

ICHOLOGY OF THE PLIOCENE BOWDEN SHELL BED, SOUTHEAST JAMAICA

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At least 45 of the approximately 600 species of molluscs documented from the Bowden shell bed exhibit evidence of bioerosion in the form of completely or incompletely penetrative (failed) small round holes. Assessment of previously illustrated material, together with new collections made by us, shows that these borings are assignable to the ichnotaxon *Oichnus* Bromley, 1981, in particular *O. paraboloides* Bromley, 1981 and *O. simplex* Bromley, 1981. Observations suggest that the borings were not a result of parasitism nor simple random excavations by bioeroding organisms. Rather, they are interpreted as a result of opportunistic predatory activities of cannibalistic gastropods, *O. paraboloides* probably having been produced by naticids and *O. simplex* by muricids.

Key words — Bowden shell bed, Pliocene, ichnology, borings, *Oichnus*, molluscs.

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elements of these previously described ichnotaxa. This is hardly surprising as, apart from the borings *Teredolites* Leymerie, which were developed in allochthonous xylic substrates, these ichnotaxa were produced *in situ* in generally soft, fine-grained marlstones characterising most of the sequence. Yet the Bowden shell bed is not entirely devoid of evidence of biogenic (ethologic) activity, albeit clearly allochthonous, and therefore, it is the purpose of this short contribution to record this in more detail than previously documented.

In his outstanding monographic studies of the molluscan fauna of the Bowden shell bed, Woodring (1925, 1928) figured many specimens that exhibited clear evidence of bioerosion in the form of small round holes (borings) that either completely or incompletely penetrated the host shells. Woodring (1928, p. 36) astutely stated, 'The nearly rounded holes that can be seen on many of the photographs of both gastropods and pelecypods are evidence of the activities of some predaceous carnivorous gastropods...', a conclusion reiterated herein. In this short contribution we provide a summary list of those species of molluscs figured by Woodring (1925, 1928) that exhibit evidence of bioero-

INTRODUCTION

Our interest in the ichnology of the Bowden shell bed arose initially from the discovery of a relatively diverse, though generally poorly preserved, assemblage of ichnotaxa within marlstones of the Bowden Formation as a whole (Pickerill *et al.*, 1996, 1998). The highly fossiliferous, massively bedded layers of the Bowden shell bed, interpreted as products of sediment gravity flows (Woodring, 1965; Robinson, 1969, Pickerill *et al.*, 1996, 1998), contain no

sion of the type (Table 1) and which hopefully will prove useful to researchers unable to access these important documents. Additionally, based on our own collections from the shell bed, we describe and figure comparable examples of such structures, and place these and Woodring's illustrated material into a modern ichnotaxonomic framework. In so doing this permits us to initially discuss, in our opinion, the somewhat controversial nomenclature of small round holes or pits made in lithic substrates.

As reviewed by several authors (for example, Bromley, 1970, 1992, 1994; Warme, 1975; Warme & McHuron, 1978; amongst others) the bioerosion of lithic substrates in marine environments reflects the work of a broad phylogenetic spectrum of organisms. The resultant ichnotaxa, which may reflect a variety of behavioural strategies, encompass a wide range of morphologies (Bromley, 1994). Even morphologically simple structures analogous to those documented herein can be produced by a variety of taxa capable of boring activities. Nevertheless, the relatively large collections on which this study is based, together with a survey of the literature, has enabled us to make at least some commentary on both the function of the structures and the possible taxonomic affinities of the organisms responsible for their production.

NOMENCLATURE

The nomenclature of small round borings was initially eloquently addressed by Bromley (1981), who formulated the ichnogenus *Oichnus* to accommodate circular to subcircular penetrations or pits (incomplete or failed penetrations) found in lithic substrates, particularly skeletal material. Bromley (1981) distinguished two morphotypes, *O. simplex* and *O. paraboloides*, the former being characterised by simple cylindrical or subcylindrical borings with axes more or less perpendicular to the penetrated substrate surface, and the latter characterised by also being more or less perpendicular, but possessing a spherical, paraboloid form. Subsequently, Brett (1985) described a new ichnotaxon, *Tremichnus*, for perpendicular, circular-parabolic pits or embedment structures that occurred on fossil echinoderms, primarily crinoids, and that did '...generally not penetrate through plates...' (Brett, 1985, p. 626). Brett differentiated *Tremichnus* from *Oichnus* based on its interpretation as a combined embedment-boring rather than simple borehole, its virtually unique association with the stereom of crinoids and, unlike *Oichnus*, its frequent overlapping. Additionally, *Tremichnus* was stated to '...rarely penetrate the substrate...' (Brett, 1985, p. 627). The four ichnospecies recognised by Brett, namely, *T. paraboloides*, *T. cystieus*, *T. minutus* and *T. puteolus*, were differentiated essentially on size, presence or absence of gall-like swellings and cystose masses of stereomatic secretions, and presence or absence of raised rims or inner ring-like

grooves. More recently, Bromley (1993) described a third ichnospecies of *Oichnus*, namely *O. ovalis*, for oval, sub-parabolically-tapering small borings. Bromley (1993) emended his original diagnosis of *Oichnus* to exclude incomplete penetrations or embedment structures similar to those documented by Brett (1985) as *Tremichnus*. In so doing, Bromley (1993, p. 170), in his discussion of his emended diagnosis of *Oichnus* stated, 'By so excluding these pits, the emended diagnosis of *Oichnus* is an improvement on the original.'

