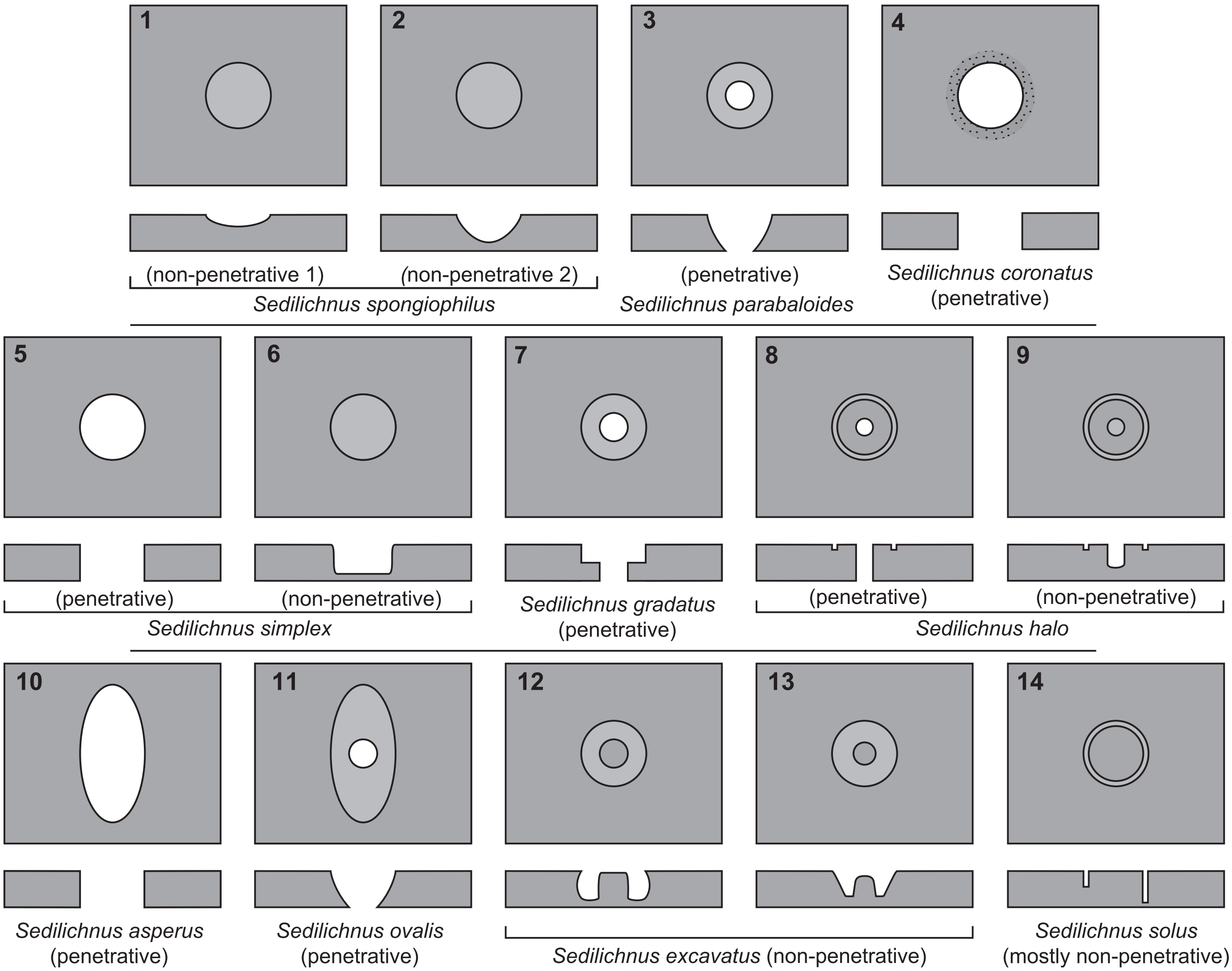


FIGURE 3—Outlines and cross-sections of *Sedilichnus* in shells (adapted from Nielsen and Nielsen, 2001; Blissett and Pickerill, 2003; Donovan and Jagt, 2002, and Nielsen et al., 2001).

It has been noted that at least some of the material originally assigned to *Tremichnus paraboloides* comprise bioclaustrations (Brett, 1985; Tapanila, 2005) *Sedilichnus spongiophilus* is restricted to forms wherein evidence indicates that the trace was formed by active boring by a tracemaker rather than solely as a systemic response of a living substrate to the activities of a parasite or a commensal organism.

SEDILICHNUS SIMPLEX Bromley, 1981

1976 muricacean boring THOMAS, p. 488, fig. 1/1, 4–6, 9.
1981 *Oichnus simplex* BROMLEY, p. 60, pl. 2, figs. 2–6.
1981 perforations KIER, p. 657, fig. 1.
1989 *Oichnus simplex* RUIZ-MUÑOZ AND GONZÁLEZ-REGALADO, p. 88, fig. 1.
1991 *Oichnus simplex* FEIGE AND FÜRSICH, p. 129, pl. 4, fig. 5.
1992 predatorial borings BENGSTON AND ZHAO, p. 368, fig. 1A–1K.
1998 *Oichnus simplex* PICKERILL AND DONOVAN, p. 163, pl. 1, figs. 1–3, pl. 2, figs. 2–4.
1999 *Oichnus simplex* TADDEI RUGGIERO, p. 170, fig. 1C–1E, 1G, 1H.
2000 bored valves KAPLAN AND BAUMILLER, p. 500, fig. 1.
2001 *Oichnus simplex* NIELSEN AND NIELSEN, p. 103, figs. 1A, 1B, 5.
2002 predatory boreholes HARPER AND WHARTON, p. 19, fig. 1B.
2003 drill holes CERANKA AND ZLOTNIK, p. 493, fig. 1.
2001 *Oichnus simplex* NIELSEN ET AL., p. 5, figs. 3, 4
2003 *Oichnus simplex* SANTOS ET AL., p. 138, fig. 7B.
2004 *Oichnus simplex* BLISSETT AND PICKERILL, p. 183, fig. 7/6.

←
(1976); scale bar=5 mm; *9*, modern trace identical to *Sedilichnus ovalis* in the shell of the common whelk *Buccinum undatum,* Economy Point, Nova Scotia; scale bar=5 mm; *10*, modern trace identical to *Sedilichnus excavatus* in the shell of the mud snail *Littorina saxatilis,* Economy Point, Nova Scotia; scale bar=2 mm; *11*, modern trace identical to *Sedilichnus excavatus* in the shell of the common whelk *Buccinum undatum* (Linnaeus, 1758) from Economy Point, Nova Scotia; scale bar=5 mm.

