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REGULAR RESEARCH ARTICLE

Invertebrate borings from the Eocene of Seven Rivers, parish of St. James, western Jamaica

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Abstract

The fossil biota of the Eocene Yellow Limestone Group of Jamaica is diverse in vertebrates and, particularly, invertebrates. However, its invertebrate trace fossils remain understudied. Herein, we document the borings of the Seven Rivers vertebrate site in western Jamaica. This is in the Litchfield Formation, high in the Lutetian (about mid-Middle Eocene). The suite of borings identified from this site comprises *Apectoichnus longissimus* (Kelly and Bromley); *Entobia* isp.; *Oichnus simplex* Bromley; and *Oichnus paraboloides* Bromley. Substrates infested by *Entobia* isp. include both molluscs and sirenian ribs. *Oichnus* ispp. occur only in bivalves and are mainly non-penetrative, which may be a taphonomic artifact. Tubes of the common *A. longissimus* are preserved free from any woody substrates, which have presumably rotted away; however, one specimen has a dark, carbonaceous external film and others have carbonized wood inclusions. The occurrence of *A. longissimus* in the Jamaican rock record coincides with periods of sub-aerial exposure.

Keywords Litchfield Formation · Trace fossils · Systematics · *Entobia* · *Gastrochaenolites* · *Apectoichnus*

Introduction

The Yellow Limestone Group of Jamaica has yielded a diverse biota including numerous micro- and macrofossil groups (see, for example, many of the papers in Wright and Robinson 1993). However, the ichnological diversity of this suite of formations awaits elucidation. Hitherto, trace fossils have commonly received, at best, only passing mention in papers on other aspects of the Yellow Limestone Group (see, for example, Donovan et al. 1990, fig. 2) with rare exceptions (Donovan and Blissett 1998). Indeed, and perhaps unexpectedly, despite the fact that Yellow Limestone Group is a popular target for experts on many fossil groups, the Paleogene ichnology of Jamaica is best known from two less 'collector-friendly' units: the Paleocene–Lower Eocene Richmond Formation (Pickerill and Donovan 1991; Pickerill et al. 1992, 1993; Pickerill and Mitchell 1999; Donovan et al. 2005, 2015); and the Eocene formations of the White Limestone Group (Blissett and Pickerill 2003, 2004, 2007; Donovan et al. 2015). Neither of these units is renowned for the ease with which their macrobiota can be found and collected (note the comments of Donovan 2004, p. 3), unlike, for example, the subject of the present paper, the Litchfield Formation of the Yellow Limestone Group (Mitchell in press).

We submit that the paucity of systematic ichnological studies of the Yellow Limestone Group of Jamaica is an oversight rather than a true reflection of its diversity of trace fossils (Donovan et al. 2015, p. 380). The present paper is the first contribution of what we hope will become at least a healthy trickle of papers on this subject. Herein, we describe the borings of the Seven Rivers vertebrate site in the parish of St. James, western Jamaica, which form part of the collections of the Florida Museum of Natural History, University of Florida, Gainesville (UF), and the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC (USNM). We recognize that this assemblage is incomplete, consisting only of invertebrate borings on shells and vertebrate

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bones, and specimens released from decomposed xylic substrates. The measured section of Mitchell (in press, fig. 3) demonstrates that these were associated with burrows made by invertebrates, namely *Thalassinoides* isp. and *Ophiomorpha* isp., and vertebrate trace fossils (crocodile coprolites).

Locality and horizon

The Seven Rivers site in the parish of St James, western Jamaica, is the most important vertebrate site in the Paleogene of Jamaica (Domning et al. 1997; Domning 2001; Portell et al. 2001; Donovan et al. 2007). It is situated at and around [NGR 5285 8810]; see the Jamaica metric edition 1:50,000 sheet #6, 'The Cockpit Country'. Mitchell (in press) provides GPS co-ordinates. The site itself is a man-made drainage ditch.

The site was discovered by the junior author in the early 1990s. At this time, it was shown as Cretaceous (Maastrichtian) on the provisional geological sheet (Bateson undated), but the discovery of sea cow ribs and diagnostic invertebrates demonstrated that it was undoubtedly within the outcrop of the Eocene Yellow Limestone Group. Remapping by Mitchell (in press, figs. 2–4) has shown conclusively that the Seven Rivers site is within the Litchfield Formation, Yellow Limestone Group. This is near the top of the Lutetian (about mid-Middle Eocene) and coeval with the other important vertebrate site of the Yellow Limestone Group, the Dump Limestone lenticle (Berg 1969; Robinson 1969; Donovan et al. 1990).