Taxonomically, the ichnogeneric nomenclatural scheme proposed by Brett (1985) and later supported by Bromley (1993) is confusing, for the following reasons. Initially, it should be recalled that ichnotaxa are named solely on morphology, significant and accessory behavioural signatures (*sensu* Fürsich, 1974) being utilised for the distinction of ichnogenera and ichnospecies, respectively. The taxonomic affinities of the producing organism(s) and the behavioural activity they reflect are irrelevant with respect to nomenclature of the resultant traces (Bromley & Fürsich, 1980; Bromley, 1990; Pickerill, 1994). In the diagnosis of *Tremichnus*, Brett (1985, p. 626) emphasised that the ichnotaxon occurred '... on the plates of echinoderms, primarily crinoids, with or without associated thickening or gall-like deformation of the plates.' That *Tremichnus* was restricted to echinoderms and gall-like swellings could or could not be present are irrelevant ichnotaxobases (*sensu* Bromley, 1990). Host specificity cannot be considered an ichnotaxobase in any sense and, equally as important, gall-like swellings (or cystose masses or stereomatic secretions) develop within the host and do not constitute part of the bioerosional structure *per se*.

Brett's (1985) differentiation of *Tremichnus* from *Oichnus* based on the former being a combined embedment-boring and the latter a strictly boring structure is also irrelevant taxonomically. Although his interpretation of *Tremichnus* is, at least in part, undoubtedly correct (but see Franzén, 1974; Eckert, 1988; Bromley, 1994, p. 139, table 5.2), we reiterate that morphology should be the exclusive criterion for distinguishing ichnotaxa (see, for example, Fürsich, 1974; Bromley & Fürsich, 1980; Johnson *et al.*, 1994; Pickerill, 1994) and functional interpretations should play no role in nomenclature. Furthermore, that examples of *Tremichnus* commonly overlap (intersect) is a palaeoecological consideration that again has no bearing on overall morphology. This, for example, was also emphasised by Alpert (1974) in his inclusion, by priority, of vertical burrows of *Tigillites* Rouault within *Skolithos* Haldeman. The only difference between these two ichnotaxa was that *Tigillites* was historically adopted for vertical burrows that were densely crowded and, as noted by Alpert (1974), burrow spacing should not be utilised as a taxonomic character. Ichnologists have almost universally accepted this recommendation, so that *Tigillites* is no longer adopted for vertical burrows irrespective of their spatial density. Besides, examples of overlapping *Oichnus* are also well

known in the literature (see, for example, Sohl, 1969; Boucot, 1990).

Finally, we note that it has previously been stated that both *Oichnus* and *Tremichnus*, irrespective of their origin, may or may not completely penetrate the host (Bromley, 1981; Brett, 1985). Complete or incomplete penetration of a host will depend on a variety of factors (see Boucot, 1990), among which the most important are probably the behavioural and taxonomic affinities of the producing organism(s) and the thickness of the host substrate, each of which can be extremely varied. Nevertheless, whether or not complete penetration of the host is achieved cannot be considered a useful ichnotaxobase as it does not reflect the overall morphology of the bioerosional structure that is produced. Furthermore, for example, if *Tremichnus* fully penetrates its host and no growth deformities accompany the penetration (consistent with some examples described by Brett, 1985), then it is impossible to distinguish from *Oichnus*. Likewise, failed or incompletely penetrative borings of *Oichnus* cannot be differentiated from *Tremichnus* in the absence of growth deformities more typically, though not universally, associated with the latter ichnotaxon. With examples such as these, assignment to one or the other of these ichnotaxa would be extremely problematic and highly subjective. This could explain, at least in part, why several recent authors may have been reluctant to assign such material to one or the other of these ichnotaxa (for example, Chatterton & Whitehead, 1987; Rohr, 1991; Baumiller, 1993; Baumiller & Macurda, 1995), despite both having already been established, preferring to retain their specimens in open nomenclature.

Consequently, given these considerations, we herein regard *Tremichnus* as a subjective junior synonym of *Oichnus*. Although beyond the scope of this contribution, *Tremichnus* is considered a candidate for taxonomic reassessment, particularly as one of the significant considerations adopted by Brett (1985) in his distinction of its four ichnospecies was size, which, as discussed by Pickerill (1994), is at best a poor ichnotaxobase. Accordingly, all the small borings and pits documented are herein assigned to one or another of the currently recognised ichnospecies of *Oichnus*.

MATERIAL AND METHODS

New material examined as part of the present study was picked from bulk samples collected from the Bowden shell bed, unit 2 (see Pickerill *et al.*, 1998). Bulk samples (totaling about 25 kg) were collected, dried in an oven and then wet sieved into a series of size fractions. Picking of finer grained samples was undertaken using a binocular microscope. Specimens for scanning electron microscopy (SEM) were mounted on aluminium stubs using double-sided adhesive tape or 'Elmer's' glue. Scanning electron microscopy was undertaken by S.K.D. at the University of Liverpool (Pl. 1, Figs 1-4), under the supervision of Mr C.J.

Veltkamp, and at the University of New Brunswick by Ms S. Belfry (Pl. 1, Figs 5, 6; Pls 2, 3).

SYSTEMATIC ICHNOLOGY

Ichnogenus Oichnus Bromley, 1981

Diagnosis — 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).