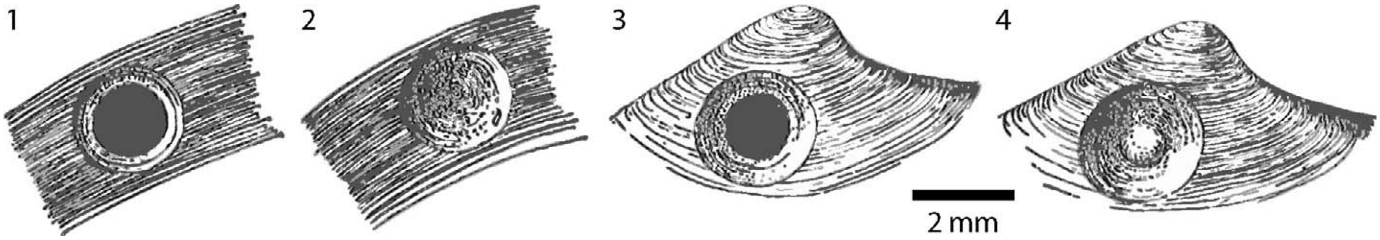


FIGURE 4—Line drawings of naticid and muricid gastropod borings. Adapted from Fretter and Graham (1962). *1*, shell of bivalve penetrated by the naticid gastropod *Nucella* sp.; this hole is representative of *S. paraboloides*; *2*, shell of bivalve incompletely penetrated by *Nucella*; this pit is representative of *S. spongiophilus*; *3*, shell of bivalve penetrated by the naticid gastropod *Natica*; this hole is representative of *Sedilichnus paraboloides*; *4*, shell of bivalve incompletely penetrated by *Natica*; note the small enraised boss at the centre of the pit; this trace is representative of *Sedilichnus excavatus*.

2006 *Oichnus simplex* TADDEI RUGGIERO ET AL., p. 181, figs. 3, 12, 14–17.
2006 drill hole, BAUMILLER ET AL., p. 315, fig. 2D–2H.
2007 *Oichnus simplex* BLISSETT AND PICKERILL, p. 90, pl. 3, fig. 6.
2007 *Oichnus simplex* DALY, p. 219, figs. 4/6, 7/1.
2007 *Oichnus simplex* DONOVAN AND HARPER, p. 62, fig. 2.
2008 *Oichnus simplex* ZAMORA ET AL., p. 20, fig. 3/13.
2010 *Oichnus paraboloides* WILSON ET AL., p. 97, fig. 3C.

Diagnosis.—"*Sedilichnus* that penetrate, having a simple cylindrical or subcylindrical form, axis more or less perpendicular to the substrate surface. Where the substrate is not penetrated right through, the distal end is flattened hemispherical." (Bromley, 1981, p. 60).

Description.—*Sedilichnus simplex* exhibit crisp, sharp margins (Figs. 1.2, 1.3, 3.5, 3.6). In some specimens an etched relief may be present on the boring walls however this has been shown to relate to the ultrastructure of the substrate rather than to scratchmarks emplaced during boring activities (Bromley, 1981). Thus, this etched relief is not considered a valid ichnotaxobases for ichnospecies differentiation (Bromley, 1981). The holotype and associated material range in size from 1.4 to 1.8 mm. Diminutive specimens (40 to 400 μm in diameter) occur on *Cloudina* from the Neoproterozoic of China (Bengston and Zhao, 1992).

Holotype.—MGUH 15351, Campanian (upper Cretaceous), Ivö Klack, Scania, Sweden.

Occurrence.—Neoproterozoic to Holocene, cosmopolitan.

Remarks.—As with all *Sedilichnus* ichnospecies, size is not considered a significant ichnotaxobases in *S. simplex*. Specimens described by Nielsen and Nielsen (2001) from foraminifera range in size from 2–60 μm. Diminutive examples also occur on ostracods (Muñoz, 1997). Specimens on bivalves, brachiopods and echinoids can range in size from 0.2 mm to 4.0 mm in diameter (Fig. 1.2, 1.3) (Bromley, 1981; Kier, 1981; Baumiller et al., 2006; Daley et al., 2007). *Sedilichnus simplex* is the only ichnospecies within this ichnogenus that includes both penetrative and non-penetrative forms (Fig. 1.2, 1.3).

SEDILICHNUS PARABOLOIDES Bromley, 1981

1976 naticean boring THOMAS, p. 488, fig. 1/1–3, 7.
1981 *Oichnus paraboloides* BROMLEY, p. 62, pl. 1, figs. 4,5, pl. 2, fig. 1.
1988 naticid borehole AITKEN AND RISK, p. 345, fig. 1A, 1C, 1D.
1988 muricacean borehole AITKEN AND RISK, p. 345, fig. 1C, 1D.
1989 *Oichnus paraboloides* RUIZ-MUÑOZ AND GONZÁLEZ-REGALADO, p. 88, figs. 2, 3.
1991 *Oichnus paraboloides* FEIGE AND FÜRSICH, p. 129, pl. 4, fig. 2, 3.
1994 abortive predatory borehole MORRIS AND BENGTSON, p. 18, fig. 14/17–19.
1995 boring GILI ET AL., p. 101, pl. 1, fig. 2A.
1996 *Oichnus paraboloides* PEK AND MIKULAS, p. 109, pl. 1, figs. 1–14, pl. 2, figs. 1, 2, 4–6, pl. 3, figs. 1–9, pl. 4, figs. 1–9, pl. 5, figs. 1–11, pl. 6, figs. 1–6.
1998 *Oichnus paraboloides* PICKERILL AND DONOVAN, p. 163, pl. 1, figs. 4–6, pl. 2, fig. 1, pl. 3, figs. 1–7.
2004 *Oichnus paraboloides* BLISSETT AND PICKERILL, p. 183, fig. 7/6.
2004 *Oichnus ovalis* GIBERT ET AL., p. 435, fig. 5d.
2004 *Oichnus paraboloides* LORENZO AND VERDE, p. 324, fig. 3D–3I.
2006 *Oichnus paraboloides* DIETL AND KELLEY, p. 104, fig. 1.
2006 *Oichnus paraboloides* TADDEI RUGGIERO ET AL., p. 181, fig. 13.
2006 *Oichnus paraboloides* SIGNORELLI ET AL., p. 301, figs. 4–8.
2006 drill hole, BAUMILLER ET AL., p. 315, fig. 2A–2C.
2007 *Oichnus paraboloides* BLISSETT AND PICKERILL, p. 89, pl. 3, fig. 2.
2007 borehole DALEY ET AL., p. 167, fig. 2A.
2007 *Oichnus paraboloides* DONOVAN AND HARPER, p. 61, fig. 1.
2008 *Oichnus paraboloides* ZAMORA ET AL., p. 20, fig. 3/1.
2009 parabolic drill holes KLOMPMAKER, p. 775, figs. 2, 5.
2010 drill holes MARTINELL ET AL., p. 223, fig. 3a, 3b.
2011 *Oichnus paraboloides* CHATTOPADHAY, p. 41, figs. 4, 6.

