

Ichnology of the Late Pleistocene Port Morant Formation of Southeastern Jamaica

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ABSTRACT.—Late Pleistocene lagoonal siliciclastic strata (approximately 10 m thick) of the Port Morant Formation, exposed on the southeastern side and east of Port Morant Harbour, southeast coastal Jamaica, contain a relatively abundant and moderately diverse ichnofauna that is described herein in detail. The sequence contains soft-sediment ichnotaxa (*Ophiomorpha nodosa* Lundgren, 1891; *Palaeophycus tubularis* Hall, 1847; *Thalassinoides paradoxicus* (Woodward, 1830)) and those formed as a consequence of bioerosion (*Caulostrepis* cf. *contorta* Bromley and D'Alessandro, 1983, *C. cretacea* (Voight, 1971), *C. taeniola* Clarke, 1908; *Clionoides thomasi* Fenton and Fenton, 1932; *Entobia ovula* Bromley and D'Alessandro, 1984, *Entobia* isp. or ispp.; *Gastrochaenolites* cf. *cluniformis* Kelly and Bromley, 1984, *G.* cf. *torpedo* Kelly and Bromley, 1984; *Meandropolydora* cf. *sulcans* Voight, 1965; *Oichnus paraboloides* Bromley, 1981, *O. simplex* Bromley, 1981). Only *P. tubularis*, *O. paraboloides* and *O. simplex* have previously been described from the Jamaican rock record; the remainder are therefore formally documented for the first time. The sequence can be subdivided into three units. In ascending stratigraphic order, unit 1 comprises an erosionally-based boulder conglomerate, and units 2 and 3 of clay-rich, calcareous, fine- to coarse-grained sandstones. Small scleractinian coral patch reefs and isolated heads occur at the base of unit 2, and laterally discontinuous (southwards) pebble conglomerates are present at the base of unit 3. Soft-sediment ichnotaxa occur in units 2 and 3, whereas bioerosional ichnotaxa occur in association with unit 1, the patch reefs of unit 2, and two abundantly fossiliferous horizons near the top of unit 3.

INTRODUCTION

Despite the long history of paleontological research in Jamaica (see Wright and Robinson, 1993), it is only since the early 1990s that systematic trace fossil studies of note have been undertaken (see, for example, Pickerill and Donovan, 1991, 1998; Pickerill et al., 1992, 1993a, 1993b, 1993c, 1996). This is unfortunate because many Jamaican sedimentary rock sequences display well-preserved and variably diverse ichnofaunal assemblages. The main purpose of this contribution is to record and systematically describe ichnotaxa that occur in one such sequence, namely the late Pleistocene Port Morant Formation. In so doing, this paper will formally document, for the first time from Jamaica, many previously unrecorded ichnotaxa. Additionally it will add to a much-needed ichnological database for Pleistocene strata in the Caribbean as a whole.

Most figured collectible material is repositied in the New Brunswick Museum, Saint John, New Brunswick (prefixed NBMG) or the Geology Museum, University of the West Indies, Mona (prefixed UWIGM).

LOCATION AND GEOLOGICAL SETTING

The late Pleistocene (last interglacial; Sangamonian?) Port Morant Formation, Upper Coastal Group, crops out in clifflines and roadside exposures surrounding and immediately to the southeast of Port Morant Harbour, southeast coastal Jamaica (Fig. 1). Where its basal contact is exposed south of Pera Point (Fig. 1), it erosionally overlies the early Pleistocene Old Pera Beds of the Manchioneal Formation. This location, the stratotype, also exhibits, in steep to essentially vertical cliffs, the most complete and continuously exposed vertical section of the formation, comprising approximately 10 m of horizontally bedded

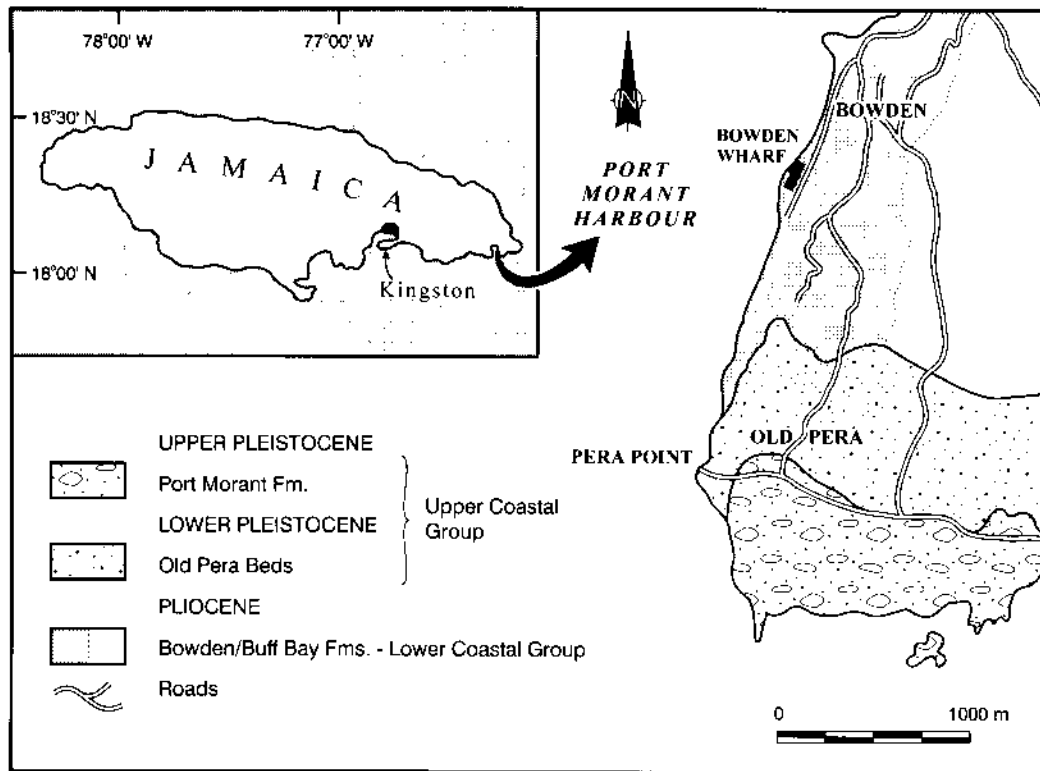


FIG. 1. Location and simplified geological map of the eastern side of Port Morant Harbour, southeast coastal Jamaica.

or gently (<5°) southward-dipping strata (Fig. 2a). Elsewhere in the area exposures of the sequence are sporadic and discontinuous, and are of a contrasting lithofacies (see below). Donovan et al. (1994) and Collins et al. (1997) informally divided the strata from the stratotype into three units and this simplified division is followed herein. These units are referred to, from base to top, as units 1-3. It is from these exposures that all ichnological observations were made.

Unit 1 comprises an erosionally-based, massive boulder conglomerate horizon (Fig. 2a, b), laterally variable in thickness but up to 1 m or slightly more. The lower horizons of this conglomerate consist of large and irregular platy slabs of sandstone lithologically identical to the underlying Old Pera Beds and which appear to be virtually in situ. Overlying cobbles and boulders comprise similar sandstones, but are obviously more rounded and reworked, accompanied by sporadic reworked coral boulders and

volcanic clasts. Additional faunas in the conglomerate include echinoid tests and radioles (Donovan et al., 1994). Where exposed, the top of unit 1 appears to be bound by veneers or extremely thin layers of crustose corallian algae.