Type ichnospecies — *Oichnus simplex* Bromley, 1981, by original designation.

Remarks — As outlined above, we regard *Tremichnus* Brett, 1985, as a junior synonym of *Oichnus* Bromley, 1981, and therefore adopt Bromley's (1981) original, rather than his emended (Bromley, 1993), diagnosis for the ichnotaxon. The ensuing systematic palichnology is based on bored material collected by ourselves, which constitutes 215 molluscan shells that collectively exhibit a total of 302 borings. Ichnospecies are described consecutively with respect to their relative abundance. All material is housed in the collections of the University of New Brunswick.

Oichnus paraboloides Bromley, 1981

Pl. 1, Figs 4-6; Pl. 2, Fig. 1; Pl. 3, Figs 1-7

Description — Smooth or vertically etched, spherical, paraboloid, complete ($n = 146$) or incomplete ($n = 24$) holes that penetrate the molluscan shells more or less perpendicular to their external surfaces. Outer edges typically countersunk and, where penetrative, borings terminate in a central hole of narrower diameter. Countersinking commonly, but not invariably, extends the length of overall penetration. Incomplete penetrations terminate in smooth, convex-upward bases. External countersunk diameters range from 0.2-3.1 mm, with a mean of 0.8 mm, and the majority between 0.5 and 0.7 mm.

Oichnus simplex Bromley, 1981

Pl. 1, Figs 1-3; Pl. 2, Figs 2-4

Description — Simple, smooth or vertically etched, cylindrical to subcylindrical, complete ($n = 64$) or incomplete ($n = 20$) holes with axes more or less perpendicular to substrate and no countersunk outer edges. Completely penetrative examples may or may not possess an essentially horizontal shelf at their inner extremities; the final penetrations through these shelves are round, of reduced diameter in comparison to the initial penetrations and may be centrally or, more typically, slightly eccentrically positioned. Boring diameters range from 0.3-2.8 mm, with a mean of 0.7 mm,

and the majority between 0.4 and 0.7 mm.

Oichnus isp.
Pl. 1, Fig. 6

Description — Circular, sediment-filled where presumably completely penetrative ($n = 12$), or incipiently developed, failed ($n = 36$) holes, with axes more or less perpendicular to substrate. Diameters range from 0.3 to 2.6 mm, with a mean of 0.7 mm and the majority between 0.5 and 0.8 mm. Overall 3-dimensional form is impossible to ascertain.

Remarks — Material documented herein is collectively referred to simply as borings as the size range (maximum diameter) of 0.2-3.1 mm overlaps the currently accepted definitions of microborings (less than 1 mm) or macroborings (greater than 1 mm) (Golubic *et al.*, 1975; Bromley, 1994). Although conichnospecific borings have, as previously noted, been figured in numerous bivalves and gastropods from the Bowden shell bed by Woodring (1925, 1928) and in a scaphopod (*Dentalium* sp.) by Donovan (1990), until now their systematics have remained undescribed. Included within *Oichnus* isp. are examples that cannot confidently be assigned to *O. paraboloides* or *O. simplex* because of (i) the incipient development and hence the extremely shallow depth of the initial penetrations that are obviously failed (for example, Pl. 1, Fig. 6), (ii) as a result of subsequent infill, precluding 3-dimensional observation of the overall form of completely penetrative examples, and (iii) preferential breakage or incomplete preservation at boring sites. However, available evidence does suggest that in such examples assignment to *O. ovalis* Bromley, 1993, can easily be dismissed because an initial round, rather than oval, penetration is clearly in evidence. Absence of countersinking suggests that most, if not all, are probably assignable to *O. simplex*, but this cannot be convincingly demonstrated.

Although size is a poor ichnotaxobase (Pickerill, 1994), and therefore should preferably not be considered in any ichnotaxonomic decisions, we do note that there are two fundamental variations in morphology of completely penetrative *O. paraboloides* and *O. simplex*, as currently defined (Bromley, 1981), in material from the Bowden shell bed. *Oichnus paraboloides* borings possess initial countersunk penetrations that may (Pl. 1, Fig. 4) or may not (Pl. 1, Fig. 6) extend to their distal extremities, and *O. simplex* may (Pl. 1, Fig. 1) or may not (Pl. 1, Fig. 2) possess a flattened distal shelf. Similar variation has been documented by many previous authors (for example, Sohl, 1969; Brett, 1985; Aitken & Risk, 1988; Kabat, 1990), suggesting that it is not uncommon. The 1985 *International Code of Zoological Nomenclature* recognises names proposed for subichnospecific taxa (Ride *et al.*, 1985, Article 45) and we feel that this obvious morphological variation perhaps deserves closer attention ichnotaxonically. After all, names in ichnotaxonomy are merely conventional

symbols or cyphers that serve as a means of reference, and call to mind immediately and unequivocally the concept intended by their transmitters (Pickerill, 1994). Although beyond the intent and scope of this contribution, we therefore suggest that future workers give careful consideration to potential additional nomenclature of these varied morphotypes.

