Swiss Journal of Palaeontology (2018) 137:103–107
https://doi.org/10.1007/s13358-018-0146-0

SHORT CONTRIBUTION

Substrate is a poor ichnotaxobase: a new demonstration

Stephen K. Donovan[1,2] · **Timothy A. M. Ewin**[3]

Received: 24 January 2018 / Accepted: 1 March 2018 / Published online: 14 March 2018

Abstract
Substrate is a poor ichnotaxobase, yet it has been widely used for distinguishing the clavate (club-shaped) borings commonly produced by bivalves. A chert nodule from the Upper Cretaceous of Morocco encloses the external mould of a clast of unknown composition (rock? wood?) which had been extensively bored, producing both small cylindrical and large clavate pits. Numerous small, short borings are referred to *Oichnus* isp. cf. *O. simplex* Bromley; *Oichnus* is otherwise commonly limited to shelly substrates. More significantly, the clavate borings may either be *Gastrochaenolites turbinatus* Kelly and Bromley, considered confined to rock and shelly substrates, or be *Teredolites clavatus* Leymerie, thought to be limited to wood. These borings are morphologically indistinguishable, only being differentiated by substrate, and thus, they are considered to be synonymous herein. *Gastrochaenolites clavatus* (Leymerie) has priority and is the type species of *Teredolites* Leymerie, now considered a junior synonym of *Gastrochaenolites* Leymerie. Thus, the clavate borings of this specimen are identified as *Gastrochaenolites clavatus* (Leymerie).

Keywords Ichnosystematics · Taphonomy · *Oichnus* · *Gastrochaenolites* · *Teredolites* · *Apectoichnus*

Introduction

Size is a poor ichnotaxobase (Pickerill 1994, p. 11), yet size undoubtedly influences, in part, the apportioning of traces between ichnospecies and ichnogenera. Trace fossils are not biological entities per se, but rather are sedimentary structures generated by the activities of plants and animals. Thus, the primary consideration of the systematics of trace fossils is the form or shape; because they are sedimentary structures, not biological species, their size is not really a consideration except to help differentiate between certain ichnospecies within a given ichnogenus (such as *Paleodictyon* Meneghini; Uchman 1995, text-figs. 21–23). For example, small round holes in shells are assigned to the ichnogenus *Oichnus* Bromley 1981 (Pickerill and Donovan 1998; Wisshak et al. 2015; Donovan and Pickerill 2017). Microborings of similar morphology should also be assigned to *Oichnus* (see, for example, Blissett and Pickerill 2007, pp. 88–90). In addition, how large can a small round hole be before it ceases to be *Oichnus*? In truth, *Oichnus* is produced by the activities of a variety of small invertebrates, commonly predatory, parasitic, or excavating a domicile, and is unlikely to be anything else but small. A big round hole is invariably a random section through a reworked sedimentary substrate (shell, mudrock, and limestone) and made by, for example, a boring bivalve (= *Gastrochaenolites* Leymerie 1842; for big round holes, see Donovan 2011).

Clavate (club-shaped) borings are generated by several genera of bivalves, and are referred either to *Gastrochaenolites* Leymerie, if penetrating a rocky or shelly substrate, or to *Teredolites* Leymerie 1842, if the structure is in wood. As expounded by Donovan (2018), this separation is based in part on our conception of the producing organisms; the bivalve *Gastrochaena* Spengler (and others) produces clavate borings in rocky and shelly substrates, whereas *Teredo* Linnaeus (and others) generates clavate borings in wood. This distinction has been widely accepted (Kelly and Bromley 1984). However, the specimen described below, which preserves only the borings and not

Handling editor: D. Marty.

✉ Stephen K. Donovan
Steve.Donovan@naturalis.nl

1 Taxonomy and Systematics Group, Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands

2 Department of Earth Sciences, University of New Brunswick, Fredericton, NB E3B 5A3, Canada

3 Department of Earth Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, England

the substrate, raises important questions regarding this substrate-based distinction.