Systematic ichnology

Remarks Some of the images used herein first appeared in Donovan et al. (2015, fig. 5) and were referred to derivation from "… Donovan and Portell, in press …" in the caption (p. 368 therein). This paper has been withdrawn from Domning and Portell (in press), revised and is now published herein.

Ichnogenus *Entobia* Bronn 1837

Type ichnospecies Entobia cretacea Portlock 1843, p. 360, by the subsequent designation of Häntzschel (1962, p. W230), from the Campanian(?) of Magilligan, Co. Londonderry, Northern Ireland, UK (Bromley 1970, p. 78).

Diagnosis (Slightly modified after Bromley and D'Alessandro 1984, p. 238.) "Boring in carbonate or phosphatic substrates comprising a single chamber or networks or boxworks of galleries connected to the surface by several or numerous apertures. Morphology changes markedly with ontogeny. The galleries show progressive increase in diameter during growth; in some forms, inflation at more or less regular distances produces a system of closely interconnected chambers; in other forms, chamber development is restricted to only a brief ontogenetic stage; in still other forms, no cameration is developed. The surface of the boring bears a cuspate microsculpture that may be lost in gerontic specimens. Fine apophyses arise from all or most surfaces of the system."

Remarks Unlike the body fossils of sponges, which remain rare throughout the fossil record of Jamaica and the Caribbean (Blissett et al. 2007; Donovan and Stemann 2007), the borings of the family Clionaidae (Bromley 2004, p. 459)—that is, *Entobia* ispp.—are locally common and have been found at many horizons in the Jamaican Cenozoic (see, for example, Donovan and Blissett 1998; Donovan et al. 2015). The occurrence of common *Entobia* in sirenian ribs at Seven Rivers (Fig. 1a, b) has necessitated a minor revision of the original diagnosis to include such calcium carbonate/phosphatic substrates. However, it is debatable if substrate composition is a valid ichnotaxobase (Donovan and Pickerill 2002; Donovan 2018; Donovan and Ewin 2018; contra Höpner and Bertling 2017).

Entobia isp.
Figure 1a–c, g
2015 *Entobia* isp.; Donovan et al., p. 370, Table 2, Fig. 5a–c, e.

Material Four infested bivalves, UF 166613 and 166940 (both in *Carolia jamaicensis* Dall, 1898, valves; Fig. 1c), and UF 166635 and 166881 (both infesting ostreid valves). Two specimens, UF 166937 (Fig. 1g) and 166938, are preserved as infills of single chambers. Bored sirenian ribs, USNM 546140 to 546142 (Fig. 1a, b).

Horizons Specimens variously from beds 2 (UF 166940), 8 (UF 166613) and 18, particularly 18-C (UF 166881, 166937, 166938, USNM 546140 to 546142) of Mitchell (in press, fig. 3) and spoil (UF 166613).

Description External, and both external and internal (UF 166881) surfaces of valves and bones perforated by numerous, irregularly distributed, circular to elliptical holes of differing sizes (Fig. 1b, c). Specimens free of substrate are individual chambers (Fig. 1g), preserved as thin, smooth, infilled calcite lining to borings preserving small, sub-spherical main chambers with short (but incomplete) necks.

Remarks Specimens of *Entobia* isp. are apparent as perforations on the surfaces of bones (Fig. 1b) and bivalves (Fig. 1c). Note that the three specimens in which *Entobia* is recognized only on the external surface of the valve do not