DISCUSSION

Completely penetrative or failed examples of *Oichnus* have been interpreted to result from chemical and/or mechanical bioerosion by predatory gastropods, nematodes, brachiopods and even octopodid cephalopods (Bromley, 1981, 1993) or soft-bodied organisms with specialised organs capable of dissolving calcium carbonate substrates (Chatterton & Whitehead, 1987). Of these various groups, predatory gastropods are favoured by most workers (for example, Chatterton & Whitehead, 1987; Aitken & Risk, 1988; Roy *et al.*, 1994) and, of these, particularly representatives of the families Muricidae and Naticidae produce borings that can readily be assigned to *O. simplex* and *O. paraboloides*, respectively. However, as demonstrated by Bromley (1993), *O. ovalis* was almost undoubtedly produced by octopodids. Combined embedment-boring *Oichnus* have been interpreted as attachment sites by myzostomids (von Graff, 1885), sessile epizoic agglutinated foraminifera (Franzén, 1974) and, perhaps more correctly, sites of parasitic organisms of unknown affinities (Brett, 1985; Eckert, 1988). The parasitic relationship is particularly attractive when growth deformities of the host are present (e.g. Brett, 1985; Eckert, 1988; Donovan, 1991), suggesting, of course, that both the epizoan (or paraendolith; Bromley, 1992) and host were alive during embedment. As was noted by Baumiller (1990) and Baumiller & Macurda (1995), parasitism may also be indicated by the presence of multiple and healed borings, indicating that drilling was not fatal, and the presence of attachment scars implying a long-term association between host and parasite.

Borings identified by us at the ichnospecific rank from the Bowden shell bed can all be regarded as one or the other of *O. paraboloides* or *O. simplex*; despite careful search, we regard *O. ovalis* as decidedly absent. Production by octopodid cephalopods can perhaps therefore easily be dismissed. Furthermore, despite the fact that many borings are incompletely penetrative, none possess associated growth deformities, evidence of healing or attachment scars. This suggests that the borings were not a result of parasitism, but, instead, were produced by either predators or simple excavations made by bioeroders, although not necessarily for predatory purposes. Criteria for the recognition of predatory borings have been summarised by Carriker & Yochelson (1968). These authors, noting that the most common extant predators capable of shell boring were gastropods, suggested that criteria enabling their

recognition as such, at least in modern shells, included circular or subcircular shape, holes drilled perpendicular to shells, presence of no more than one completed hole, host specificity, and location at a site on a shell that was likely to penetrate soft tissue on the interior. In contrast, Baumiller (1993) summarised the evidence for excavations made by bioeroders, and not necessarily predators, as obliquely penetrative holes, multiple holes in a single shell, random distribution of holes on shells, presence of entrance and exit holes, and alignment of holes penetrating adjacent shells. The following section assesses, wherever possible, these various criteria with respect to the borings described herein.

Oichnus is, by definition, circular to subcircular and is produced more or less perpendicular to the shell surface (Bromley, 1981). Of particular significance in assessing borings in the Bowden shell bed is that in virtually all instances where we observed a shell to be completely penetrated, it was only by a single boring even in those examples also possessing associated, but incomplete, penetrations. In only rare examples (two specimens) did we observe two completed penetrations in a single shell, these both being assignable to *O. simplex* (Pl. 1, Fig. 2). Third, as the majority of bivalves in our collections were disarticulated it was easy to determine that, at least in this class, all the failed examples of *Oichnus* were produced externally. The geometry of completely penetrative *O. paraboloides* similarly indicates an external origin. Admittedly, with completely penetrative *O. simplex*, an initial external or internal penetration was impossible to assess. Similarly, as most *Oichnus* borings found in various species of gastropod occur in their apertural regions, and which are not infilled with sediment, an initial external penetration was clearly obvious. Fewer examples present in earlier-formed whorls were essentially infilled with sediment thereby precluding, in several cases, not only a definitive ichnospecific assignment, but also evidence of an initial external or internal penetration. However, on balance, given the available evidence, it is reasonable to suggest that the majority of borings were initiated externally rather than internally and were therefore not simply random excavations made by bioeroders. Fourth, given the fact that Woodring (1925, 1928) identified approximately 600 species of benthic molluscs from the shell bed, of which at least 45 exhibit evidence of boring (Table 1), we are unable to comment on any possible trends regarding host specificity. The considerable number of taxa that exhibit borings possibly suggests that host specificity, at least in this sequence, is not an important consideration and that boring was opportunistic. However, although potentially an avenue for further investigation, this particular aspect is well beyond the scope of this contribution. Nevertheless, it is clear that at least in several species in our collections, where adequate numbers were available, that the borings are site specific and obviously not randomly developed. For example, this is clearly demonstrated in the two gastropod species *Natica* (*N.*) *castrenoides* Woodring and *Acteocina* *lepta* Woodring (Pl. 3). In *A. lepta* (Pl. 3, Figs 1-3), *O. paraboloides* occurs in

the last whorl and to the left of the aperture at sites therefore most likely to penetrate soft tissue even when the prey was fully or even partially retracted into its shell (compare with Rohr, 1991). In *N. (N.) castrenoides* (Pl. 3, Figs 4-7), *O. paraboloides* is located immediately below and generally slightly to the right of the final whorl below the aperture. Interestingly, we have observed many additional specimens of *Acteocina* *lepta* that were clearly broken in this region, but do not possess *Oichnus* elsewhere on the shell. This may suggest, parallelling the observations of Roy *et al.* (1994), that such damaged shells may well have been initially bored at similar locations, but that subsequent breakage preferentially occurred at these sites, thereby precluding any unequivocal evidence of boring activity. Other molluscs also exhibit evidence of incipient breakage, and fracturing in such shells typically occurs in association with the borings (Pl. 2, Figs 2-4; Pl. 3, Fig. 1).