Unit 2, approximately 3 m thick, comprises soft and friable, beige to tan, fine- to medium-grained, clay-rich, calcareous sandstones. The unit is highly bioturbated and differential cementation has particularly emphasized large burrow systems of *Thalassinoides* and *Ophiomorpha* (Fig. 2c, d). As a result of intense weathering of the generally poorly-cemented sandstones, primary bedforms are difficult to discern; where observed, horizontal laminations or thinly layered mudstone-rich and fine-grained sandstone-rich alternations predominate. Of particular interest is the development of sporadically distributed in situ scleractinian coral colonies, some attaining heights of 2 m, that extend verti-

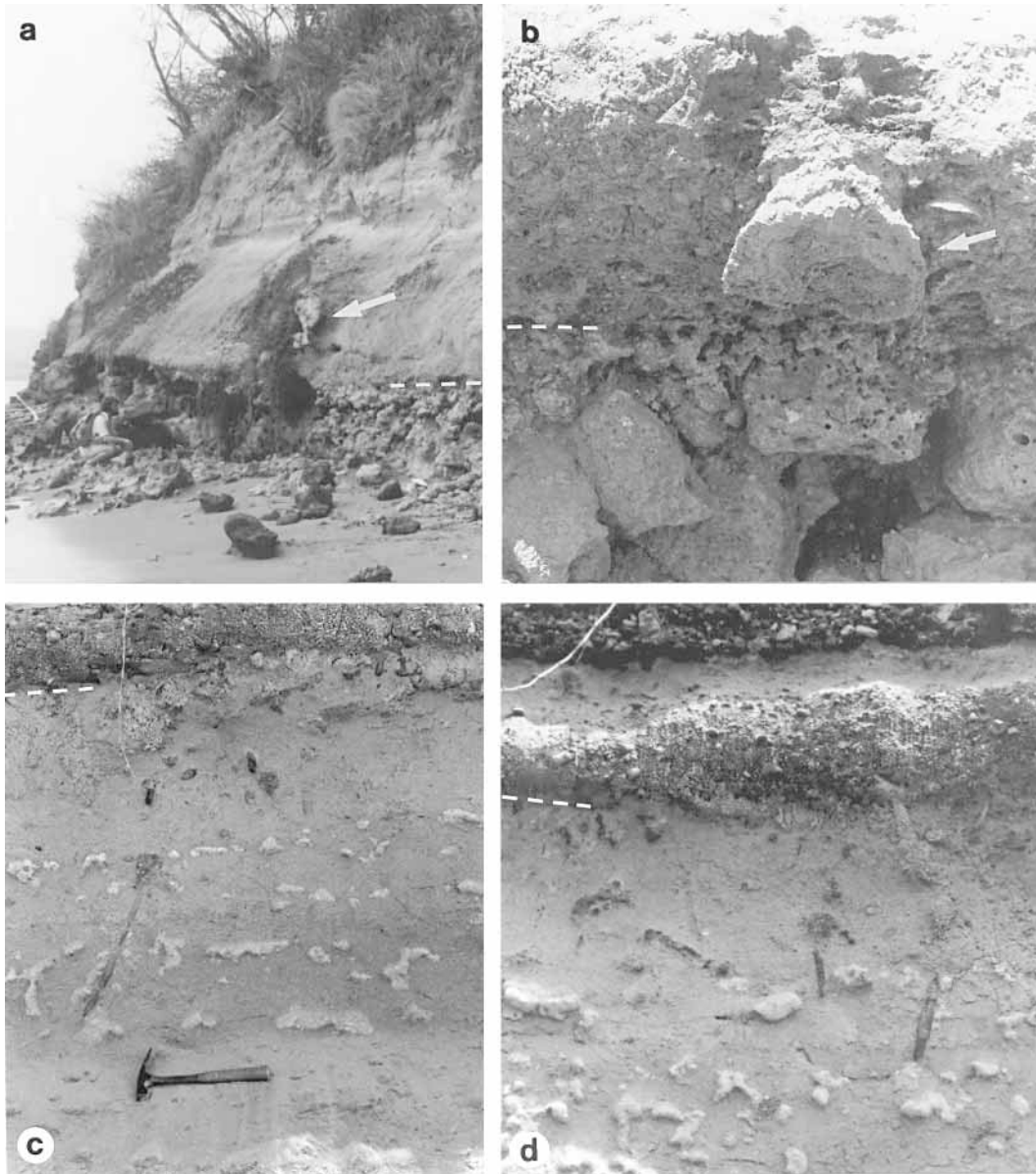


FIG. 2. a, b. Contact between boulder conglomerates of unit 1 and calcareous sandstones of unit 2 (lined) just south of Pera Point. Note the large in situ coral colonies (arrowed) developed from the top surface of unit 1. Figure (lower left) for scale in a; horizontal field of view in b is approximately 1.5 m. c, d. Contact between calcareous sandstones of unit 2 and erosive pebble conglomerate layers at the base of unit 3 (lined). Note the extensive development of *Ophiomorpha nodosa* Lundgren (black colored) and particularly *Thalassinoides paradoxicus* (pale colored). Hammer in c is 28 cm long and horizontal field of view in d is approximately 2 m.

cally from their primary attachment surfaces at the top of unit 1 (Fig. 2a, b). Otherwise, macrofaunas are extremely rare.

Unit 3 is approximately 6 m thick, its lower contact being arbitrarily placed

where there is an influx of erosionally-based, cross-bedded pebble conglomerate layers and interbedded, bioturbated, pebbly sandstones (Fig. 2c, d). The former layers are, however, laterally discontinuous,

generally thinning and disappearing southwards to be substituted entirely by muddy, calcareous, beige to tan, bioturbated fine- to coarse-grained, calcareous sandstones that in places are very fossiliferous. The sandstones are poorly bedded, variably cemented both vertically and laterally, and contain a generally high proportion of volcanic detritus including scattered pebbles up to 60 mm in diameter. In contrast to unit 2 these strata contain an abundant and diverse shelly fauna dominated by molluscs, but also including echinoids (Donovan et al., 1994), crustaceans (Collins et al., 1997) and even very rare fish teeth (Purdy et al., 1996). These faunas are particularly common at two locations toward the top of unit 3 on both sides immediately on the landward side of the elongate peninsula to the extreme south of Pera Point (Fig. 1).

SYSTEMATIC PALICHTHOLOGY

1. *Soft-sediment ichnotaxa*

Soft-sediment ichnotaxa are ethologic structures produced on or within substrates that are unlithified. They can be clearly differentiated from bioerosional ichnotaxa (see Ekdale et al., 1984) and, as both categories clearly form integral components of the Port Morant Formation ichnocoenose, are herein differentiated as such. Following conventional procedures (for example, Häntzschel, 1975), ichnotaxa in each category are described alphabetically.

Ichnogenus *Ophiomorpha* Lundgren, 1891
Ophiomorpha nodosa Lundgren, 1891
 (Figs. 2a, b; 3a)

Description.—Several tens of variably but generally poorly-preserved specimens in unit 2, particularly towards its upper horizons (Fig. 2d), and typically exposed in vertical section only. Each comprises a vertical to steeply inclined sediment-filled tube that has a wall lined with agglutinated pelletoidal sediment that effects an external nodose appearance (Fig. 3a). The pellets are 4-7 mm in diameter, ovoid and densely packed. Burrow fill is typically coarser in grain size than the host strata and is structureless. Individual burrows are invariably apparently unbranched, very rarely

branched; where branched, bifurcations are Y-shaped and slightly enlarged. Diameters range from 10 - 50 mm and commonly vary within a single shaft, though in several examples the diameter is relatively constant. Length is variable, up to 350 mm, commonly less than 200 mm.

Discussion.—The horizontal and vertical branching, agglutinated pelletoidal, crustacean-produced burrows of *Ophiomorpha*, its synonyms and ichnospecies have been discussed by Frey et al. (1978) and Uchman (1995). Distinction of its various valid ichnospecies, *O. annulata* Książkiewicz, *O. borneensis* Keij, *O. irregulair*e Frey, Howard and Pryor and *O. nodosa* Lundgren, is based on the nature and disposition of the pelletoidal material constituting the walls, rather than overall burrow configuration (see Frey et al., 1978; Howard and Frey, 1984; Uchman, 1995). In this context the Port Morant specimens most closely resemble *O. nodosa*, itself characterized by dense, regularly to irregularly distributed, discoid, ovoid or polygonal pellets. In contrast, *O. annulata* possesses elongate pellets arranged perpendicular to the long axis of the burrow, *O. borneensis* has regularly distributed but bilobate pellets, and in *O. irregulair*e the pellets are only sparsely developed but sporadically may form pelletal masses (see Frey et al., 1978; Frey and Howard, 1990).