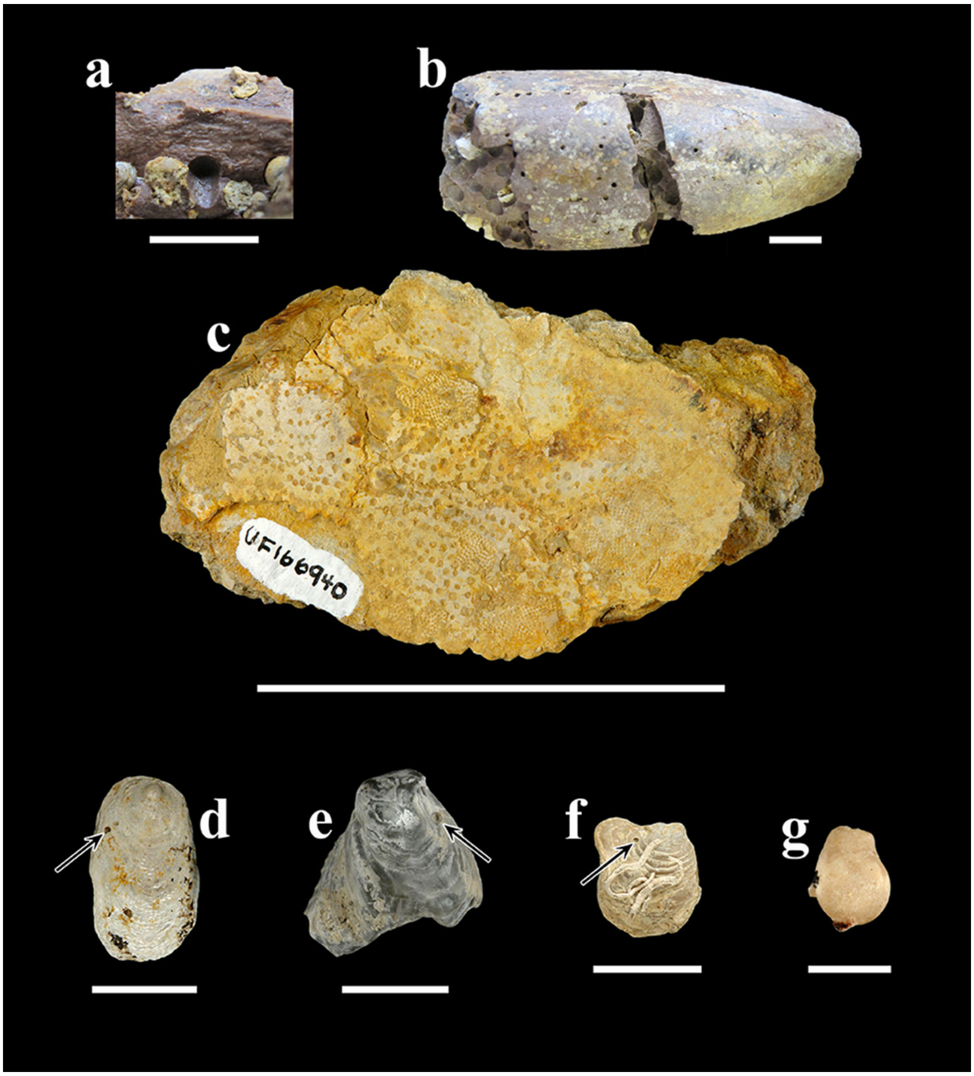

Fig. 1 Borings in biomineralized substrates from the Eocene of Seven Rivers, Jamaica (**a–c, f, g** after Donovan et al. 2015, fig. 5a–e, respectively). **a–c, g** *Entobia* isp. **a** USNM 546142, rib fragment bored with some chambers infilled by white calcite. **b** USNM 546140, rib fragment showing apertures (right and left of center) and infilled chambers (left). **c** UF 166940, surface expression of a dense infestation in an ostreid; scale bar represents 50 mm. **g** UF 166937, calcite infill of a chamber. **d–f** Small round holes in shells, *Oichnus* ispp. **d** *Oichnus paraboloides* Bromley, UF 166840, non-penetrative pit in *Anomia*. **e** *Oichnus paraboloides* Bromley, UF 166844, non-penetrative pits in an ostreid. **f** *Oichnus simplex* Bromley, UF 166847, non-penetrative pit in an ostreid; scale bar represents 2 mm. Scale bars represent 10 mm unless stated otherwise

expose the inner surface; these are only seen on broken ribs. UF 166881 is a post-mortem infestation of an ostreid; the other bivalves may have been infested either in vivo or post-mortem.