In summary, therefore, we believe that *Oichnus* in molluscs of the Bowden shell bed were not a result of parasitism nor random excavations by bioeroders; rather, the above observations suggest they are essentially the result of predatory activities. Interestingly, in this context, it is perhaps notable that none of the four terrestrial gastropod species (*Lucidella costata* Simpson, *Incerticyclus bakeri* (Simpson), *Pleurodonte bowdeniana* Simpson and *P. bernaldi* Kimball) confidently assignable to the Bowden shell bed by Goodfriend (1993) exhibit evidence of boring activity. Presumably, soft tissue in these species had decayed prior to or soon after their introduction into the marine environment so that boring for predatory purposes would have been obviated. The absence of borings in these terrestrial species also lends further support that *Oichnus* in molluscs of the Bowden shell bed were not simply random excavations by bioeroders. If our interpretation as predatory activities is correct, what then is the nature and affinities of the producing organisms? As previously outlined, and discussed by Bromley (1981), a variety of taxa are capable of producing borings similar to *Oichnus*, though most authors would agree that in latest Cretaceous and younger strata *O. simplex* and *O. paraboloides* are almost universally produced by muricid and naticid gastropods respectively (Aitken & Risk, 1988; Kabat, 1990). Indeed, undoubtedly drilling naticids are known to reach high abundances, and even dominate, in several Cretaceous and Cenozoic molluscan-dominated associations (Fürsich & Jablonski, 1984) similar to those of the Bowden shell bed, undoubtedly a reflection of their diversification (along with muricids) in the late Mesozoic and early Cenozoic (Sohl, 1969; Baumiller & Macurda, 1995). Although representatives of several other Cenozoic and present-day gastropods are capable of boring activities, their fossil record is extremely poor and either too little is known with respect to even their present-day boring habits or, alternatively, their resultant excavations clearly differ morphologically from *Oichnus*. For example, the three families of mesogastropod tonnaceans known to be capable of boring, the Cymatiidae, Tonnidae and Cassidae, are only rarely preserved in the

fossil record (Sohl, 1969) and only the borings of cassids are reasonably documented (Bromley, 1981). The latter are approximately circular in cross-section, but possess jagged and irregular edges (Hughes & Hughes, 1971) that obviously contrast with the smooth margins of *Oichnus*. Similarly, although capulid mesogastropod borings have been described (for example, Orr, 1962; Matsukama, 1978), they are oval or tear-shaped in cross-section. The final group of boring gastropods, the pulmonate oleacinids and zonitids, are known only to rasp irregular-shaped holes and little has been described with respect to their boring habits (Bromley, 1981).

Predatory gastropods possess chemo-receptive mechanisms for detecting and locating prey, which, once subdued, are then cannibalised essentially by chemical (acid secretion) methods. Naticids typically produce boreholes that are site selective (Carriker, 1981; Kabat, 1990) and parabolic in cross-section with countersunk outer edges and a centred, round inner opening (Bishop, 1975; Chatterton & Whitehead, 1987; Savazzi & Reymont, 1989; Kabat, 1990), features typical of *O. paraboloides*. In contrast, site selection in muricids is less clearly understood, but appears to be at random on prey valves following an extended period of exploration of the shell surface (Carriker, 1981). Their resultant borings are cylindrical in cross-section, are not countersunk and commonly have a shelf at their inner edge (Bishop, 1975), features consistent with *O. simplex*. These observations are also consistent with *O. paraboloides* and *O. simplex* documented by us from molluscs in the Bowden shell bed. We therefore conclude, though admittedly on somewhat circumstantial evidence, that these borings were produced by unknown naticid and muricid gastropods, respectively.

SUMMARY AND CONCLUSIONS

Of the approximately 600 species of benthic molluscs described by Woodring (1925, 1928) from the Bowden shell bed, at least 45 exhibit clear evidence of bioerosion in the form of completely or incompletely penetrative (failed) small round borings. These borings, supplemented by additional examples collected by us, are all assignable to one or another of the various ichnospecies of *Oichnus* Bromley, herein considered a senior synonym of *Tremichnus* Brett. *Oichnus paraboloides* is the most common ichnospecies, *O. simplex* is also well represented and *O. ovalis* is decidedly absent. Fifteen species of bivalves and 30 species of gastropods are bored (Table 1), suggesting that host specificity was not an important consideration with respect to prey selection of the overall molluscan assemblages. Observations suggest that *Oichnus* borings were not a result of parasitism nor simple random excavations by bioeroding organisms. Rather, functionally the borings are best interpreted as a consequence of predation by carnivorous, opportunistic organisms (Woodring, 1928). Of the various organisms capable of producing *Oichnus*, as

reviewed by Bromley (1981, 1993), predatory gastropods are considered to have been the most likely culprits. Although somewhat circumstantial, comparison with both extant and previously reported fossilised examples of *O. paraboloides* and *O. simplex* suggests production by naticid and muricid gastropods, respectively, both families being well represented in the Bowden shell bed.