In 1992 specimens of *O. nodosa* were relatively common in unit 2. Bulldozing activities in 1993 regrettably removed many of the better-preserved examples and most are now largely inaccessible, generally occurring towards the top of the unit in steep cliffs (Fig. 2c, d). Their presence there can be indicated by their relatively darker color (in comparison to *Thalassinoides paradoxicus*) (Fig. 2c, d). This darker coloration is presumably a consequence of weathering of the walls, which contain an increased proportion of clay minerals, iron oxides and sulphides, and is a characteristic of the ichnotaxon (Frey et al., 1978).

This is the first formal record of *O. nodosa* in the Jamaican rock record. Notably, Howard and Frey (1984) observed that sparsely branched vertical components of the ichnospecies predominated in near-shore, higher-energy environments, whereas densely branched horizontal com-

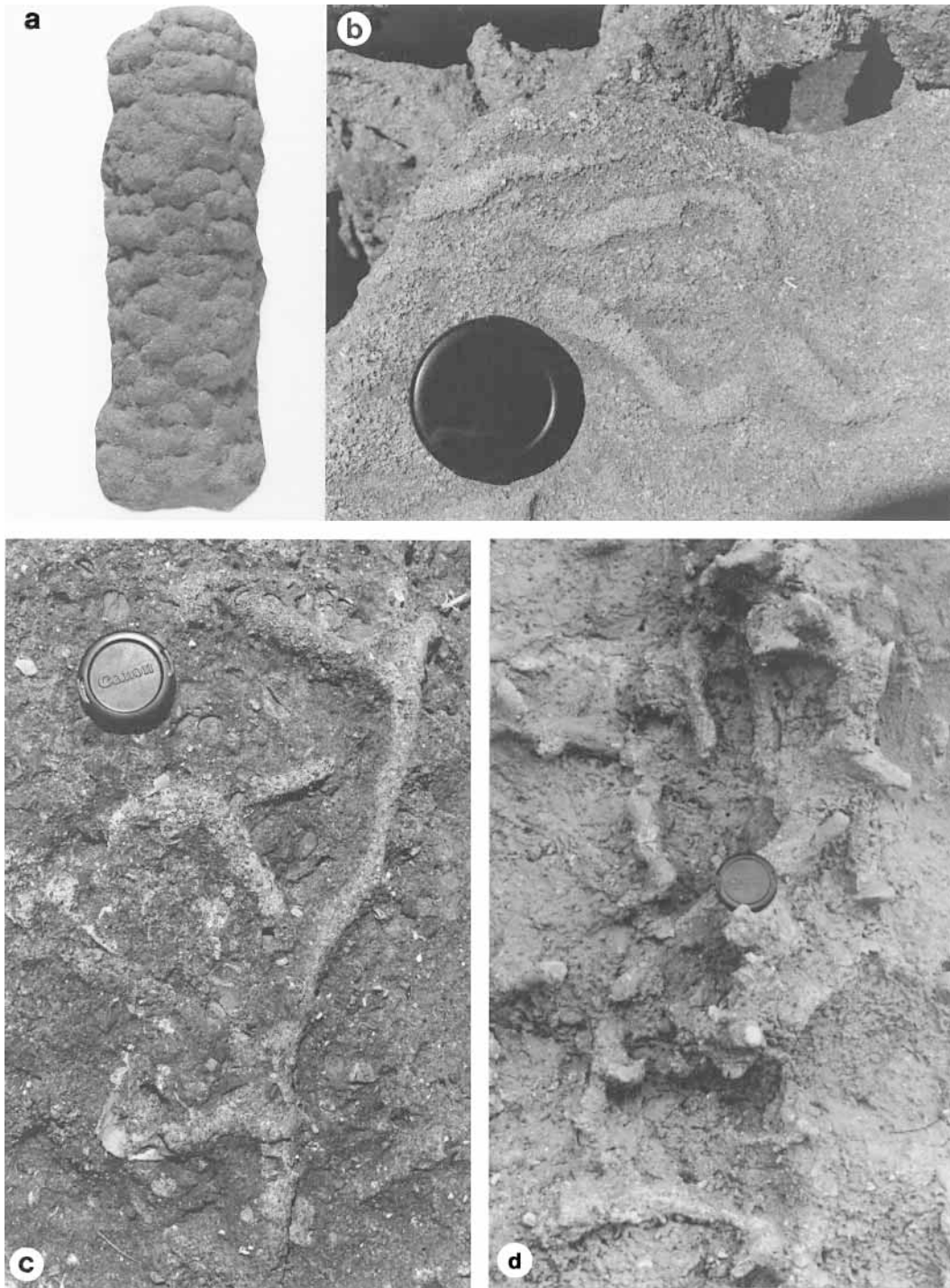


FIG. 3. a. *Ophiomorpha nodosa* Lundgren from unit 2, $\times 1$. b. *Palaeophycus tubularis* Hall from unit 3. c, d. *Thalassinoides paradoxicus* (Woodward) from unit 3; c is on a bedding plane surface and d is in vertical section. Lens hood is 55 mm in diameter; specimens b - d uncollectible.

ponents were commonplace in offshore, low-energy settings.

Ichnogenus *Palaeophycus* Hall, 1847
Palaeophycus tubularis Hall, 1847
(Fig. 3b)

Description.—Four examples, preserved in positive hyporelief on the sole of an uncollectible block of sandstone from unit 3. Specimens comprise simple, horizontal, curved to slightly sinuous burrows, each 12–14 mm in diameter and up to 110 mm in length. Burrows are unbranched; burrow fill is of the same grain size as the enclosing sediment and massive. Burrow margins possess a thin unsculptured mudstone lining.

Discussion.—The presence of a thin, albeit poorly-preserved, unsculptured lining readily permits assignment of these simple internally unstructured burrows to *P. tubularis*. The other common ichnospecies, *P. sulcatus* (Miller and Dyer), *P. alternatus* Pemberton and Frey and *P. striatus* Hall possess linings that are sculptured, while *P. heberti* Saporta is characterized by an unornamented margin but is thickly lined (see Pemberton and Frey, 1982). The thin linings on *P. tubularis* weather away rapidly on exposure and, as in several of the examples herein, are commonly not preserved (compare with Howard and Frey, 1984). Because in much of the sequence the outcrop is in steep to vertical cliffs, the ichnotaxon may be more common than it appears, having potentially been misidentified by us as isolated segments of *Thalassinoides paradoxicus* burrows.

Palaeophycus represents passive sedimentation within an open dwelling burrow constructed by predaceous or suspension-feeding organisms, predominantly annelids (Pemberton and Frey, 1982). *Palaeophycus tubularis* was recorded from the Jamaican rock record by Pickerill and Donovan (1991).

Ichnogenus *Thalassinoides* Ehrenberg, 1944
Thalassinoides paradoxicus (Woodward, 1830)
(Figs. 2c, d; 3c, d)

Description.—Numerous examples from units 2 and 3 of variably preserved, sparse to densely branched, variably oriented, burrow systems. Preservation is mostly in

vertical section as incomplete and only sporadically exposed burrow segments (Fig. 2c, d), more rarely as extensively developed 3-dimensional boxwork burrow systems (Fig. 3d), and rarely as partial systems on bedding plane surfaces (Fig. 3c). An individual system comprises an interwoven mosaic of sinuous to straight, branched burrows typically of variable diameter; the latter usually varies from about 1 cm to more than 3 cm. Branching patterns are very irregular, with many branches terminating, apparently blindly, after relatively short distances. Branch junctions are both Y- and T-shaped, the former generally being more common; burrow diameters are normally enlarged at points of bifurcation, and bulbous enlargements may occur in unbranched burrow segments. Burrow cross-sections, where observable, are broadly circular; margins are smooth and unstructured. Burrow fill is variable and may be coarser, finer or of the same grain size as the host material; internally, where a fill is viewable it is structureless.