The individual, infilled chambers liberated from, presumably, crumbling sirenian bones resemble the bivalve boring *Gastrochaenolites orbicularis* Kelly and Bromley, 1984, which has not been reported from the Antilles hitherto (Donovan and Hensley 2006, table 2). The small size and preservation free of a substrate are unusual. However, our original interpretation of these specimens, that they were produced by juvenile boring bivalves invading a relatively thin shelly, aragonitic substrate which was subsequently lost due to diagenesis, was erroneous. A collection of sirenian bones, mainly ribs and all from unit 18, shown to S.K.D. by Professor D.P. Domning (August 29, 2012), included several specimens that were densely infested by *Entobia*, preserved both as natural excavations and calcitic casts (Fig. 1a, b). Although unknown from Seven Rivers, *Gastrochaenolites* ispp. are a common component of the Cenozoic rock record of Jamaica (see, for example, Donovan et al. 2001; Donovan 2002) and the wider Antilles (Donovan and Hensley 2006; Donovan et al. 2014).

Ichnogenus *Oichnus* Bromley 1981

Type ichnospecies Oichnus simplex Bromley 1981, p. 60, by original designation.

Diagnosis (After Donovan and Pickerill 2002, p. 87.) “Small, circular, subcircular, oval or rhomboidal holes or pits of biogenic origin in hard substrates, commonly perpendicular to subperpendicular to substrate surface. Excavation may pass directly through substrate as a penetration, most commonly where the substrate is a thin shell, or may end within the substrate as a shallow to moderately deep depression or short, subcylindrical pit, commonly with a depth:width ratio of ≤ 1, with or without a central boss.”

Remarks Oichnus ispp. are locally common in diverse shelly substrates of the Cenozoic of Jamaica (see, for example, Pickerill and Donovan 1998; Donovan and Harper 2007; Donovan et al. 2015).

Oichnus simplex Bromley, 1981
Figure 1f
2015 *Oichnus simplex* Bromley; Donovan et al., p. 370, table 2, fig. 5d.

Material One specimen, UF 166847 (a non-penetrative pit in a valve of an ostreid; Fig. 1f).

Horizon Bed 18-C of Mitchell (in press, fig. 3).

Diagnosis (After Bromley 1981, p. 60.) "*Oichnus* 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."

Description Simple, small (< 0.5 mm), sub-rounded, incomplete hole with axis perpendicular to substrate and no countersunk edge.

Remarks This pit may represent failed predation by a muricid gastropod (see discussion in Pickerill and Donovan 1998, pp. 164–166). As muricids in this fauna are commonly large (see Portell in press), this tiny trace may have been bored by a juvenile. The valve is encrusted by calcareous worm tubes and a bryozoan (Fig. 1f).

Oichnus paraboloides Bromley, 1981
Figure 1d, e
2015 *Oichnus paraboloides* Bromley; Donovan et al., p. 370, table 2.

Material UF 166840 (one non-penetrative pit in a valve of *Anomia*; Fig. 1d), 166841 (one penetrative borehole and a second incomplete borehole or pit in a valve of *Anomia),* 166844 (four non-penetrative pits in a valve of ostreid; Fig. 1e) and 166874 (three non-penetrative pits in a valve of *Anomia*).

Horizon All specimens are from bed 18-C of Mitchell (in press, fig. 3).

Diagnosis (After Bromley 1981, p. 62.) "*Oichnus* having a spherical paraboloid form, truncated in those cases where the boring penetrates right through the substrate. Where it does not so penetrate, the paraboloid may be deformed by a slightly raised central boss."

Description Small (largest specimen about 1 mm in diameter), paraboloid, rounded to elliptical, mainly incomplete holes with axis perpendicular to substrate. Outer edges countersunk.

Fig. 2 Infills of bivalve borings, *Apectoichnus longissimus* (Kelly and Bromley), released from rotted xylic substrates from the Eocene of Seven Rivers, Jamaica. **a** UF 166582. **b** UF 166596. **c** UF 166597 (after Donovan et al. 2015, fig. 5f). Scale bars represent 50 mm

Remarks These pits and the complete borehole may represent examples of failed and successful predation, respectively, by naticid gastropods (see discussion in Pickerill and Donovan 1998, pp. 164–166). Naticids in this fauna are commonly small, as are *O. paraboloides* (see Portell in press). Why so many of these pits should be non-penetrative in such a thin shell as *Anomia* is unknown. However, the one borehole is cut by a crack in the valve which links to the second pit in this specimen. It may be that successful predation reduces the chance of preservation by mechanically weakening the valve (Roy et al. 1994; Pickerill et al. 2002, pp. 115–116).