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Table 1. Bored molluscs of the Bowden shell bed, Bowden Formation, southeast Jamaica, illustrated by Woodring (1925, 1928). Borings are *Oichnus* isp. unless indicated otherwise. Key: * = *Oichnus paraboloides* Bromley, 1981; ** = possibly irregularly punctured; + = although no bored scaphopods were figured by Woodring, Donovan (1990, fig. 4J) illustrated a bored *Dentalium* sp.; ¹ = an associated figure shows the interior of this valve, but it does not appear to be perforated (= unsuccessful boring?); ² = possibly broken rather than bored; ³ = Woodring (1928, pl. 26, fig. 8) illustrated a specimen of this species that has a slot in the shell that may be due to annelid predation (or mechanical breakage); ⁴ = specimen appears to have broken in region of boring. Note that the molluscan taxonomic assignments of Woodring have not been revised. Shadows on the insides of some shells undoubtedly mask borings; figures that show an internal view of a bivalve shell are quoted in parentheses.

Class BIVALVIA (see Woodring, 1925)

Family LEDIDAE		
	<i>Leda subcerata</i> Woodring *	Pl. 1, fig. 8
	<i>Leda clara</i> Guppy *	Pl. 1, figs. 18, (19)
Family ARCIDAE		
	<i>Glycymeris prepennacea</i> Woodring	Pl. 2, figs. 6, (7)
	<i>Barbatia islopa</i> Woodring	Pl. 3, figs. 7, (8)
Family OSTREIDAE		
	<i>Ostrea folioides</i> Woodring	Pl. 7, figs. 3, (4)
Family CRASSATELLITIDAE		
	<i>Crassatellites jamaicensis</i> Dall	Pl. 11, fig. 12 ¹
Family LUCINIDAE		
	<i>Codakia vendryesi</i> Dall	Pl. 14, figs (3, 4)
	<i>Lucina bowdenensis</i> Woodring	Pl. 14, fig. 8
	<i>Myraea pertenera</i> (Dall) *	Pl. 14, fig. 15 ¹
	<i>Phacooides podagrinus</i> Dall	Pl. 15, figs. 8, 12
	<i>Phacooides actinus</i> Dall	Pl. 17, figs (6, 8)
	<i>Divaricella prevaricata</i> Guppy *	Pl. 17, fig. 12
Family CARDIIDAE		
	<i>Cardium thauastum</i> Woodring **	Pl. 19, figs. 12H, (13H)
Family VENERIDAE		
	<i>Calloocardia elethusa</i> Woodring	Pl. 20, fig. 13
Family TELLINIDAE		
	<i>Tellina hendersoni</i> Dall *	Pl. 23, fig. 4

Class SCAPHOPODA (see Woodring, 1925)

None +

Class GASTROPODA (see Woodring, 1928)

Family ACTEONIDAE		
	<i>Acteon eurystoma</i> Woodring *	Pl. 2, fig. 2
Family ACTEOCINIDAE		
	<i>Acteocina lepta</i> Woodring *	Pl. 2, fig. 5H
Family TEREBRIDAE		
	<i>Terebra bowdenensis</i> Woodring *	Pl. 3, fig. 8
	<i>Terebra monida</i> Woodring	Pl. 3, fig. 17H
	<i>Terebra ischna</i> Woodring	Pl. 3, fig. 18
Family TURRIDAE		
	<i>Crassispira aegis</i> Woodring	Pl. 4, fig. 12
	<i>Compsodrilla urceola</i> Woodring	Pl. 5, fig. 1
	<i>Compsodrilla senaria</i> Woodring	Pl. 5, fig. 4
	<i>Syntomodrilla espyra</i> Woodring	Pl. 5, figs. 11, 12
	<i>Ithycythara psilooides</i> Woodring	Pl. 6, fig. 7
	<i>Bactrocythara obtusa</i> (Guppy)	Pl. 6, figs. 15, *, 16
	<i>Brachycythara</i> sp.	Pl. 7, fig. 1
	<i>Vaughanites leptus</i> Woodring *	Pl. 9, fig. 1
Family CONIDAE		
	<i>Conus multiliratus</i> Böse *	Pl. 11, fig. 3
Family CANCELLARIIDAE		
	<i>Cancellaria barretti</i> Guppy **	Pl. 12, fig. 6
	" <i>Cancellaria</i> " sp. **	Pl. 13, fig. 2
Family XANCIDAE		
	<i>Xancus textilis</i> (Guppy) ²	Pl. 15, fig. 3
Family FASCIOLARIIDAE		
	<i>Fusinus engonius</i> Woodring	Pl. 15, fig. 9
Family PYRENIDAE		
	<i>Columbella platymema</i> Woodring	Pl. 16, fig. 10
Family MURICIDAE		
	" <i>Muricopsis</i> " <i>collatus</i> (Guppy) *	Pl. 17, fig. 11
Family CERITHIIDAE		
	<i>Bittium praeformatum</i> Guppy ³	Pl. 25, fig. 10
Family TURRITELLIDAE		
	<i>Turritella guppyi</i> Cossmann	Pl. 26, fig. 9 ⁴
Family RISSOINIDAE		
	<i>Rissoina guppyi</i> Cossman *?	Pl. 28, fig. 10
Family HIPPONICIDAE		
	<i>Hipponix ceras</i> Woodring	Pl. 29, figs 10, 11, 13
Family NATICIDAE		
	<i>Stigmulae vererugosum</i> (Cossman) *?	Pl. 30, fig. 10
	<i>Tectonatica pusilla</i> (Say) *?	Pl. 30, fig. 12
Family OPALINAE		
	" <i>Plicicula</i> " <i>dasystoma</i> Woodring *?	Pl. 32, fig. 6
Family TURBINIDAE		
	<i>Astrea sublongispina</i> (Maury)	Pl. 33, fig. 2
Family TROCHIDAE		
	" <i>Circulus</i> " <i>bicarinatus</i> (Guppy) *	Pl. 37, fig. 12
	<i>Episcynia naso</i> (Pilsbry and Johnson)	Pl. 37, fig. 20

PLATE 1

Scanning electron micrographs of small borings in molluscs of the Bowden shell bed, Bowden Formation, southeast Jamaica, illustrating variation in morphology of *O. paraboloides* and *O. simplex*. All specimens coated with 60% gold-palladium.