Discussion.—The numerous reports of the open-framework, branching burrow systems of *Thalassinoides* are testimony to its abundance in many rock sequences, particularly of Mesozoic and younger age, throughout the world. In modern environments, similar structures are produced by marine organisms that include cerianthis anenomes, balanoglossan enteropneusts, and fish (Myrow, 1995), but most importantly by decapod crustaceans, primarily thalassinoid shrimps, such as callianassids (Bromley, 1996). Systematics of the ichnogenus are complex and have been debated by several authors (e.g., Kennedy, 1967; Fürsich, 1973; Bromley and Frey, 1974). Myrow (1995) discussed the four commonly occurring ichnospecies, namely *T. saxonicus* (Geinitz), *T. ornatus* (Kennedy) *T. paradoxicus* (Woodward) and *T. suevicus* (Rieth), and formulated a fifth, *T. horizontalis* Myrow. The remaining ichnospecies of *Thalassinoides*, and not discussed by Myrow (1995), namely *T. tandoni* Badve and Ghare, *T. minimus* Aron and *T. foedus* Mikulás, are not worthy of ichnospecific distinction (Keighley and Pickerill, 1997).

The Port Morant material, particularly where preservation is reasonably good

(Fig. 3c, d), exhibits all the main characteristics of *T. paradoxicus* as outlined in Kennedy (1967), Howard and Frey (1984) and Frey and Bromley (1985), and is therefore regarded as conichnospecific. Such definitive parameters collectively include: (i) the irregular development of extensive 3-dimensional boxwork burrow systems; (ii) the presence of sinuous and straight burrow segments that branch randomly from adjacent segments, with the successive branches typically of variable and inconsistent diameter; (iii) the existence of many such branches that apparently terminate after relatively short distances; and (iv) the presence of characteristically enlarged Y- and T-shaped bifurcations. In less well-preserved material, particularly that observed essentially only in vertical section (for example, Fig. 2d), other ichnospecies are potentially present though this is equivocal.

Although *T. suevicus* has been recorded from the Jamaican rock record (Pickerill and Donovan, 1991), this is the first recording of *T. paradoxicus*. Notably, in a recent study of the crustaceans from the Port Morant Formation, Collins et al. (1997) identified two species of callianassid shrimps, *Neocallichirus peraensis* Collins, Donovan and Dixon, and *Glypturus acanthochirus* Stimpson. These organisms may have produced the numerous *T. paradoxicus* burrows in this formation.

2. Bioerosional ichnotaxa

Bioerosion is the process by which organisms sculpt or penetrate hard substrates. The resultant biogenous structures qualify as trace fossils and are named as ichnotaxa (Ekdale et al., 1984; Bromley, 1994). As reviewed by Pleydell and Jones (1988), such ichnotaxa are characteristic of, but not exclusively limited to, rocky shorelines, hardgrounds and reefs. When present in siliciclastic sequences, they occur generally in association within substrates provided by organisms with a calcareous exoskeleton, and this is true of the Port Morant Formation. In most cases in this study the bioerosion structures are preserved as natural casts, unless where indicated, within mostly decalcified or unrecognizable shells

of bivalves, as well as in association with gastropods and scleractinian corals.

Ichnogenus *Caulostrepsis* Clarke, 1908

Remarks.—Three ichnospecies of *Caulostrepsis* can be differentiated in the Port Morant Formation and are described utilizing the homologized terminology proposed by Bromley and D'Alessandro (1983). All occur within indeterminate ostreaceids and the prosobranch mesogastropod *Strombus gigas* Linnaeus, typically in association with the borings *Entobia ovula* Bromley and D'Alessandro, *Entobia* isp. or isp., and *Gastrochaenolites* cf. *cluniformis* Bromley and D'Alessandro.

Caulostrepsis cf. *contorta*

Bromley and D'Alessandro, 1983
(Fig. 4d)

Description.—A single cluster of smooth, helicoidally-arranged cylindrical galleries. Individual whorls are closely juxtaposed but do not intersect; diameter of the cylinders is 0.7-0.8 mm. Their variable orientation suggests that the cluster is either a single structure twisted along its axis (a characteristic feature of the ichnospecies) or that more than one gallery is present. No vane is present except for a weak development in association within a single whorl.

Caulostrepsis *cretacea* (Voight, 1971)

(Figs. 4a, c; 6a)

Description.—Smooth, elongate, U-shaped galleries with fused limbs and no central vane, but characteristically with a central axial depression that extends from the distal U-bend along the entire exposed length. Galleries are variably oriented, straight to curved, but never tortuous. Length, mostly incomplete, up to 15 mm; width 1.5-3 mm, typically decreasing aperturally. Transverse sections constricted distally and flattened-elliptical aperturally. Rare examples exhibit apertural fusion of the two limbs into a single tube.

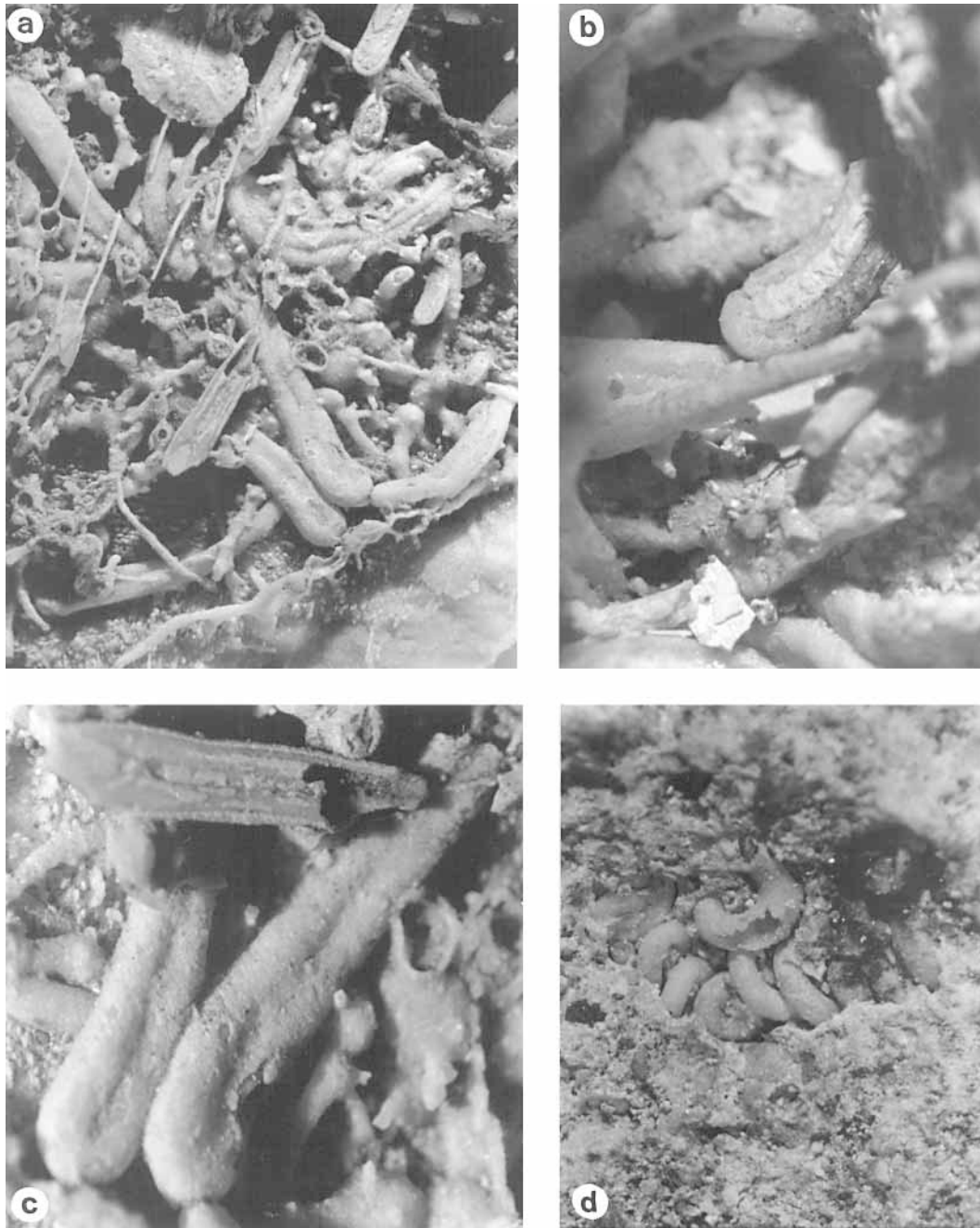


FIG. 4. Ichnospecies of *Caulostrepsis* Clarke in indeterminate ostracid shells from unit 3. a, *C. cretacea* (Voigt) in association with *Entobia ovula* Bromley and D'Alessandro, c being an enlargement of the two examples exhibited at bottom center in a. Specimen NBMG 10118; a $\times 3$, c $\times 6.5$. b. *C. taeniola* Clarke exhibiting a distinctive vane. Specimen NBMG 10119; $\times 10$. d. *C. cf. contorta* Bromley and D'Alessandro. Specimen NBMG 10120; $\times 6$. Note that both *C. cretacea* and *E. ovula* also occur in NBMG 10119.