The terminology of borings used herein follows Häntzschel (1975) and Kelly and Bromley (1984). The specimen discussed herein is deposited in the Department of Earth Sciences, The Natural History Museum, London, UK (BMNH).

Geological occurrence

The specimen was purchased at the Tucson Gem and Mineral Show 2013 (by BMNH staff Dr. M. Munt and the junior author of this paper). Unfortunately, only scant data regarding locality and stratigraphy are known. It is reportedly from a region to the west of Boujdour, Western Sahara, and is thought to have come from the same region as large numbers of fossil gastropods beautifully preserved in chalcedony that are well known to commercial dealers and private collectors. However, the precise locality and stratigraphic details (of both the nodule and the gastropods) remain obscure as all collecting has been undertaken through surface collection (rather than at outcrop) by local commercial collectors who have so far not revealed their source (K. Martyn, pers. comm. to T.A.M.E., 2016). The age of the gastropods loosely associated with the nodule has been provisionally identified as either Eocene or Upper Cretaceous, but with the latter preferred (M. Munt, pers. comm. to T.A.M.E., 2017). As such, we regard the nodule as Late Cretaceous in age, but this should be treated as provisional. Other larger pieces of chert, generally cylindrical in shape and over 1 m long, are also known to commercial dealers (K. Martyn, pers. comm. to T.A.M.E., 2016); however, these were not available for this study.

Description

The specimen is a chert nodule, BMNH PEI 5339, about 162 × 130 × 102 mm, but incomplete, with a cavity about 122 × 65 × 62 mm. The chert nodule was presumably shaped more or less like a rugby ball when complete, whereas the cavity is more irregular (Fig. 1a). The chert is rich in lithic inclusions and small vuggy cavities, with coarse banding sub-parallel to the main cavity and the outer surface of the clast (Fig. 1a, b). The outer surface is 'clinkery', almost like a volcanic bomb. The cavity is an external mould of a clast, now lost, which supported abundant borings; no direct evidence to the lithology of the clast has been recognized. Apart from the borings, the original clast shows evidence of weathering before the formation of the surrounding nodule, as evidenced by borings at the clast margin being truncated and which presumably would have been whole when originally formed (far right, Fig. 1b); the presence of a crack in the original clast, which also bisects the clavate borings, being infilled with chert (centre, Fig. 1b); and the rough and irregular surface of the clast (top right of Fig. 1c). However, this weathering could equally have been formed in rock or wood.

Borings filled with chert are numerous and of two morphologies (Fig. 1). Particularly, common are short, smooth, parallel-sided shafts. These may be single or clustered; variation in size suggests that these shafts were made in two or more spatfalls. Some specimens are long, extending from the surface of the clast to the clavate borings, mainly to the neck, but also to low in the chamber. They most resemble the tips of smooth, blunt echinoid spines.

The second morphology of borings is larger and club-shaped (clavate), including at least ten individuals; again, variation in size suggests two or more spatfalls. The borings have a narrow aperture, a tapering (rarely sinuous) neck, and a long chamber (sensu Kelly and Bromley 1984, text-Fig. 1). The neck-to-chamber transition is gradual and indistinct. The base is broadly domed and lacks any discernible sculpture. The four largest clavate borings form a rough line (Fig. 1a–c) is their bases, but not their apertures. A second group is more closely clustered (Fig. 1a, b, d) and smaller.

Some of the clavate borings support one or, commonly, more of the small borings (Fig. 1d). These are invariably short; such borings into the surface of the clast are commonly wider and longer.