Ichnogenus *Apectoichnus* Donovan 2018

Type ichnospecies Teredolites longissimus Kelly and Bromley 1984, pp. 804, 806, text-figs. 9b, 11, by original designation (Donovan 2018, p. 96) from the Aptian (Lower Cretaceous) of Kent, south-east England.

Diagnosis (After Donovan 2018, p. 96.) "Elongate borings, commonly circular in section, smooth-sided, straight or sinuous to contorted and intertwined, with or without a calcareous lining. The boring may change direction and cause a constriction of the tube, but tubes are commonly of more or less constant diameter. May be solitary or gregarious."

Remarks In Jamaica, *Apectoichnus longissimus* has been recognized hitherto (as *Teredolites longissimus*) from the Upper Pliocene turbidites of the Bowden Member including its basal unit, the Bowden shell bed (Pickerill et al. 1996; Donovan et al. 1998). The Bowden Member contains allochthonous examples of *A. longissimus*, preserved within their host xylic substrates. *Apectoichnus longissimus* is preserved as short lengths of isolated calcite tubes in the Bowden shell bed. Preservation of *A. longissimus* elsewhere in the Cenozoic of the Antilles shows a range of taphonomic expressions (for example, Pickerill et al. 2003; Donovan 2014).

Apectoichnus longissimus (Kelly and Bromley 1984)
Figure 2

2015 *Teredolites longissimus* Kelly and Bromley; Donovan et al., p. 370, table 2, fig. 5f.

Material Thirty-three specimens, UF 166565–166566, 166570, 166572–166573, 166577–166582, 166584–166585, 166587–166591, 166593, 166595–166597, 166599–166600, 166602, 166605, 166607, 166719–166724 (Fig. 2). Some of these numbers may refer to two fragments of the same tube that it has not been possible to reconstruct.

Horizon All specimens are from bed 8 of Mitchell (in press, fig. 3).

Diagnosis As for the ichnogenus.

Description Cylindrical, unbranched, gray (when clean) calcite tubes, never complete, but some are of considerable length (100+ mm). Tubes more or less tapering gently distally, although some specimens show apparently proximal contractions. Tube section rounded, commonly circular. Tubes sinuous to highly contorted, only straight over short distances. Distal termination either conical or bulbous. Geniculations of tubes uncommonly swollen. Tubes commonly infilled with sedimentary rock, rarely with woody inclusions; although sedimentary rock has dropped out of some specimens, the internal walls are invariably masked by adhering mudrock.

Growth lines on outside of tube perpendicular to long axis, formed by a cone-in-cone arrangement of successive layers. Walls up to 40% of tube diameter proximally, the concentric arrangement of layers apparent on broken ends. Walls commonly thicken proximally, although the base of some specimens may be particularly thick.

Remarks These specimens are not immediately apparent as *Apectoichnus*. None of them is preserved in a woody substrate, although UF 166582 has, in part, a dark carbonaceous external film that is suggestive of a xylic origin and other specimens include carbonized woody inclusions (including UF 166570, 166593). They are interpreted as *A. longissimus* tubes that were released into the sediment after their enclosing woody substrates rotted away. Particularly, some of the convoluted tubes are reminiscent of the type series (Kelly and Bromley 1984, text-fig. 11) and other, closely packed associations of this species (see, for example, Savrda and Smith 1996, fig. 1; Savrda et al. 2005, fig. 5).

Discussion

The small suite of trace fossils described above provides limited palaeoecological information about the Seven Rivers site. Because of its pseudoplanktonic lifestyle, *A. longissimus* is an archetypal facies-crossing trace fossil. However, it is the commonest trace fossil in this assemblage, which may have been a function of Jamaica's proximity to the Yucatán Peninsula of Mexico and its shoreline at this time (Domning et al. 1997; Donovan et al. 2007). As the Caribbean Plate ground its way east, Jamaica became completely submerged (Draper 1987) and far distant from any landmass. It was only after renewed tectonic activity had raised the Jamaican landmass above sea level that *Apectoichnus* was again found in the Jamaican rock record (Pickerill et al. 1996; Donovan et al. 1998). Thus, a nearby coastline is apparently a decisive factor determining the presence of *Apectoichnus* in the rock record of Jamaica. In contrast, *Entobia* and *Gastrochaenolites* Leymerie, 1842 are typical ichnofossils in a wide range of shallow-water, open-marine settings.

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