Caulostrepsis taeniola Clarke, 1908
(Figs. 4b; 6a)

Description.—Essentially as *C. cretacea* except: (i) each specimen possesses a distinct central vane, commonly with a flattened spreite-like structure (Figs. 4b, 6a); (ii) as a consequence, transverse sections are dumbbell or 8-shaped at their apertural extremities (Fig. 6a); and (iii) individual galleries may be enlarged to form a tongue-like shape at the distal extremities (Fig. 4b). Most specimens are observed in transverse section so that maximum observed, but incomplete, lengths are only 9 mm.

Discussion.—Bromley and D'Alessandro (1983) emended the ichnotaxonomy of *Caulostrepsis* and provided a detailed review of its valid ichnospecies and their distinguishing criteria. Of the five ichnospecies formally recognized by them, *C. cretacea* is the only one with typically fused, inward-facing walls. The original position of the median wall is commonly only indicated by a shallow axial depression and does not exhibit apertural extensions. In *C. taeniola* both limbs are interconnected by a distinctive vane, but the simple longitudinal U-shaped and flattened gallery is retained. Notably, in several examples of *C. taeniola* documented herein, the spreite-like structures within the central vane, as also illustrated by Häusel (1905) and refigured in the *Treatise on Invertebrate Paleontology* (Häntzschel, 1975, p. W125, Fig. 77, 5a, b), are clearly evident (for example, Fig. 4b) unlike the material exhibited in Bromley and D'Alessandro (1983). Other species of this ichnogenus are geometrically far more complex, a result of the development of apertural structures or contortions or clusterings of the limbs (see Bromley and D'Alessandro, 1983). The latter are clearly exhibited by the cluster of *C. cf. contorta* (Fig. 4d), which is a geometrically varied and complex ichnospecies that rarely exhibits a helicoidal form similar to that shown by the tentatively identified example documented herein. Regrettably, with this example the central vane, stated by Bromley and D'Alessandro (1983) to be generally well developed in this ichnospecies, is only weakly visible, perhaps due to incomplete

preservation resulting from weathering. Geometrically the specimen is remarkably similar to a helicoidal example of *C. contorta* figured by Bromley and D'Alessandro (1983, p. 305, pl. 23, Fig. 2), which also does not possess the central vane throughout the entire structure. Nevertheless, the general absence of the central vane precludes positive ichnospecific assignment.

Assuming no other ichnospecies are present in the studied material (all from unit 3), because of the variable orientation of many examples of the ichnotaxon, assignment to *C. cretacea* or *C. taeniola* when preserved in sections perpendicular to their long dimensions is difficult. Assignment to one or the other was, however, attempted based on cross-sectional shape, with *C. cretacea* being elliptical or oval and *C. taeniola* exhibiting dumbbell or 8-shaped configurations (Bromley and D'Alessandro, 1983). Within the six samples of indeterminate ostraceids and three of *Strombus gigas*, there are approximately 45 examples of each, with no demonstrable mutual exclusivity.

Caulostrepsis and its various ichnospecies result from euendolithic or paraendolithic activities of polychaete annelids of various families (Bromley, 1978, 1994), but most probably spionids (Barrier and D'Alessandro, 1985). This ichnotaxon has not been formally recorded in the Jamaican rock record, though it was noted to occur in the sequence by Pickerill and Donovan (1997).

Ichnogenus *Clionoides*
Fenton and Fenton, 1932

Clionoides thomasi Fenton and Fenton, 1932
(Fig. 5a, b)

Description.—Preserved on the external surface of an indeterminate species of *Spondylus* Linnaeus (probably *S. americanus* Hermann) from unit 3, and in association with *Entobia* isp., the specimens comprise a series of isolated, straight to gently curved, linear and empty grooves that do not fully penetrate the shell of the spondylid. They range in length from 7-15 mm, in width from 0.5-2 mm, and exhibit a variable depth of typically less than 2 mm. At least 9 individual grooves can be ascertained, but there may be additional speci-

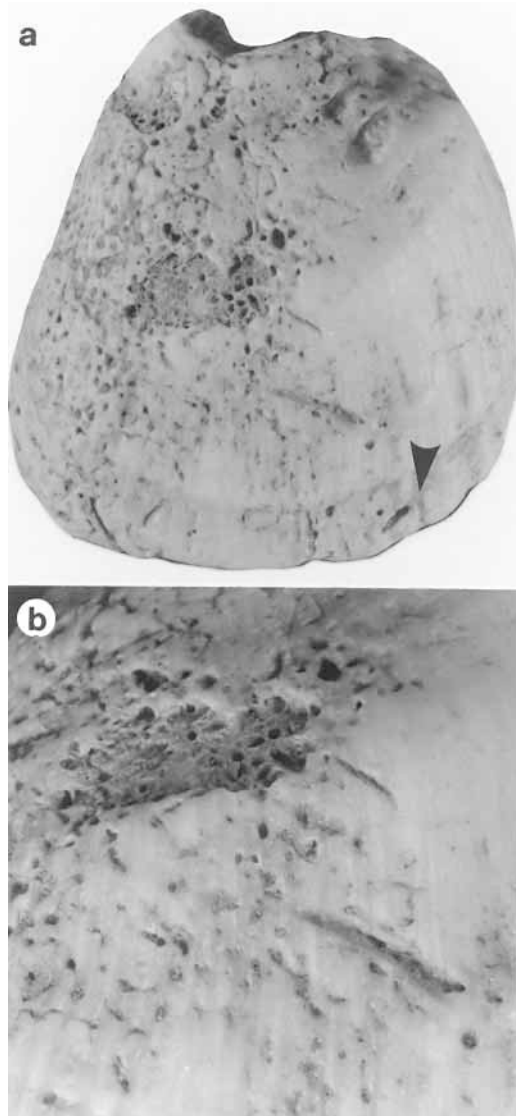


FIG. 5. a, b. *Clionoides thomasi* Fenton and Fenton and *Entobia* isp. on the external valve of *Spondylus* sp. In a, the arrow (bottom right) indicates a branched *C. thomasi*; b is an enlargement of the examples of *C. thomasi* in lower center in a. Specimen NBMG 10121; a $\times 0.8$, b $\times 1.7$. Specimen from unit 3.

mens obscured by relatively dense networks of *Entobia* isp. (to the left in Fig. 5a). Apart from a single example (arrowed in Fig. 5a), the groove structures are unbranched.

Discussion.—Though little used since its original description by Fenton and Fenton (1932), we regard the descriptor as useful in

classifying these relatively simple bioerosional structures. They somewhat resemble the bivalve boring *Petroxestes* Wilson and Palmer though this ichnotaxon is deeper, larger, possesses rounded terminations, and is unbranched. As the epithet suggests, *Clionoides* was initially interpreted by Fenton and Fenton (1932) as the product of boring monactinellid sponges. Their material (Fenton and Fenton, 1932, p. 59, Figs. 1-3; some later reproduced in Häntzschel, 1975, p. W125, Fig. 77, 2a, b) is remarkably similar in overall width and length to that described herein. Fenton and Fenton also noted that branching of the structures, though present, was infrequent. Thus, particularly as we are unaware of any additionally formulated ichnospecies, we regard assignment to *C. thomasi* as appropriate. Given the morphology of the borings, it is unlikely that sponges were responsible for their production, as was also emphasized by Jux (1964) who favored polychaete annelids, a conclusion supported herein.