Discussion

Both forms of borings in BMNH PEI 5339 present problems of classification. At least some of the small borings are reminiscent of the chambers of *Entobia* ispp., but they are not linked by lateral canals (Fig. 1c, d). Rather, they are small round holes/pits in a hard substrate and are most probably domiciles. The original diagnosis of *Oichnus* stated: "Circular to subcircular holes of biogenic origin bored into hard substrates. The hole may pass right through the substrate as a penetration, where the substrate is a thin shell; or end within the substrate as a shallow to deep depression or short, subcylindrical pit" (Bromley 1981, p. 60; see also Donovan and Pickerill 2002, p. 87). The borings in the present specimen "… end within the substrate as a … deep depression …" Therefore, these pits are referred to *Oichnus* isp.; the parallel-sided shafts embolden us to suggest that they are closest to the type species, *Oichnus simplex* Bromley, 1981. *Oichnus simplex* is most commonly identified from shelly substrates; here, the producer was boring into rock (mudrock? limestone?) or

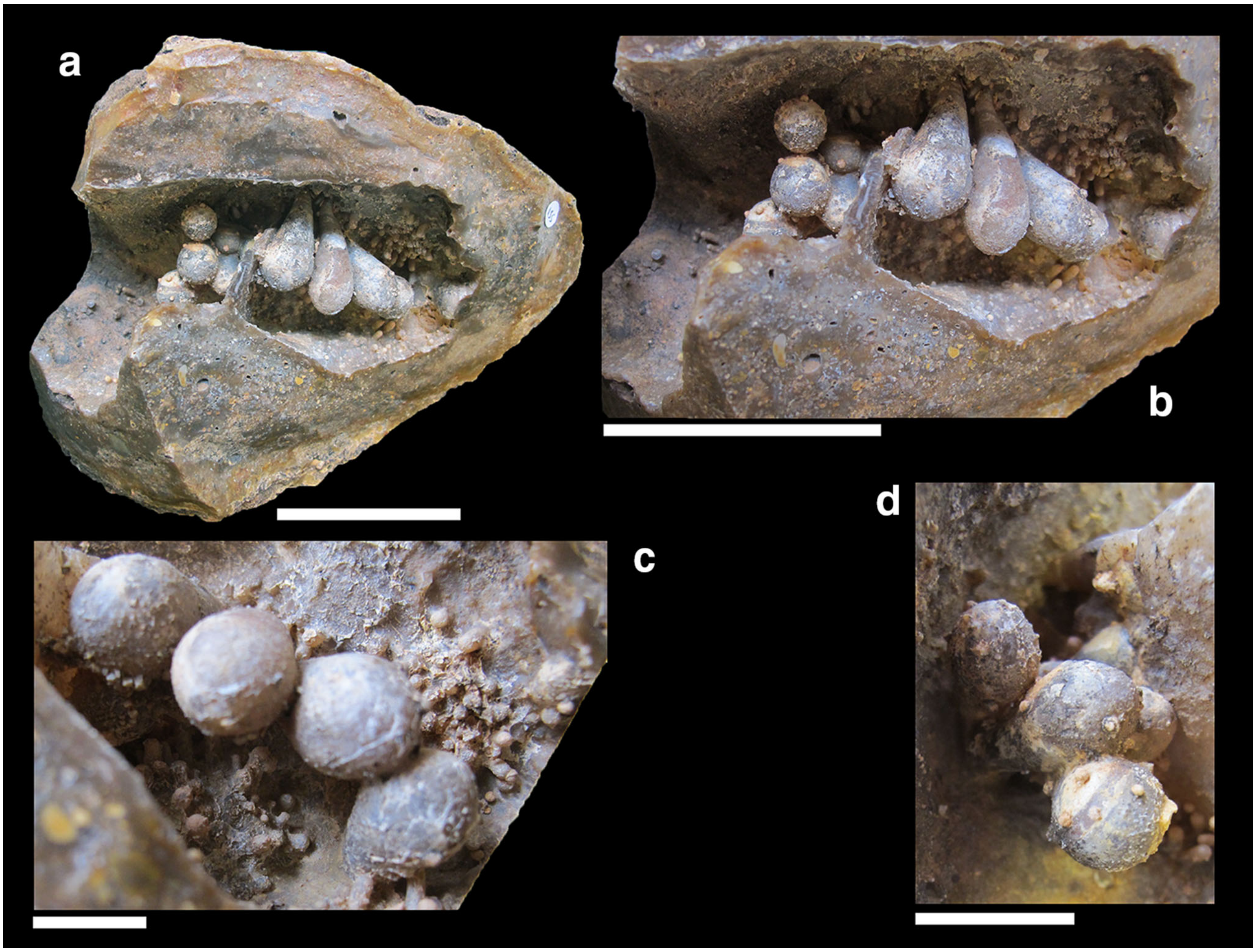

Fig. 1 Bored clast preserved as an external mould in chert, BMNH PEI 5339, from the Upper Cretaceous of Morocco. **a** Broken interior view of clast showing heterogeneous nature of chert, external mould of lost internal substrate (wood? limestone?), sheet-like fracture filled with chert (near centre), and chert-filled borings. **b** Enlargement of borings showing the contrast in size and number of specimens of the two morphologies, as well as a boring which has been partially truncated by weathering (far right). **c** Linear array of four clavate borings, *Gastrochaenolites clavatus* (Leymerie), flanked by numerous small, simple borings, *Oichnus* isp. cf. *O. simplex* Bromley. Note also the roughness of the clast surface. **d** Clavate borings bearing small, simple borings. Specimen uncoated. Scale bars represent 50 mm (**a, b**) or 10 mm (**c, d**)

wood, yet the message of this paper, as amplified below, is that substrate is not important in classification. Most probably, these pits were domiciles.