- Fig. 1. Completely penetrative *O. simplex* in the bivalve *Crassitellites* sp., x 23.
- Fig. 2. Two completely penetrative *O. simplex* both with a basal horizontal yet penetrated shelf at their inner extremity, in the bivalve *Crassitellites* sp., x 22. Note also the two failed borings of *O. simplex* proximal to the umbonal region.
- Fig. 3. Incompletely penetrative (failed) borings of *O. simplex* in the bivalve *Crassitellites* sp., x 22.
- Fig. 4. Completely penetrative *O. paraboloides* in the bivalve *Barbatia* sp., x 17.
- Fig. 5. Incompletely penetrative *O. paraboloides* in the bivalve *Crassitellites* sp., x 22.
- Fig. 6. Incompletely penetrative *O. paraboloides* and *Oichnus* isp. (arrowed) in the bivalve *Crassitellites* sp., x 22.

PLATE 1

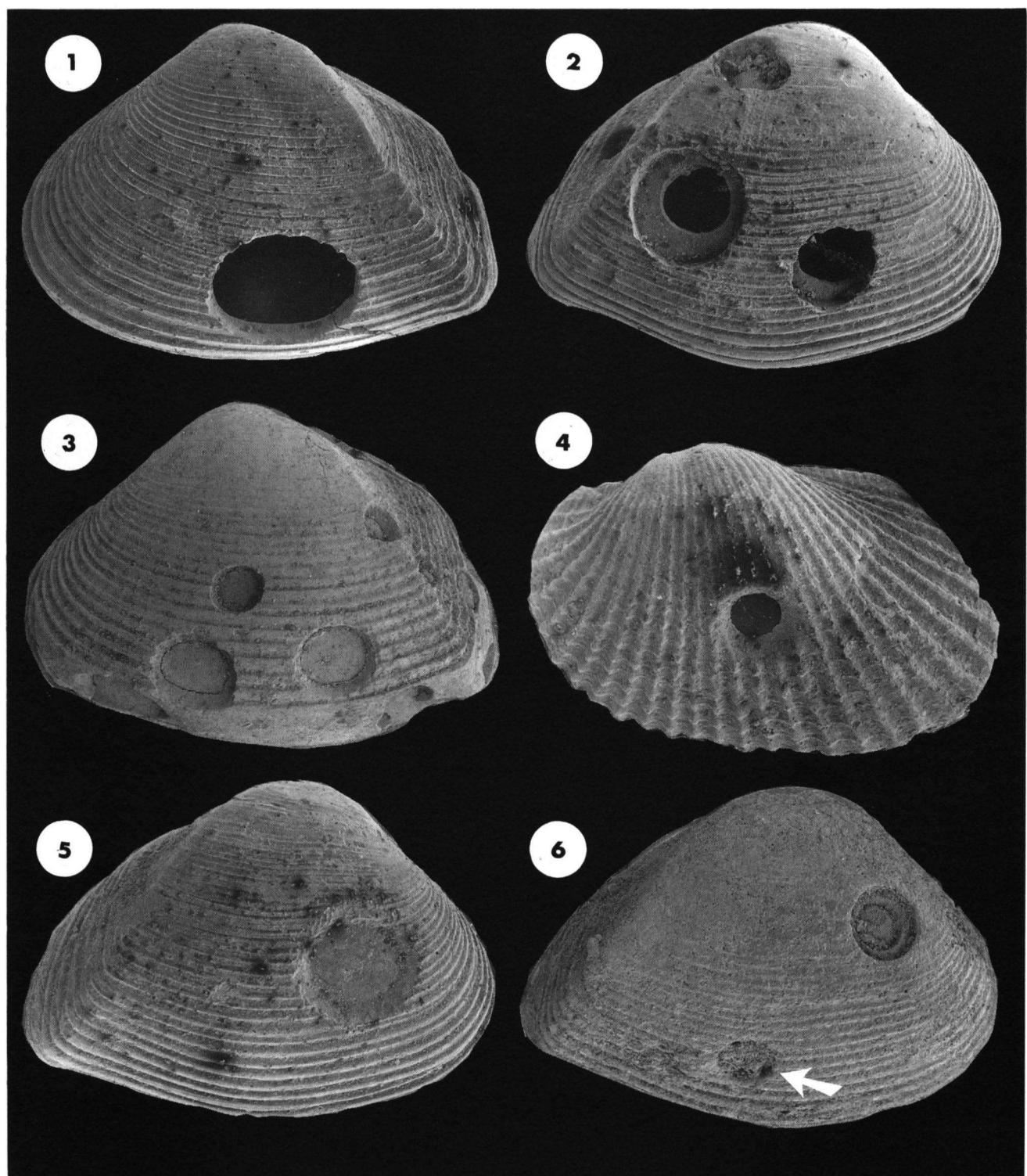


PLATE 2

Scanning electron micrographs of small borings in molluscs of the Bowden shell bed, Bowden Formation, southeast Jamaica. All specimens coated with 60% gold-palladium.