This is the first formal recording of the ichnotaxon from the Jamaican rock record.

Ichnogenus *Entobia* Bronn, 1837

Remarks.—Historically, the terminology applied to the anatomical parts of the clionid sponge boring *Entobia*, and its synonyms and numerous ichnospecies, has proven convoluted. We follow the nomenclatural scheme proposed by Bromley and D'Alessandro (1984). The single ichnospecies confidently recognized by us from the Port Morant Formation mimics the occurrence of *Caulostrepsis*.

Entobia ovula Bromley and D'Alessandro, 1984
(Figs. 6a; 9a)

Description.—Several tens of examples each comprise a camerate entobian with poorly-developed, slender, generally unbranched exploratory threads that connect to closely-spaced, regularly sub-cylindrical, oval or globose crowded chambers that sporadically are organized in rows and branched at various angles. Individual chambers, typically small, 0.5-1.5 mm in

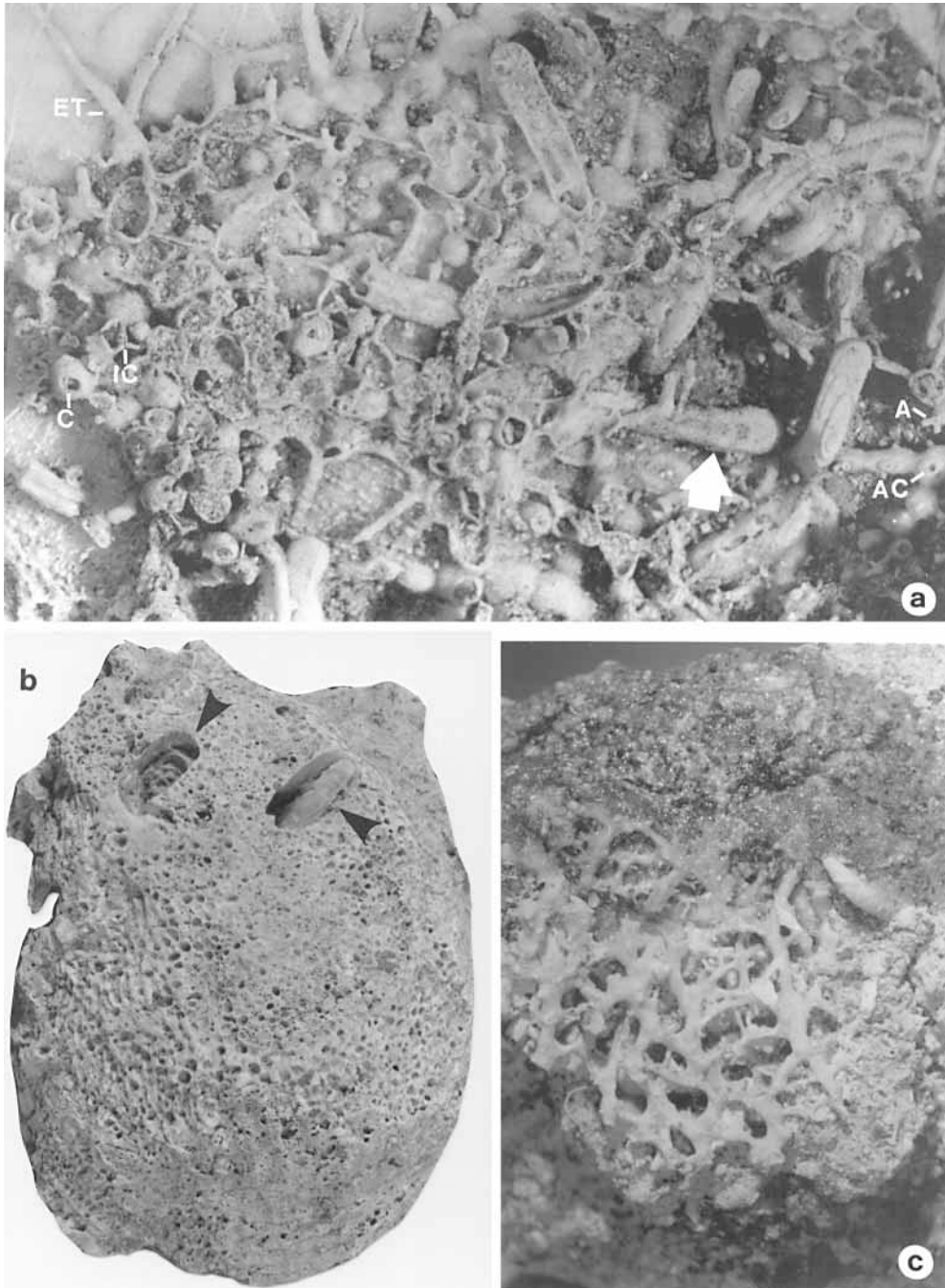


FIG. 6. a. *Entobia ovula* Bromley and D'Alessandro associated with *Caulostrepsis cretacea* (Voight) and *C. taeniola* Clarke (example arrowed) within an indeterminate ostraucid shell. For *E. ovula*, examples of exploratory threads (ET), chambers (C), intercameral canals (IC), apophyses (A) and apertures and apertural canals (AC) are indicated as such (see text for details). Specimen NBMG 10120; $\times 4$. b. *Entobia* isp. preserved on the exterior of *Spondylus* sp. Note also the two examples (arrowed) of *Gastrochaenolites* cf. *cluniformis* Kelly and Bromley that preserve their producing bivalve *Rocellaria* (*Gastrochaena*) *hians* Gmelin. Specimen NBMG 10122; $\times 0.7$. c. Juvenile phase of *Entobia* isp. on an indeterminate ostraucid shell; $\times 3.5$. All specimens from unit 3.

maximum diameter depending on growth phase (see below), usually possess a single, small, central, circular aperture with well-developed outward-tapering apertural canals. Intercameral canals variably developed; when observed, they are commonly short, or substituted by a constriction giving the chambers a fused appearance. Slender apophyses may extend from individual chambers, but are not commonly developed.

Entobia isp. or ispp.
(Figs. 5a, b; 6b, c; 8a)

Description.—Detailed description of this material is unnecessary because it comprises tens of examples that are impossible to assess at the ichnospecies rank. This is a result of (i) preservation as fragmentary and incomplete segments of the boring, particularly those examples restricted to juvenile phases (Fig. 6c); (ii) intensely weathered or poorly-preserved specimens; and (iii) specimens that are preserved on shell exteriors only, and do not fully penetrate their host, thus precluding 3-dimensional analysis (Fig. 6b).

Discussion.—The many and varied morphological parameters used to distinguish the numerous ichnospecies of *Entobia* have been discussed by Bromley and D'Alessandro (1984). Of these criteria, size, arrangement and fusion/non-fusion of chambers, and presence and dimensions of the various canal systems, were considered the most significant. However, even within a single ichnospecies a unique morphology is not necessarily present owing to ontogenetic variation between juvenile and gerontic areas within individual boring systems. The well-preserved Port Morant material clearly exhibits such variation, with initial penetration by juveniles being represented simply by exploratory threads, and successive development leading to the introduction of chambers with associated apertural systems and variably developed intercameral canals. In terms of the five growth phases (A-E) proposed by Bromley and D'Alessandro (1984) for entobians, the material clearly illustrates the initial A through C phases (many clionid sponges progress no further than C).

Entobia ovula is characterized by initial exploratory threads that are little-branched and typically poorly developed. Subsequently-developed chambers are typically ovoid or globose, may be arranged in straight strings, and associated apophyses are slender, but not numerous. Apertural systems are distinct and intercameral canals are short or reduced to a constriction (Bromley and D'Alessandro, 1984). All these features typify the well-preserved Port Morant specimens which, therefore, we regard as conichnospecific. As noted above, all other specimens are regarded as *Entobia* isp., though more than a single ichnospecies could be present. All examples were observed in molluscs from unit 3.

This is the first formal documentation of *Entobia* from the Jamaican rock record, though the ichnotaxon was noted to occur in the sequence by Pickerill and Donovan (1997). It occurs particularly in association with indeterminate ostreaceids, *Strombus gigas* and *Spondylus* sp.