The identity of the clavate borings is also problematic. The principal ichnotaxobase used for clavate borings has been substrate, either rocky/shelly (*Gastrochaenolites* Leymerie) or wood (*Teredolites* Leymerie); the importance of morphology has been at the level of ichnospecies. The specimens in Fig. 1 are close to two ichnospecies, most particularly *Gastrochaenolites turbinatus* Kelly and Bromley and *Teredolites clavatus* Leymerie, neither of which has a discernible neck region; that is, the chamber-to-neck transition is recognized in neither ichnospecies (Kelly and Bromley 1984, text-figs. 3G, 8C, 9A, 10). Unfortunately, the diagnosis of *T. clavatus* is more concerned with substrate than morphological features: "Clavate *Teredolites* predominantly perpendicular to the grain in woody substrates having length/width ratio usually less than 5″ (Kelly and Bromley 1984, p. 804). On the same page, the diagnosis of the ichnogenus *Teredolites* is "Clavate borings in woody substrate …" and, thus, that of *T. clavatus* actually tells us little more. If substrate is dismissed as an ichnotaxobase, as we believe that it should be, it is apparent that *G. turbinatus* is a junior synonym of *T. clavatus*. The latter is not worthy of a separate ichnogeneric name and should be considered *Gastrochaenolites clavatus* (Leymerie). As both ichnogenera were erected in the same publication, this is the option that will involve the least ichnospecific confusion.

Note at this juncture that *Teredolites longissimus* Kelly and Bromley, 1984, the only other nominal species hitherto attributed to this ichnogenus, is morphologically highly distinct from all *Gastrochaenolites* ispp. and, particularly, *T. clavatus*. It has recently been reclassified as the type species of a new ichnogenus, *Apectoichnus* Donovan, 2018, based on its distinct morphology and not its substrate.

In short, the type (and, currently, only) species of *Teredolites*, *T. clavatus* Leymerie, is similar in form to *Gastrochaenolites* spp. (compare Kelly and Bromley 1984, text-figs. 3, 9A with 9B). Therefore, how much does substrate matter? The schemes of Pickerill (1994, p. 10) followed Bromley (1990) in recognizing general form, branching, burrow fill, and burrow boundaries as recognizable ichnotaxobases, whilst Bertling et al. (2006, Table 2) summarized recommended ichnotaxobases as morphology (overall shape), orientation, ornamentation, and internal structure. Note that none of these experts included substrate as an ichnotaxobase (contra Höpner and Bertling 2017).