Diagnosis.—Penetrative *Sedilichnus* having a spherical paraboloid form that is truncated where the boring penetrates through the substrate.

Description.—*Sedilichnus paraboloides* are one of the more common forms of *Sedilichnus*. The boring narrows from the external opening to the internal opening (Figs. 1.4–1.10, 2.3, 4.1, 4.3). In the holotype and associated material the external opening ranges from 3.8 to 4.1 mm in diameter whereas the internal opening ranges from 1.8 to 2.2 mm in diameter (Bromley, 1981).

Holotype.—MGUH 15352, basal Rhodos Formation, Pleistocene, Monte Smith, Rhodos Town, Rhodes, Greece.

Occurrence.—Cambrian to Holocene, cosmopolitan.

Remarks.—*Sedilichnus paraboloides* likely reflect the activities of several different organisms. Many borings that are clearly attributable to the activities of naticid gastropods on modern bivalves are morphologically consistent with this ichnotaxa (Figs. 1.4–1.10, 4.1). Some boreholes created by the muricid gastropod *Nucella* are also consistent with this ichnospecies (Fretter and Graham, 1962; Fig. 4.3). Other examples are attributed to turbellarian flatworms (Kabat, 1990; Kelley and Hansen, 2003). Diminutive examples described by Nielsen and Nielsen (2001) are unlikely to have been bored by a gastropod predator as they

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fall well under the size range these organisms would be likely to make (25–30 μm vs. >1 mm in gastropod predation traces). Diminutive examples have also been noted on ostracods (Muñoz, 1997; Reyment, 1999).

SEDILICHNUS OVALIS Bromley, 1993

1993 *Oichnus ovalis* BROMLEY, p. 170, figs. 3–5.
1995 boring GILI ET AL., p. 105, pl. 3, fig. 6.
1999 *Oichnus ovalis* TADDEI RUGGIERO, p. 170, fig. 1F.
2002 *Oichnus ovalis* HARPER, p. 293, figs. 1, 2.
2006 *Oichnus ovalis* TADDEI RUGGIERO ET AL., p. 179, figs. 11, 12.
2007 *Oichnus ovalis* BLISSETT AND PICKERILL, p. 89, pl. 3, figs. 2, 5.
2007 *Oichnus ovalis* GIBERT ET AL., p. 793, fig. 9d.
2010 drill holes MARTINELL ET AL., p. 223, fig. 3b, 3c.

Diagnosis.—Oval *Sedilichnus* tapering subparabolically from a larger external opening to a smaller inner one. External opening oval to rounded rhomboid in outline. Internal opening circular to subcircular or oval in outline.

Description.—*Sedilichnus ovalis* vary in shape, from truly oval forms to those that are approximately rhombohedral in external outline. The opening on the inner surface is smaller than the external opening (Figs. 2.7, 2.8, 3.11). The outer margin of the boring may be sharp and angular or rounded (Bromley, 1993).

Holotype.—MGUH 22057, Pliocene, unnamed limestone unit in foreshore zone in bay south of Cape Vagia and 1 km east of Kolymbia, Rhodes, Greece.

Occurrence.—Cenozoic to Holocene, cosmopolitan.

Remarks.—*Sedilichnus ovalis* have been observed on a variety of Cenozoic gastropods, bivalves, brachiopods and Foraminifera. Bromley (1993) made a strong case that octopods are a likely tracemaker of this ichnotaxon. Nixon (1979) showed that the large external opening is excavated by the octopus radula whereas the internal oval opening is excavated by tooth-like structures on the salivary papilla. Diminutive forms (on microfossils such as foraminifera) likely record the activities of other, non-octopod predators.

SEDILICHNUS CORONATUS Nielsen and Nielsen, 2001

2001 *Oichnus coronatus* NIELSEN AND NIELSEN, p. 108, fig. 1E–1G.
2011 *Oichnus coronatus* STRENG ET AL., p. 598, fig. 1g.

Diagnosis.—*Sedilichnus* "having a simple cylindrical or subcylindrical form, oriented more or less perpendicular to the substrate surface. The external opening is surrounded immediately by a halo having granular texture" (Nielsen and Nielsen, 2001, p. 108).

Description.—*Sedilichnus coronatus* differ from *S. simplex* solely in the presence of a surficial etched halo or corona surrounding the rim of the penetration (Fig. 3.4). In the material illustrated in Nielsen and Nielsen (2001) the halo has a granular texture and appears to affect only the surface of the foraminifera. Specimens in microfossils range in size form 12–25 μm with the halos ranging from 2 to 24 μm in size.

Holotype.—MGUH 24769, early Holocene, Great Australian Bight, on test of a benthic foraminiferan.

Occurrence.—Holocene of Australian Bight and Gulf of Aqaba, Red Sea; Pleistocene of Rhodes.

Remarks.—These simple *Sedilichnus* are similar to S. *simplex,* differing solely in the presence of an altered halo surrounding the hole (Fig. 3.4). The halo has been interpreted to reflect construction by the tracemaker (Nielsen and Nielsen, 2001) implying that part of the attachment structure of the parasitic organism remained external to the host organism while the boring organ occurred roughly central in the parasite. Nielsen and Nielsen (2001) indicate that these forms occur on both benthic and planktonic foraminifera.

Although identification of this ichnotaxon in the literature is thus far limited to microfossils such as dinoflagellates and foraminifera (Nielsen and Nielsen, 2001; Streng et al., 2011) we anticipate that it will also be recognized on macrofossils as well. The etched halo likely results from chemical dissolution and/or mechanical abrasion associated with the attachment of the parasite to the host skeletal test.

SEDILICHNUS GRADATUS Nielsen and Nielsen, 2001

2001 *Oichnus gradatus* NIELSEN AND NIELSEN, p. 110, fig. 2E–2H.
2007 *Oichnus gradatus* BLISSETT AND PICKERILL, p. 89, pl. 3, fig. 4.

Diagnosis.—*Sedilichnus* "that abruptly changes diameter from wide externally to narrow internally. The two parts are concentric." (Nielsen and Nielsen, 2001, p. 110).