Ichnogenus *Gastrochaenolites*
Leymerie, 1842

Gastrochaenolites cf. *cluniformis*
Kelly and Bromley, 1984
(Figs. 6b; 7c, d; 8a, b)

Description.—Several hundreds of broadly club- to spherical-shaped structures in their long dimension (Fig. 8a, b), and circular to ovate at their single openings (Fig. 7c, d), that penetrate a variety of siliciclastic and calcareous substrates. Observed lengths, though commonly incomplete due to truncation by present-day weathering, are 12-50 mm; widths correspondingly vary between 10-30 mm. Most borings are oriented approximately normal or steeply inclined to the host substrate. Bases are smooth and rounded and very rarely possess a linear ridge; nature of the necks/apertures (terminology of Kelly and Bromley, 1984) are typically unobserved. Most borings are smooth internally and externally, and empty, though many (Figs. 6a, 8a, b) retain the conjoined valves of their producer, the gastrochaenid bivalve *Rocellaria* (*Gastrochaena*) *hians* Gmelin, interestingly the only extant tropical member of the genus (Abbott and Morris, 1995).

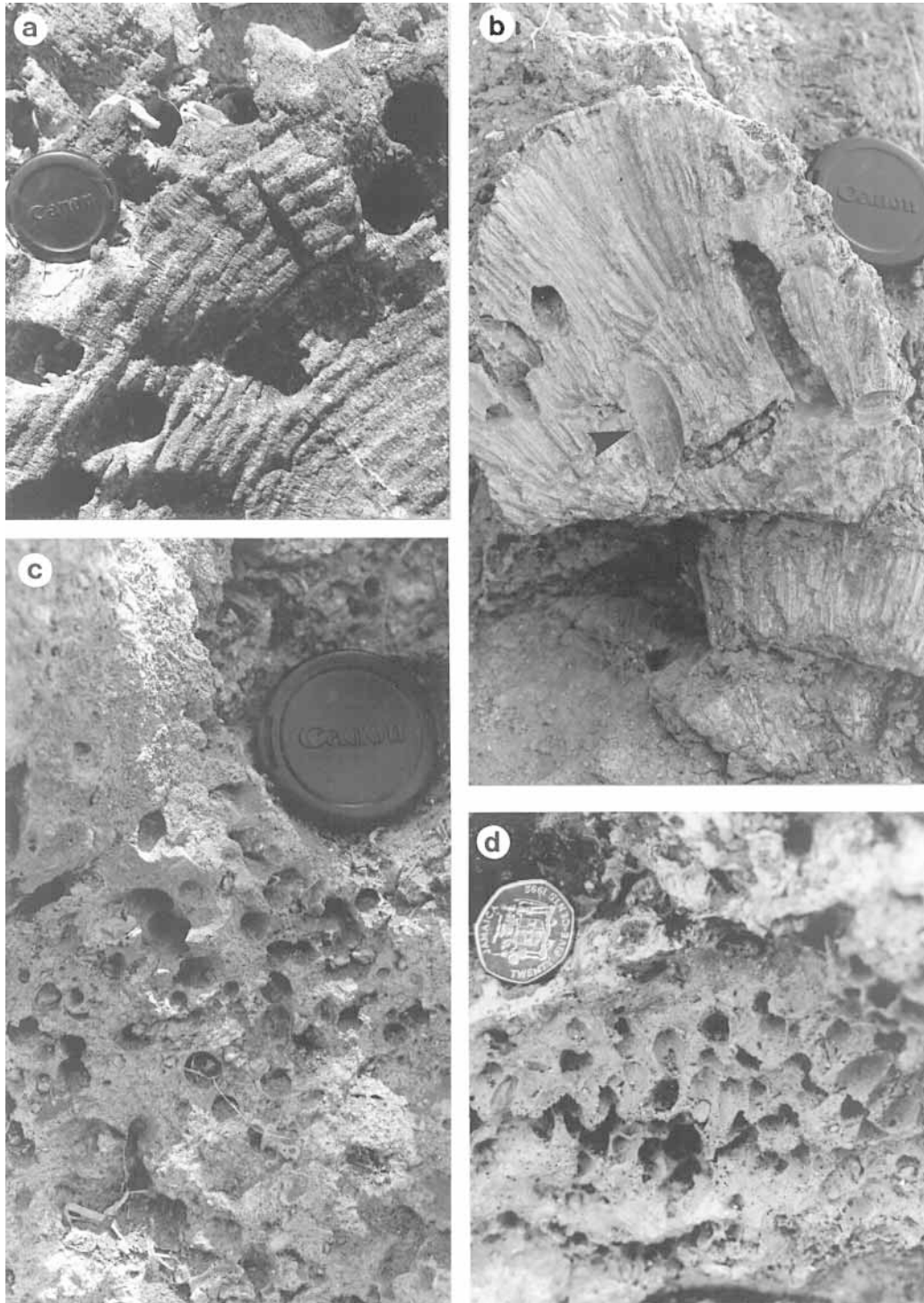


FIG. 7. a, b. *Gastrochaenolites* cf. *torpedo* Kelly and Bromley within in situ corals at the base of unit 2. Note the thin lining in the example (arrowed) in b. c, d. *Gastrochaenolites* cf. *cluniformis* Kelly and Bromley in siliciclastic boulders of unit 1. Lens hood is 55 mm in diameter and coin in d is 24 mm wide; all specimens uncollectible.

Gastrochaenolites cf. *torpedo*
 Kelly and Bromley, 1984
 (Fig. 7a, b)

Description.—Several tens of large, elongate, straight, but variably oriented borings within corals at the base of unit 2. Lengths up to 160 mm and single observable openings 30-50 mm wide. The borings are smooth, unlined, or rarely possess a thin calcareous lining (Fig. 7b) and a smooth parabolic base. Necks and apertures are unobserved but external openings are typically round (Fig. 7a). Several examples retain the conjoined valves of their producer, the boring mytilid *Lithophaga antillarum* (Orbigny), a large, thin-shelled species whose extant representatives bore into carbonate substrates in very shallow-water marine environments (Morris, 1975).

Discussion.—Kelly and Bromley (1984) provide an elegant review of *Gastrochaenolites* and its various ichnospecies which, in part, are distinguished on the nature of the neck, aperture and base, and the transverse cross-sectional shape of the borings along their lengths. Because of the preservation of the Port Morant material, several of these parameters were indeterminate. Nevertheless, two ichnospecies are present and of the eight recognized by Kelly and Bromley we tentatively assign the material to *G. cluniformis* and *G. torpedo*. The former possesses a similar longitudinal shape to the Port Morant material, as well as a smooth and rounded base characterized, though not exclusively so, by the development of a median ridge. The latter is large, elongate, lined or unlined and is known to have been produced by species of *Lithophaga* (Kelly and Bromley, 1984). Jones and Pemberton (1988) noted that their Pleistocene examples of *G. torpedo* were among the largest examples (up to 140 mm long), but several of the Jamaica specimens surpass this value.

Gastrochaenolites cf. *cluniformis* occurs in abundance within sandstone and coral boulders and cobbles of unit 1 (Fig. 7c, d), and less commonly within in situ corals at the base of unit 2 (Fig. 8a, b) and in the molluscs *Strombus gigas* and *Spondylus* sp. from unit 3 (Fig. 8a). Notably, volcanic clasts in

unit 1 are not bored, suggesting that the producing bivalves were substrate selective, preferring poorly lithified siliciclastics or carbonates. In contrast, *G. cf. torpedo* is restricted to carbonate substrates provided by the corals *Solenastrea bourmoni* Edwards and Haine, *Porites asteroides* Lamarck, *Siderastrea siderea* (Ellis and Solander), *Montastrea cavernosa* (Linnaeus) and *Diploporia strigosa* (Dana) that occur at the base of unit 2. Interestingly, *Lithophaga* can generally only bore into calcareous substrates, as the chemical employed is a calcium complexing secretion and not an acid (see Bromley, 1970; Jones and Pemberton, 1988). Therefore, this explains the absence of *G. cf. torpedo* in the siliciclastic cobbles and boulders of unit 1.