If this argument is rejected that *Teredolites clavatus* is a *Gastrochaenolites*, then how should we classify the clavate borings in Fig. 1? Are they *Gastrochaenolites turbinatus* or *Teredolites clavatus*? Despite the excellent preservation shown by these specimens, because the substrate is unknown, there is no possible way of determining this using existing logic of classification. Yet, if we consider some other sedimentary structure—say, cross bedding—it remains cross bedding whatever the mineralogy of the grains or the substrate. The utility of substrate when analysing a clavate boring is in giving an indication of the nature of the boring organism (Bromley 2004, p. 462), but that is an ancillary consideration. Too often, it is biological determinations that overrule the simple requirement to classify a trace based on its form (e.g., Donovan 2010). The Latinized binomens used to name trace fossils do not make them organisms, yet it is an historic accident (Osgood, 1975) that continues to confuse ichnologists, sedimentologists, and palaeontologists that they are so. They are not.

On the basis of recognized ichnotaxobases, and not of substrate, *T. clavatus* is a *Gastrochaenolites*. In consequence, *Teredolites* is a junior synonym of *Gastrochaenolites* (Appendix 1). This synonymization is not, we emphasize, just to allow one specimen (Fig. 1) to be comfortably placed within ichnological classification. Rather, the reverse is true; this specimen exposes a persistent flaw in ichnotaxonomic practice. The specimen is an illustration that has helped clarify our thoughts on the value (or otherwise) of substrate as an ichnotaxobase. Our arguments are pertinent whether the specimen in Fig. 1 is referred to or not.

Acknowledgements We thank Professor A. Uchman (Jagiellonian University, Kraków, Poland) for comments on an earlier version of this paper, and Dr. M. Munt (Dinosaur Isle Museum, Isle of Wight, Hampshire, UK) and Mr. K. Martyn (Moussa Direct Ltd, Cambridge, UK) for specimen acquisition and helpful discussions relating to the specimen locality and stratigraphy. We thank an anonymous reviewer, and Dr. J.W.M. Jagt (Natuurhistorisch Museum Maastricht, Netherlands) and Dr. E.A. Jagt-Yazykova (Uniwersytet Opolski, Poland), for their supportive reviews.

Appendix 1

Systematic ichnology

Ichnogenus *Gastrochaenolites* Leymerie, 1842.

Type ichnospecies. *Gastrochaenolites lapidicus* Kelly and Bromley 1984.

Other ichnospecies. *Gastrochaenolites ampullatus* Kelly and Bromley 1984; *Gastrochaenolites anauchen* Wilson and Palmer 1998; *Gastrochaenolites clavatus* (Leymerie 1842); *Gastrochaenolites cluniformis* Kelly and Bromley 1984; *Gastrochaenolites cor* Bromley and d'Alessandro 1987; *Gastrochaenolites dijugus* Kelly and Bromley 1984; *Gastrochaenolites hospitium* Kleemann 2009; *Gastrochaenolites oelandicus* Ekdale and Bromley 2001; *Gastrochaenolites orbicularis* Kelly and Bromley 1984; *Gastrochaenolites ornatus* Kelly and Bromley 1984; *Gastrochaenolites pickerilli* Donovan 2002; *Gastrochaenolites torpedo* Kelly and Bromley 1984; *Gastrochaenolites vivus* Edinger and Risk 1994.

Diagnosis. (Modified after Kelly and Bromley 1984, p. 797.) Clavate borings, with or without a calcareous lining. The aperture region of the boring is narrower than the main chamber, and may be circular, oval, or dumbbell shaped. The aperture may be separated from the main chamber by a neck region which in some cases may be widely flared. The main chamber may vary from subspherical to elongate, having a parabolic to rounded truncated base and a circular to oval cross section, modified in some forms by a longitudinal ridge or grooves to produce an almond or heart-shaped section. Typical substrates are rock (commonly mudrock or limestone), shell or, less commonly, wood.

References

Bertling, M., Braddy, S. J., Bromley, R. G., Demathieu, G. R., Genise, J., Mikuláš, R., et al. (2006). Names for trace fossils: a uniform approach. *Lethaia, 39,* 265–286.

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

Bromley, R. G. (1981). Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geològica Hispànica, 16,* 55–64.

Bromley, R. G. (1990). *Trace Fossils: Biology and Taphonomy*. London: Unwin Hyman.