Description.—*Sedilichnus gradatus* differ from other forms in the 'stepped' nature of the boring, essentially comprising a narrow diameter boring in the centre of a larger diameter boring (Figs. 2.1, 3.7). In the type material the diameter of the inner shelf ranges from 1 to 7 μm in size whereas the diameter of the outer margin of the trace ranges from 4–15 μm in size (Nielsen and Nielsen, 2001). The margins of the two components are perpendicular whereas the inner platform is parallel to the external surface of the host organism (Nielsen and Nielsen, 2001).

Holotype.—MGUH 24773, Holocene, Great Australian bight, on test of a benthic foraminiferan.

Occurrence.—Holocene of Australian Bight, Gulf of Aqaba, Red Sea and West Greenland; Pleistocene of Rhodes.

Remarks.—To our knowledge this trace fossil has, to date, only been described from foraminifera. It is suggested that the boring parasite may have excavated a body cavity for itself (the platform) and bored in with a central boring organ. This trace fossil occurs on both benthic and planktonic foraminifera (Nielsen and Nielsen, 2001).

SEDILICHNUS HALO (Neumann and Wisshak, 2009)

2000 predatory boreholes HARPER AND WHARTON, p. 19, fig. 1D.
2009 *Oichnus halo* NEUMANN AND WISSHAK, p. 117, figs. 1–3.

Diagnosis.—*Sedilichnus* "with a central hole (or pit) with smooth walls surrounded by one or more circular depressions." (Neumann and Wisshak, 2001, p. 117).

Description.—The combination of a central, penetrative hole/pit and an outer circular groove forming a halo around the hole (Figs. 2.2, 2.3, 3.8, 3.9) are unique to *S. halo*. The type specimen, and three paratypes, occur on the test of the holasteroid echinoid *Echinocarys* sp. The outer groove diameter from 6.9 to 8.3 mm, with the central, steep-walled penetration having a diameter of between 0.8 and 1.6 mm in diameter.

Holotype.—MBE 2342, Upper Cretaceous (Campanian), Heidestrasse chalk quarry in Lägerdorf, near Itzehoe, northern Germany.

Occurrence.—Upper Cretaceous to Paleocene of Germany.

Remarks.—*Sedilichnus halo* has been interpreted as a combined parasitic/attachment trace of eulimid gastropods upon an echinoderm host (Neumann and Wisshak, 2009). The Cretaceous and Paleocene examples collected from Germany (Fig. 2.2, 2.3) are identical to those produced by gastropods of the genus *Thyca pellucida* on the asteroid *Linckia laevigata* (Janssen, 1985) and appear in the rock record coincident with the first appearance of eulimid gastropods (Neumann and Wisshak, 2009). In both the modern specimens on asteroids, as well as the fossil specimens on echinoids, the *S. halo* are found exclusively on the oral surface of the host (Elder, 1979; Warén, 1980; Janssen, 1985).

SEDILICHNUS ASPERUS Nielsen and Nielsen, 2001

2001 *Oichnus asperus* NIELSEN AND NIELSEN, p. 108, fig. 2A–2D.
2001 *Oichnus* aff. *asperus* NIELSEN ET AL., p. 7, fig. 7.
2007 *Oichnus simplex* BLISSETT AND PICKERILL, p. 89, pl. 3, fig. 2.

Diagnosis.—*Sedilichnus* "having openings of regular to irregular elongate-oval outline. The margin is perpendicular to the substrate surface." (Nielsen and Nielsen, 2001, p. 110).

Description.—*Sedilichnus asperus* differs from most other ichnospecies of *Sedilichnus* by its elongate, oval outline (Figs. 2.4, 2.5, 3.10). It differs from *S. ovalis* in the proportionally large diameter of its opening/penetration and in the straight, rather than curved or angled, walls.

Holotype.—MGUH 24771, Holocene, Great Australian bight, on test of a benthic foraminiferan.

Occurrence.—Pleistocene to Holocene, cosmopolitan.

Remarks.—This trace fossil occurs on both benthic and planktonic foraminifera (Nielsen and Nielsen, 2001; Nielsen et al., 2003; Figs. 2.4, 2.5, 3.10). It has not, as yet, been reported from other taxa.

SEDILICHNUS EXCAVATUS Donovan and Jagt, 2002

1976 incomplete naticean boring THOMAS, p. 488, fig. 1/8.
1988 gastropod borings in bivalve shells AITKEN AND RISK, p. 345, fig. 1A, 1C, 1D.
2002 *Oichnus excavatus* DONOVAN AND JAGT, p. 69, figs. 2, 3.
2003 *Oichnus excavatus* BLISSETT AND PICKERILL, p. 222, fig. 2.
2004 *Oichnus* cf. *O. excavatus* DONOVAN AND JAGT, p. 23, fig. 1.
2005 *Oichnus excavatus* DONOVAN AND JAGT, p. 150, pl. 1, fig. 1.
2007 *Oichnus excavatus* BLISSETT AND PICKERILL, p. 88, pl. 3, fig. 3.
2007 *Oichnus excavatus* DALEY ET AL., p. 219, fig. 7/5–6.

Diagnosis.—Circular to elliptical, non-penetrative *Sedilichnus*, with a broad, high central raised boss or pedestal. Walls externally convex or V-shaped.

Description.—The central pedestal or 'boss' in *Sedilichnus excavatus* occurs in only two *Sedilichnus* species: *S. excavatus* and *S. solus* (Fig. 3.12–3.14). The size of the pedestal in *S. excavatus* is variable as is the angle of the slope of the external boring wall (Fig. 3.12, 3.13). In the holotype material (Donovan and Jagt, 2002) the external margin of the boring is convex outwards forming an overhanging lip (Fig. 3.12). Blissett and Pickerill (2003) revised the ichnospecific diagnosis to include examples wherein the walls are V-shaped (Fig. 3.13). In no example that we are aware of is any part of the boring penetrative. *Sedilichnus excavatus* differs from *S. solus* in having a wider trough with walls that are concave or v-shaped (Figs. 2.11, 2.12, 3.12, 3.13) rather that perpendicular to the external test surface (Figs. 2.6, 3.14).

Holotype.—NHMM 4689, Upper Cretaceous, Meersen Member, Maastricht Formation, along the Albertkanaal at Vroenhoven-Riemst (Limburg, Belgium), on the tests of the holasteroid echinoids *Hemipneustes striatoradiatus* Leske).

Occurrence.—Upper Cretaceous of northwestern Europe (Belgium and Netherlands), Eocene of the Caribbean region.