Fig. 1. Completely penetrative *O. paraboloides* in the gastropod *Acteocina lepta* Woodring, x 30. Note the vertical etching pattern on the countersunk penetration.

Figs 2-4. *Oichnus simplex* in the bivalves *Chione* cf. *sawkinsi* (2) and *Crassitellites* sp. (3,4) illustrating incipient fracturing associated with the borings, x 17 (2), x 18 (3) and x 22 (4).

PLATE 2

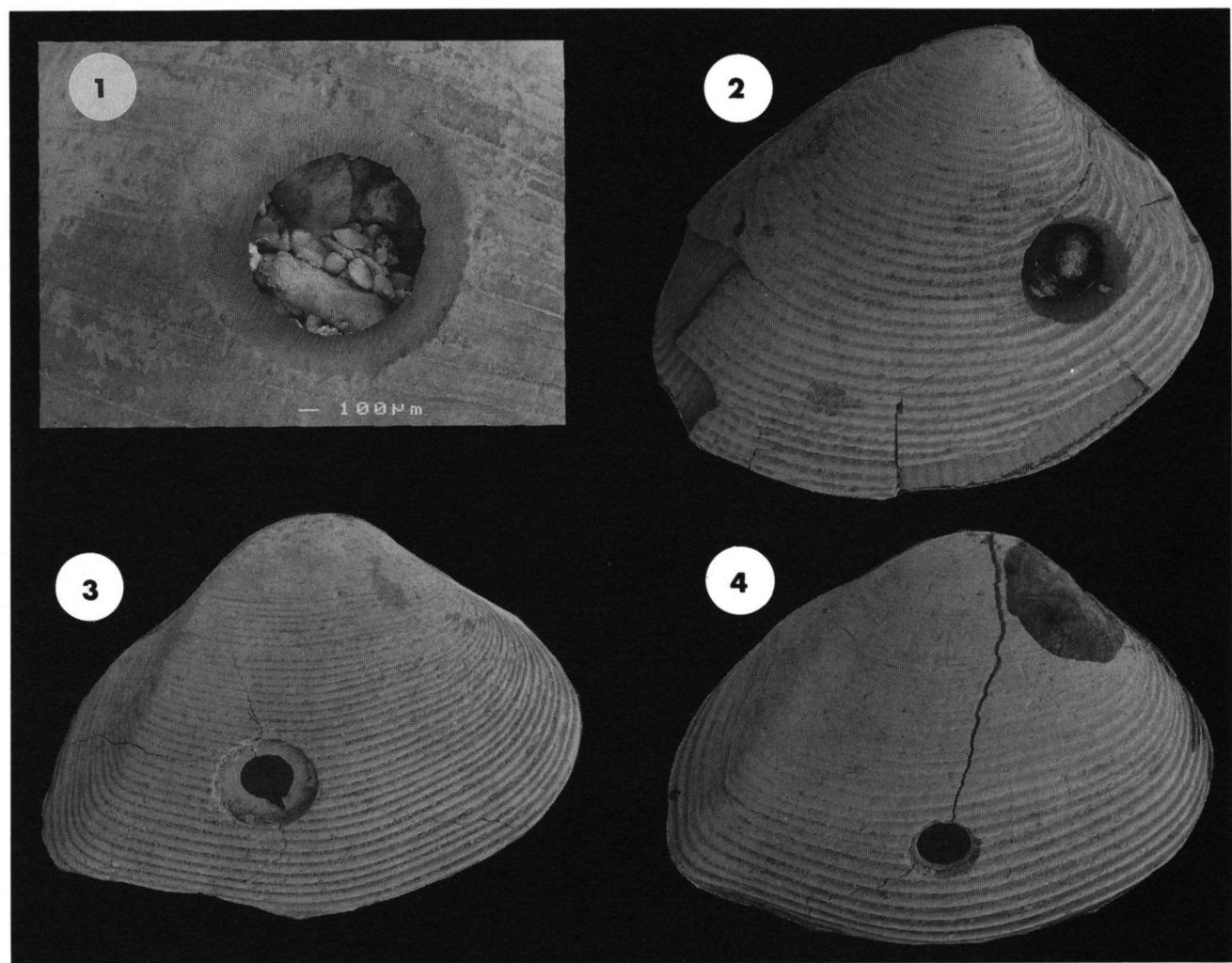


PLATE 3

Scanning electron micrographs of examples of site specificity of *O. paraboloides* in the gastropods *Acteocina lepta* Woodring (Figs 1-3) and *Natica castrenoides* Woodring (Figs 4-7) from the Bowden shell bed, Bowden Formation, southeast Jamaica. All specimens coated with 60% gold-palladium.

Figs 1-3. *Oichnus paraboloides* in *Acteocina lepta*, x 25 (1), x 22 (2) and x 19 (3). Note shell fracturing and resultant breakage immediately to the left of *O. paraboloides* in 1.

Figs 4-7. *Oichnus paraboloides* in *Natica castrenoides*, x 9 (4), x 7 (5), x 9 (6) and x 8 (7). Note that other examples of *O. paraboloides* in *A. lepta* (n = 9) (see also Woodring, 1928, pl. 2, fig. 5) and *N. castrenoides* (n = 6) are located at almost identical sites.

PLATE 3