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

Bromley, R. G., & D'Alessandro, A. (1987). Bioerosion of the Plio-Pleistocene transgression of southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia, 93,* 379–422.

Donovan, S. K. (2002). A new ichnospecies of *Gastrochaenolites* Leymerie from the Pleistocene Port Morant Formation of southeast Jamaica and the taphonomy of calcareous linings in clavate borings. *Ichnos, 9,* 61–66.

Donovan, S. K. (2010). *Cruziana* and *Rusophycus*: trace fossils produced by trilobites… in some cases? *Lethaia, 43,* 283–284.

Donovan, S. K. (2011). Aspects of ichnology of Chalk and sandstone clasts from the beach at Overstrand, north Norfolk. *Bulletin of the Geological Society of Norfolk, 60* (for 2010), 37–45.

Donovan, S. K. (2018) A new ichnogenus for *Teredolites longissimus* Kelly and Bromley. *Swiss Journal of Palaeontology, 137*, 4 pp.

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

Donovan, S. K., & Pickerill, R. K. (2017). The invalidity of the trace fossil *Tremichnus* Brett. *Geological Journal, 52,* 828–831.

Edinger, E. N., & Risk, M. J. (1994). Oligocene-Miocene extinction and geographic restriction of Caribbean corals: roles of turbidity, temperature, and nutrients. *Palaios, 9,* 576–598.

Ekdale, A. A., & Bromley, R. G. (2001). Bioerosional innovation for living in carbonate hardgrounds in the Early Ordovician of Sweden. *Lethaia, 34,* 1–12.

Häntzschel, W. (1975). Trace fossils and problematica. Second edition, revised and enlarged, xxi + 269. In C. Teichert (Ed.), *Treatise on Invertebrate Paleontology, Part W, Miscellanea, Supplement 1*. Boulder and Lawrence: Geological Society of America and University of Kansas.

Höpner, S., & Bertling, M. (2017). Holes in bones: ichnotaxonomy of bone borings. *Ichnos, 24,* 259–282.

Kelly, S. R. A., & Bromley, R. G. (1984). Ichnological nomenclature of clavate borings. *Palaeontology, 27,* 793–807.

Kleemann, K. (2009). *Gastrochaenolites hospitium* isp. nov., trace fossil by a coral-associated boring bivalve from the Eocene and Miocene of Austria. *Geologica Carpathica, 60,* 339–342.

Leymerie, A. (1842) Suite de mémoire sur le terrain Crétacé du departement de l'Aube. *Mémoires de la Société Géologique de France, 4*, 291–364. **(Not seen.)**

Osgood, R. G., Jr. (1975). The history of invertebrate ichnology. In R. W. Frey (Ed.), *The Study of Trace Fossils: A Synthesis of Principles, Problems, and Proceedures in Ichnology* (pp. 3–12). New York: Springer.

Pickerill, R. K. (1994). Nomenclature and taxonomy of invertebrate trace fossils. In S. K. Donovan (Ed.), *The Palaeobiology of Trace Fossils* (pp. 3–42). Chichester: John Wiley and Sons.

Pickerill, R. K., & Donovan, S. K. (1998). Ichnology of the Pliocene Bowden shell bed, southeast Jamaica. *Contributions to Tertiary and Quaternary Geology, 35,* 161–175.

Uchman, A. (1995). Taxonomy and palaeoecology of flysch trace fossils: the Marnoso-arenacea Formation and associated facies (Miocene, northern Apennines, Italy). *Beringeria, Würzburger geowissenschaftliche Mitteilungen, 15,* 1–115.

Wilson, M. A., & Palmer, T. J. (1998). The earliest *Gastrochaenolites* (early Pennsylvanian, Arkansas, U.S.A.): an Upper Paleozoic bivalve boring? *Journal of Paleontology, 72,* 769–772.

Wisshak, M., Kroh, A., Bertling, M., Knaust, D., Nielsen, J. K., Jagt, J. W. M., et al. (2015). In defence of an iconic ichnogenus—*Oichnus* Bromley, 1981. *Annales Societatis Geologorum Poloniae, 85,* 445–451.