Remarks.—The holotype material, and many other specimens of *Sedilichnus excavatus* occur on the tests of holasteroid echinoids (Donovan and Jagt, 2002, 2004, 2005). Subsequently additional material has been recognized on other taxa such as bivalves (Aitken and Risk, 1988) and foraminifera (Blissett and Pickerill, 2003, 2007). Failed predatory boring by the naticid gastropod *Natica* Scopoli 1777 are consistent in morphology with *S. excavatus* (Fretter and Graham, 1962; Fig. 4.4). Failed predatory borings by the naticid gastropod *Lunatia heros* Say 1822 are also consistent with this trace morphology (Fig. 2.9–2.11)

Sedilichnus excavatus are closely allied with *S. solus* (discussed below). These two ichnotaxa differ primarily in the proportional size of the groove surrounding the central pedestal or boss. In *S. excavatus*, the groove is wide, may be concave or oriented oblique to the skeletal test surface and the height of the central pedestal is commonly less than the depth of the groove (Donovan and Jagt, 2002, 2004, 2005; Blissett and Pickerill, 2003, 2007). In failed naticid borings the pedestal often consists of a small nubbin (Figs. 2.9, 4.4; Thomas, 1976). The absence of a central hole or pit in these two ichnospecies may provide support for the argument that *S. excavatus* and *S. solus* should be included in a distinct ichnogenus (and thus the retention of the ichnogenus *Fossichnus*), however we feel that the overlap in characters between such forms as *S. halo, S. paraboloides* and *S. simplex* with *S. solus* and *S. excavatus* (Fig. 3.3, 3.5, 3.6, 3.8, 3.9, 3.12–3.14) supports inclusion within a single ichnogenus. We suspect that the bulk of these forms comprise failed predation attempts and that if completed would have formed penetrative *Sedilichnus* such as *S. paraboloides* (Fig. 4.1–4.4).

SEDILICHNUS SOLUS Nielsen, Nielsen and Bromley 2003

2003 *Fossichnus solus* NIELSEN ET AL., p. 3, figs. 1, 3, 4.

Diagnosis.—Circular to elliptical, primarily non-penetrative *Sedilichnus*, with a broad central region forming a table or pedestal of unaffected skeletal substrate in the center of the trace. Boring walls vertical, perpendicular to the substrate surface.

Description.—The depth of the groove is commonly variable in individual *S. solus* (Nielsen et al., 2003). The grooves are narrow and the walls of the groove are perpendicular to near perpendicular to the surface of the bored skeletal substrate. *Sedilichnus solus* have, thus far, only been reported from foraminifera and thus specimens are small, ranging from 13–30 μm in diameter with the width of the external groove ranging from 1 to 4 μm (Nielsen et al., 2003).

Holotype.—MGUH 26767. Quaternary, Davis Strait, West Greenland.

Occurrence.—Cenozoic of the Caribbean region; Quaternary of west Greenland and Argentina.

Remarks.—*Sedilichnus solus* are similar in many regards to S. *excavatus*, in possessing a raised central pedestal surrounded by a groove. The two ichnotaxa differ primarily in the proportional width of the groove, the degree to which the inner pedestal is modified, and the perpendicular intersection of the wall with the external surface of the bored shell. In *S. solus* the groove is narrow, deep and the inner pedestal is minimally modified (Figs. 2.6, 3.14) unlike the rounded pedestal common in *S. excavatus* (Figs. 2.9–2.11, 3.12–3.14). Some *S. solus* have been shown to be associated with other *Sedilichnus* taxa, such as *S. simplex* and may represent a failed predatory boring (Nielsen et al., 2003). Consequently the circular groove which defines this ichnotaxon may, in some cases, partially penetrate through the test (Nielsen et al., 2003). To date, *S. solus* has been reported solely from foraminifera (Nielsen et al., 2003; Cardosa and Senra, 2007).

DISCUSSION

Small round holes in skeletal substrata are attributable to the activities of a broad variety of extant and extinct organisms.

Since the original descriptions of these trace fossils by Müller (1977), Bromley (1981) and Brett (1985) numerous examples have been described on a variety of skeletal substrata on fossil material ranging from the Cambrian through the Holocene as well as sub-fossil material from the Pleistocene to the modern. (e.g., Bromley, 1981; Savazzi and Reyment, 1989; Baumiller, 1990; Kowalewski, 1993; Morris and Bengston, 1994; Harper and Wharton, 2000).

As well, although most *Sedilichnus* occur in marine and marginal marine setting, trace fossils on Holocene bivalves from a freshwater lake in central Canada are consistent with *S. simplex* and *S. paraboloides* (Hagan et al., 1998). To date all *Sedilichnus* that we are aware of have been described from aquatic or marginal aquatic forms. Dunlop and Braddy (2011) assigned small circular burrows in sandstone, interpreted to be spider dwelling traces to *Oichnus bavincourti*. Although we do not attempt herein to re-classify these burrows, they are not herein included within *Sedilichnus* as they were excavated in a lithological rather than a skeletal substrate.

Unlike most other trace fossils, including many other borings, *Sedilichnus* provide evidence on the interactions between groups of living organisms. Most *Sedilichnus* were clearly emplaced on living organisms. Many penetrative forms, such as some *S. paraboloides, S. simplex* and *S. ovalis* have been shown to be predation traces on a variety of host taxa including brachiopods and bivalves. (e.g., Bromley, 1981, 1993; Kowalewski, 1993; Pietso et al., 1994; Gili et al., 1995; Harper, 2002; Baumiller et al., 2006; Daley et al., 2007; Klompmaker, 2009) (Fig. 1.1–1.6).

Although the individual ichnospecies are not clearly attributable to the activities of an individual predator, parasite or commensal taxon, in many cases augmenting the ichnospecific assignment with other information such as the size of the borings, the taxonomic affinity of the host organism, and the position on the host organism where the trace occurs, provides sufficient information for confident identification of the trace-making predator. Among the more common examples of *Sedilichnus* are holes excavated in bivalve shells by naticid and muricid gastropods (Kowalewski, 1993) (Fig. 1.1–1.10). Penetrative holes with curved to obliquely oriented edges (*S. paraboloides*; Fig. 1.4–1.10) are generally attributed to naticid predators whereas penetrative holes with straight edges perpendicular to the surface of the host test (*S. simplex*; Fig. 1.2, 1.3) are attributed to muricid gastropods (Bromley, 1981; Carriker and Yochelson, 1968; Carriker and Van Zandt, 1972; Carriker, 1981). However, characters such as the thickness of the bored shell, the structure of the bored material and the location on the host taxa where the hole was bored all have an effect on borehole morphology and may obscure the identity of the boring organism (Vermeij, 1980; Yochelson et al., 1983; Taylor et al., 1983; Kowalewski, 1992).

Many non-penetrative forms, such as many *Sedilichnus excavatus* and some *S. spongiophilus*, are clearly formed for the purposes of attachment to a stable substrate by commensals or parasites. Many other non-penetrative *Sedilichnus* such as some *S. spongiophilus,* some *S. simplex*, and many *S.excavatus* and *S. solus* are likely failed predation or failed parasitic traces (Bromley, 1981; Kowalewski, 1993; Nielsen et al., 2003). *Sedilichnus solus* on foraminifera have been shown to be, at least in part, precursor forms to penetrative *S. simplex* (Nielsen et al., 2003). Similarly, some *S. excavatus* have been shown to be precursor forms to penetrative *S. paraboloides* (Kowalewski, 1993). Likewise it is clear that some *S. spongiophilus* are precursor forms to penetrative *S. paraboloides*. In these cases the tracemaker was likely disturbed, or dislodged, prior to completion of the borehole. Such intermediate forms possess unique attributes distinct from the end member forms, thus supporting retention of these traces as distinct ichnospecies.

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REFERENCES

Adams, H. and Adams, A. 1854. The genera of Recent Mollusca 1. J. Van Viirst Publishers, London. 484 p.

Agassiz, L. 1847. Nomenclator zoologicus : continens nomina systematica generum animalium tam viventium quam fossilium, secundum ordinem alphabeticum disposita, adjectis auctoribus, libris, in quibus reperiuntur, anno editionis, etymologia et familiis, ad quas pertinent, in singulis classibus. C. L. Bonaparte, France, 393 p.

Aitken,A. E. and M. J. Risk. 1988. Biotic interactions revealed by macroborings in arctic bivalve molluscs. Lethaia, 21:339–350.

Baumiller, T. K.1990. Non-predatory drilling of Mississippian crinoids by Platyceratid gastropods. Palaeontology, 33:743–748.

Baumiller, T. K., A. Bitner, and C. C. Emig. 2006. High frequency of drill holes in brachiopods from the Pliocene of Algeria and its ecological implications. Lethaia, 39:313–320.

Bengston, S. and Y. Zhao. 1992. Predatorial borings in late Precambrian mineralized exoskeletons. Science, 257:367–369.

Bertling, M., D. J. Braddy, R. G. Bromley, G. R. Demathieu, J. Genise, R. Mikuláš, J. K. Nielsen, K. S. S. Nielsen, A. K. Rindsberg, M. Schlirf, and A. Uchman. 2006. Names for trace fossils: a uniform approach. Lethaia, 39: 265–286.

Blissett, D. J. and R. K. Pickerill. 2003. *Oichnus excavatus* Donovan and Hagt, 2002 from the Montague Formation, White Limestone Group, Jamaica. Caribbean Journal of Science, 39:221–223.

Blissett, D. J. and R. K. Pickerill. 2004. Observations from the White Limestone Group of Jamaica. Cainozoic Research, 3:167–187.

Blissett, D. J. and R. K. Pickerill. 2007. Systematic ichnology of microborings from the Cenozoic White Limestone Group, Jamaica, West Indies. Scripta Geologica, 134:77–108.

Brett, C. E. 1985. *Tremichnus*: a new ichnogenus of circular-parabolic pits in fossil echinoderms. Journal of Paleontology, 59:625–635.

Bromley, R. G. 1981. Concepts in ichnology illustrated by small round holes in shells. Acta Geològica Hispànica, 16:55–64.

Bromley, R. G. 1993. Predation habits of octopus past and present and a new ichnospecies, *Oichnus ovalis*. Bulletin of the Geological Society of Denmark, 40:167–173.

Bromley, R. G. 2004. A stratigraphy of marine bioerosion, p. 455–479. *In* D. McIlroy (ed.), The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis. Geological Society of London Special Publication 228.

Cardosa, M. N. and M. C. E. Sensra. 2007. Tafonomia de formaníferos Bentônicos em sedimentos siliciclásticos e Carbonáticos. Anuario do Instituto de Geociências, 30:101–108.

Carriker, M. R. 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: a synthesis. Malacologia, 20:403–422.

Carriker, M. R. and D. van Zandt. 1972. Predatory behavior of a shell-boring muricid gastropod, p. 157–244. *In* H. E. Winn and B. L. Olla (eds.), Behavior of Marine Animals: Current Perspectives in Research I. Invertebrates. Plenum Press, New York.

Carriker, M. R. and E. L. Yochelson. 1968. Recent gastropod boreholes and Ordovician cylindrical borings. United States Geological Survey Professional Paper 593-B:1–26.

Ceranka, T. and M. Złotnik. 2003. Traces of cassid snails predation upon the echinoids from the middle Miocene of Poland. Acta Palaeontologica Polonica, 48:491–496.

Chattopadhay, D. 2011. First evidence of predatory drilling from Upper Cretaceous Eutaw Formation, Georgia. Southeastern Geology, 48:37–44.

Conrad, T. A. 1837. Description of the marine shells from upper California, collected by Thomas Nuttall. Journal of the Academy of Natural Sciences of Philadelphia, 7:227–268.

Daley, G. M., S. Ostrowski, and D. H. Geary. 2007. Paleoenvironmentally correlated differences in a classic predator-prey system: the bivalve Chione elevate and its gastropod predators. PALAIOS, 22:166–173.

Daly, A. C. 2007. Statistical analysis of mixed-motive shell borings in Ordovician, Silurian, and Devonian brachiopod from northern and eastern Canada. Canadian Journal of Earth Sciences, 45:213–229.

Deline, B. 2008. The first evidence of predatory or parasitic drilling in stylophoran echinoderms. Acta Palaeontologica Polonica, 53:739–743.

Dietl, G. P. and P. H. Kelley. 2006. Can naticid gastropod predators be identified by the holes they drill? Ichnos, 13:103–108.

Donovan, S. K. and D. A. T. Harper. 2007. Rare borings in Pleistocene brachiopods from Jamaica and Barbados. Caribbean Journal of Science, 43: 59–64.

Donovan, S. K. and J. W. M. Jagt. 2002. *Oichnus* Bromley borings in the irregular echinoid *Hemipneustes* Agassiz from the type Maastrichtian (Upper Cretaceous, The Netherlands and Belgium). Ichnos, 9:67–74.

Donovan, S. K. and J. W. M. Jagt. 2004. Site selectivity of pits in the chalk (Upper Cretaceous) echinoid *Echinocorys* Leske from France. Bulletin of the Mizunami Fossil Museum, 31:21–24.

Donovan, S. K. and J. W. M. Jagt. 2005. An additional record of *Oichnus excavatus* Donovan and Jagt from the Maastrichtian (Upper Cretaceous of southern Limburg, The Netherlands). Scripta Geologica, 129:147–150.

Donovan, S. K. and R. K. Pickerill. 2002. Pattern versus process or informative versus uninformative ichnotaxonomy: reply to Todd and Palmer. Ichnos, 9:85–87.

Donovan, S. K., D. N. Lewis, and P. Kabrna. 2006. A dense epizoobiontic infestation of a Lower Carboniferous crinoid (*Amphoracrinus gilbertsoni* (Phillips)) by *Oichnus paraboloides* Bromley. Ichnos, 13:43–45.

Dunlop, J. A. and S. J. Braddy. 2011. *Ctenzia bavincourti* and the nomenclature of arachnid-related trace fossils. The Journal of Arachnology, 39:250–257.

Eckert, J. D. 1988. The ichnogenus *Tremichnus* in the lower Silurian of western New York. Lethaia, 21:281–283.

Elder, H. Y. 1979. Studies of the host-parasite relationship between the parasitic prosobranch *Thysa crystalline* and the asteroid starfish *Linckia laevigata*. Journal of Zoology (London), 187:369–382.

Feige, A. and F. T. Fürsich. 1991. Taphonomy of Recent molluscs of Bahia la Choya (Gulf of California, Sonora, Mexico). Zitteliana, 18:89–133.

Fretter, V. and A. Graham. 1962. British Prosobranch Molluscs: Their Functional Anatomy and Ecology. Ray Society, London, 755 p.

Gibert, J. M. de, R. Domènech and J. Martinell. 2004. An ethological framework for animal bioerosion trace fossils upon mineral substrates with proposal of a new class, fixichnia. Lethaia, 37:429–437.

Gibert, J. M. de, R. Domènech and J. Martinell. 2007. Bioerosion in shell beds from the Pliocene Roussillon Basin, France: implications for the (macro) bioerosion ichnofacies model. Acta Palaeontologica Polonica, 52: 783–798.

Gili, C., C. M. da Silva, and J. Martinell. 1995. Pliocene nassariids (Mollusca: Neogastropoda) of central-west Portugal. Tertiary Research, 15: 95–110.

Goldring, R. and J. E. Pollard. 1996. Ichnotaxonomic revision and the importance of type material. Palaeontology Newsletter, 31:7–8.

Gould, A. A. 1847. Description of New Shells received from Rev. Mr. Mason, of Burmah. Proceedings of the Boston Society of Natural History, ii:218–221.

Gray, J. E. 1847. A list of the genera of recent Mollusca, their synonyma and types. Proceedings of the Zoological Society of London, 15:129–219.

Hagan, T. H., M. Coniglio, and T. W. D. Edwards. 1998. Subfossil bioerosion of mollusc shells from a freshwater lake, Ontario, Canada. Ichnos, 6:117–127.

Harper, E. M. 2002. Plio–Pleistocene octopod-drilling behavior in scallops from Florida. PALAIOS, 17:292–295.

Harper, E. M. and D. S. Wharton. 2000. Boring predation and Mesozoic articulate brachiopods. Palaeogeography, Palaeoclimatology, Palaeoecology, 158:15–24.

Harper, J. A. 1986. Diverse fauna at Beaver County fossil locality. Pennsylvania Geology, 17:13–16.

Huebner, J. D. and D. C. Edwards. 1981. Energy budget of the predatory marine gastropod *Polinicces duplicatus*. Marine Biology, 61:221–226.

Janssen, H.-H. 1985. Three epizoic gastropods from Malaysia and the Philippines. Zeitschrift für Paristenkunde (Parisitology Research), 71:553–560.

Kabat, A. R. 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. Malacologia, 32:155–193.

Kaplan, P. and T. K. Baumiller. 2000. Taphonomic inferences on boring habit in the Richmondian *Onniela meeki* epibole. PALAIOS, 15:499–510.

Kelley, P. H. 2008. Role of bioerosion in taphonomy: effect of predatory drillholes on preservation of mollusc shells, p. 451–470. *In* M. Wisshak and L. Tapanila (eds.), Current Developments in Bioerosion. Erlangen Earth Conference Series Springer Verlag, Berlin.

Kelley, P. H. and T. A. Hansen. 2003. The fossil record of drilling predation on bivalves and gastropods, p. 113–139. *In* P. H. Kelley, M. Kowalewski and T. A. Hansen (eds.), Predator-Prey Interactions in the Fossil Record. Kluwer Academic Publishers, New York.

Kier, P. M. 1981. A bored Cretaceous echinoid. Journal of Paleontology, 55: 656–659.

Kitchell, J.A., C. H. Boggs, J. F. Kitchell, and J. A. Rice. 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. Paleobiology, 7:533–552.

Klompmaker, A. A. 2009. Taphonomic bias on drill-hole intensities and paleoecology of Pliocene mollusks from Langenboom (Mill), the Netherlands. PALAIOS, 24:772–779.

Köhler, R. 1924. Anomalies, irrégularitiés et déformations du test chez les échinides. Ann. Inst. Océanogr., N.S., 1:159–480.

Köhler, R. and G. Vaney. 1908. Description d'un nouveau genre de prosobrache parasite sur certains échinides (*Pelseneeria*). Bulletin de l'Institut océanographique de Monaco, 118:1–16.

Kowalewski, M. 1993. Morphometric analysis of predatory drillholes. Palaeogeography, Palaeoclimatology, Palaeoecology, 102:69–88.

Linnaeus, C. 1758. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Holmiæ. (Salvius), Stockholm, 824 p.

Lorenzo, N. and M. Verde. 2004. Estucturas de bioerosión en moluscos marinos Formación de la Villa Soriano. (Pleistoceno Tardío-Holoceno) de Uruguay. Revista Brasileira de Paleontologica, 7:319–328.

Martinell, J., R. Domènech, J. Aymar, and M. Kowalewski. 2010. Confamilial predation in Pliocene naticid gastropods from southern France: utility of preexisting collections in quantitative paleoecology. PALAIOS, 25:221–228.

Morris, S. C. and S. Bengston. 1994. Cambrian predators: possible evidence from boreholes. Journal of Paleontology, 68:1–23.

Müller, A. H. 1977. Zur ichnologie der subherzynen Oberkreide (Campan). Zeitschrift für geologische Wissenschaften, Berlin, 5:881–897.

Muñoz, F. R. 1997. Importancia de la bioerosión en e-ostrácados actuals del litoral de Huelva (SW España). Geogaceta, 21:195–198.

Neumann, C. and M. Wisshak. 2009. Gastropod parasitism on Late Cretaceous to Paleocene holasteroid echinoids—evidence from *Oichnus halo* isp. n. Palaeogeography, Palaeoclimatology, Palaeoecology, 284:115–119.

Nielsen, J. K. and K. S. S. Nielsen. 2002. Pattern versus process or informative versus uninformative Ichnotaxonomy: reply to Todd and Palmer. Ichnos, 9:83–84.

Nielsen, K. S. S. and J. K. Nielsen. 2001. Bioerosion in Pliocene to late Holocene tests of benthic and planktonic foraminiferans, with a revision of the ichnogenera *Oichnus* and *Tremichnus*. Ichnos, 8:99–116.

Nielsen, K. S. S., J. K. Nielsen, and R. G. Bromley. 2001. Palaeoecological and ichnological significance if microborings in Quaternary Foraminifera. Palaeontologica Electronica 6, 13 p.

Nixon, M. 1979. Has *Octopus vulgaris* a second radula? Journal of the Zoological Society of London, 187:291–296.

Olivi, G. 1792. Zoologia Adriatica, ossia catalogo ragionato degli animali del golfo e della lagune di Venezia. Bassano, Venecia, 334 p.

Peitso, E., E. Hui, B. Hartwick, and N. Bourne. 1994. Predation by the naticid gastropod *Polinices lewisii* (Gould) on littleneck clams *Protothaca staminea* (Conrad) in British Columbia. Canadian Journal of Zoology, 72: 319–325.

Pek, I. and R. Mikuláș. 1996. The ichnogenus *Oichnus* Bromley, 1981—predation traces in gastropod shells from the Badenian in the vicinity of Ceska Trebova (Czech Republic). Vestník Ceského geologického ústavu, 71:107–120.

Pickerill, R. K. and S. K. Donovan. 1998. Ichnology of the Pliocene Bowden Shell Bed, southeast Jamaica. Contributions to Tertiary and Quaternary Geology, 35:161–175.

REYMENT, R. 1999. Drilling gastropods, p. 197–204. *In* E. Savazzi (ed.), Functional Morphology of the Invertebrate Skeleton. John Wiley and Sons Ltd., New Jersey.

RÖDING, P. F. 1798. Museum Boltenianum sive catalogus cimeliorum e tribus regnis naturæ quæ olim collegerat Joa. Fried Bolten, M. D. p. d. per XL. annos proto physicus Hamburgensis. Pars secunda continens conchylia sive testacea univalvia, bivalvia & multivalvia. Hamburg, Germany, 199 p.

RUIZ-MUÑOZ, R. AND M. L. GONZÁLEZ-REGALADO. 1989. Bioerosión en ostrácados. Geogaceta, 6:87–90.

SANTOS, A., E. MAYORAL, F. MUÑIZ, I. BAJO, AND O. ADRIAENSENS. 2003. En el sector Surroccidental de la Cuenca del Guadalquivir (Provincia de Sevilla). Revista Española de Paleontología, 18:131–141.

SAVAZZI, E. AND R. A. REYMENT. 1989 .Subaerial hunting behaviour in *Natica gualteriana* (naticid gastropod). Palaeogeography, Palaeoclimatology, Palaeoecology, 74:355–364.

SAY, T. 1822. An account of some of the marine shells of the United States. Journal of the Academy of Natural Sciences of Philadelphia, 2:221–248, 257–276, 302–325.

SCOPOLI, G. A. 1777. Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae. Prague, 589 p.

SIGNORELLI, J. H., G. PASTORINO, AND M. GRIFFIN. 2006. Naticid boreholes on a Tertiary cylichnid gastropod from southern Patagonia. Malacologia, 48: 299–304.

STRENG, M., O. ESPER, AND J. WOLLENBURG. 2011. Calcareous dinoflagellate cysts from the Pleistocene (Marine Isotope Stage 31) of the Ross Sea, Antarctica. Antarctic Science, 23:597–604.

TADDEI RUGGIERO, E. 1999. Bioerosive processes affecting a population of brachiopods (upper Pliocene, Apulia). Bulletin of the Geological Society of Denmark, 45:169–172.

TADDEI RUGGIERO, E. AND G. AUNNUNZIATA. 2002. Bioerosion on a *Terebratula scillae* population from the lower Pleistocene of Lecce area (Southern Italy). Acta Geologica Hispanica, 37:43–51.

TADDEI RUGGIERO, E., G. BUONO, AND P. RAIA. 2006. Bioerosion on brachiopod shells of a thanatocoenosis of Alboran Sea (Spain). Ichnos, 13:175–184.

TAPANILA, L. 2005. Palaeoecology and diversity of endosymbionts in Palaeozoic marine invertebrates: trace fossil evidence. Lethaia, 38:89–99.

TAYLOR, J. D., R. J. CLEEVELY, AND N. J. MORRIS. 1983. Predatory gastropods and their activities in the Blackdown Greensand (Albian) of England. Palaeontology, 26:521–533.

THOMAS, R. D. K. 1976. Gastropod predation on sympatric Neogene species of *Glycymeris* (Bivalvia) from the Eastern United States. Journal of Paleontology, 50:488–499.

TODD J. A. AND T. J. PALMER. 2002. Pattern versus process or informative versus uninformative ichnotaxonomy. Ichnos, 9:83–84.

VERMEIJ, G. J. 1980. Drilling predation of bivalves in Guam: some paleoecological implications. Malacologia, 19:329–334.

WARD, L. W. AND B. W. BLACKWELDER. 1975. Chesapecten, a new genus of Pectinidae (Mollusca: Bivalvia) from the Miocene and Pliocene of Eastern North America. United States Geological Survey Professional Paper 861, 39 p.

WARÉN, A. 1980. Revisions of the genera *Thyca, Stilifer, Scalenostoma, Mucronalia* and *Echineulima* (Mollusca, Prosobranchia, Eulimidae). Zoologica Scripta, 9:187–210.

WILSON, M. A., H. R. FELDMAN, AND E. B. KRIVICICH. 2010. Bioerosion in an equatorial Middle Jurassic coral-sponge reef community (Callovian, Matmor Formation, southern Israel). Palaeogeography, Palaeoclimatology, Palaeoecology, 289:93–101.

YOCHELSON, E. L., D. DOCKERY, AND H. WOLF. 1983. Predation on sub-Holocene scaphopod mollusks from southern Louisiana. United States Geological Survey Professional Paper 1282, p. 1–13.

ZAMORA, S., E. MAYORAL, J. A. GÁMEZ VINTANED, S. BAJO, AND E. ESPÍLEZ. 2008. The infaunal echinoid *Micraster*: taphonomic pathways indicated by sclerozoan trace and body fossils from the Upper Cretaceous of northern Spain. Geobios, 41:15–29.

ZIEGELMEIER, E. 1954. Beobachtungen fiber den Nahrungserwerb bei der Naticide *Lunatia nitida* Donovan (Gastropoda, Prosobranchaia). Helgoländer wissenschaftliche Meeresunters, 5:1–33.

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