As noted above, several examples of these ichnospecies still preserve their gastrochaenid and lithophagid producers, which are generally difficult to extricate as whole shells. Fossilized shells within *Gastrochaenolites* have been reported from elsewhere (e.g., Wilson, 1986; Jones and Pemberton, 1988; Bromley, 1994), but such recordings are not always the case. For example, in an upcoming study of several hundreds of examples of *Gastrochaenolites* in littoral boulders from the Miocene of southern Spain, Doyle et al. (1998) find no evidence of their progenitors. Thus, our examples provide a somewhat fortuitous occurrence of borings preserving their producers.

Although Pickerill and Donovan (1997) documented several examples of *Gastrochaenolites* isp. from the sequence, we believe, based on the additional material described herein, that these examples are best regarded as *G. cf. cluniformis*. This still remains the first formal recording of both these ichnospecies from the Jamaican rock record.

Ichnogenus *Meandropolydora* Voight, 1965
Meandropolydora cf. *sulcans* Voight, 1965
 (Fig. 9a)

Description.—A single specimen fortuitously preserved on a small (8 × 5 mm) fragment of an indeterminate ostracoid shell from unit 3 and comprising a sinuous,

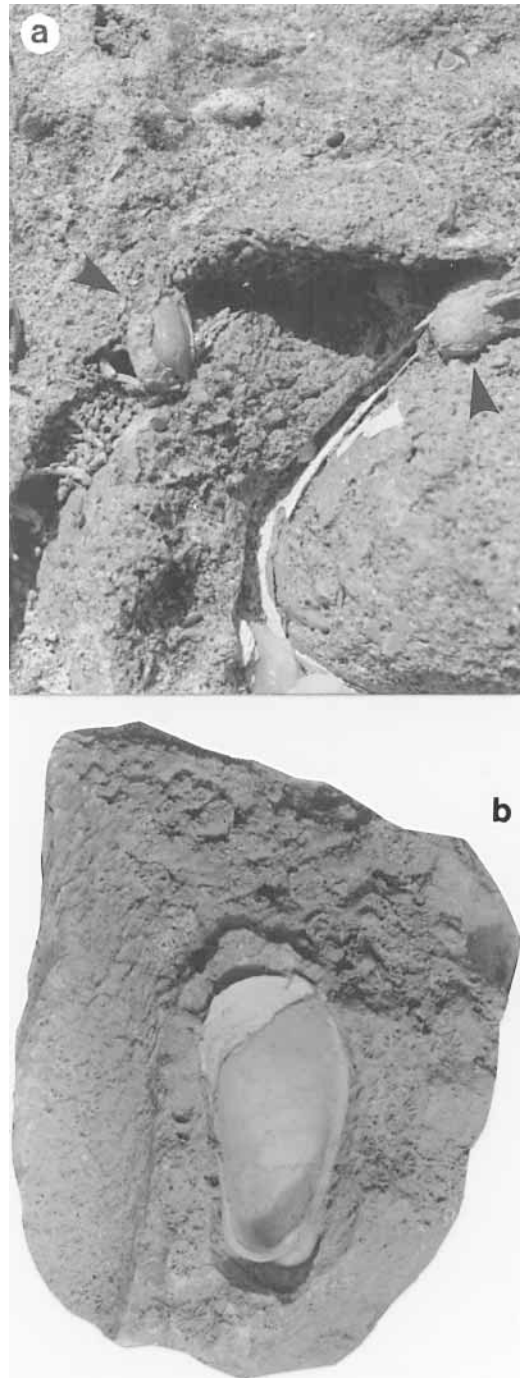


FIG. 8. a. *Gastrochaenolites* cf. *cluniformis* Kelly and Bromley (arrowed) within *Strombus gigas* Linnaeus from unit 3, both examples preserving their producer, the boring gastrochaenid *Rocellaria* (*Gastrochaena*) *hians* Gmelin. The irregular entangled network to the lower left of the example to the left comprises a network of *Entobia ovula* Bromley and D'Alessandro and *Caulostrepsis cretacea* (Voight). Specimen UWIGM 1997.1; $\times 0.7$. b. Well-preserved *Rocellaria* (*Gastrochaena*) *hians* shell in *G.* cf. *cluniformis* in a decalcified coral from the base of unit 2. Specimen NBMG 10123; $\times 1.4$.

looped and continuous, smooth, unbranched, internally structureless gallery that parallels but clearly penetrates the shell surface on at least two levels. The looped limbs do not touch or intersect and the intervening ostracoid shell material is unaffected. Diameter of the gallery, relatively constant at both levels, is approximately 0.5-0.6 mm.

Discussion.—Though incomplete, the specimen can clearly be assigned to the ichnotaxon *Meandropolydora*, discussed in detail by Bromley and D'Alessandro (1983, 1987). Of the five ichnospecies recognized by them, *M. decipiens* Voight is looped but the inner sides of the limbs are connected by a vane, and *M. elegans* Bromley and D'Alessandro possesses limbs that touch, but are normally not fused. *Meandropolydora barocca* Bromley and D'Alessandro exhibits numerous pouches, each with a spiral course and tending to arise by bifurcation of other pouches (see Bromley and D'Alessandro, 1987, Figs. 12-14); *M. crassa* Bromley and D'Alessandro is a large, branched ichnospecies occurring in lithic substrates and possessing a granulate wall. Finally, *M. sulcans* has no vane, is commonly looped and the walls are not necessarily in mutual contact. The combination of characteristics, together with the observation that *M. sulcans* is particularly common in oysters (Bromley and D'Alessandro, 1983), suggests that the described specimen can be compared to this ichnospecies.

Meandropolydora is interpreted as the domichnion of suspension-feeding polychaete annelids (Bromley, 1994), particularly spionids (Barrier and D'Alessandro, 1985). The ichnogenus has never previously been formally recorded in the Jamaican rock record.

Ichnogenus *Oichnus* Bromley, 1981
Oichnus paraboloides Bromley, 1981
 (Fig. 9c)

Description.—Smooth, spherical, paraboloid holes penetrating molluscan shells more or less perpendicular to their external surfaces. Outer edges typically countersunk and borings terminate in a central

hole of narrower diameter. The 12 examples recognized by us exhibit countersinking that extends the length of overall penetration. External countersunk diameters range from 2.5-3.0 mm and the borings occur as single penetrations within *Anadara lienosa floridana* (Conrad) (5), *Apolymetis intrastriata* (Say) (3) and *Chione cancellata* Linnaeus (4).

Oichnus simplex Bromley, 1981
 (Fig. 9b, d)

Description.—Simple, smooth, cylindrical to subcylindrical holes with axes more or less perpendicular to molluscan shell surfaces and no countersunk outer edges. Of the 24 collected examples, two possess an essentially horizontal shelf at their inner extremities which is penetrated by a hole of reduced diameter (cf. Pickerill and Donovan, 1998, pl. 1, Fig. 2); the remainder do not exhibit this basal shelf. Boring diameters range from 1.0-3.3 mm and they particularly occur as randomly distributed single penetrations in association with *Chione cancellata*, one of the most common mollusc species in the sequence. Other bored species include: *Anadara lienosa floridana*, *Anodonta alba* Link, *Apolymetis intrastriata*, *Crassostrea rhizophorae* Guilding, *Diplodonta nucleiformis* Wagner, *Strombus costatus* Gmelin, *Tellina georgiana?* Dall and *Tellina listeri* Röding.

Discussion.—All examples of *Oichnus* were observed in molluscs from unit 3. Bromley (1981, 1993) discussed in some detail the ichnotaxonomy of *Oichnus* and its three recognized ichnospecies. *Oichnus paraboloides*, which is characterized by spherical, countersunk outer edges that are otherwise absent in *O. simplex*, probably resulted from opportunistic activities of cannibalistic naticid gastropods, whereas *O. simplex* was produced by mucricids (for review, see Pickerill and Donovan, 1998). The third ichnospecies, *O. ovalis* Bromley, was undoubtedly produced by octopodids (Bromley, 1993). *O. paraboloides* and *O. simplex* are recorded and described in detail from the Jamaican rock record by Pickerill and Donovan (1998).

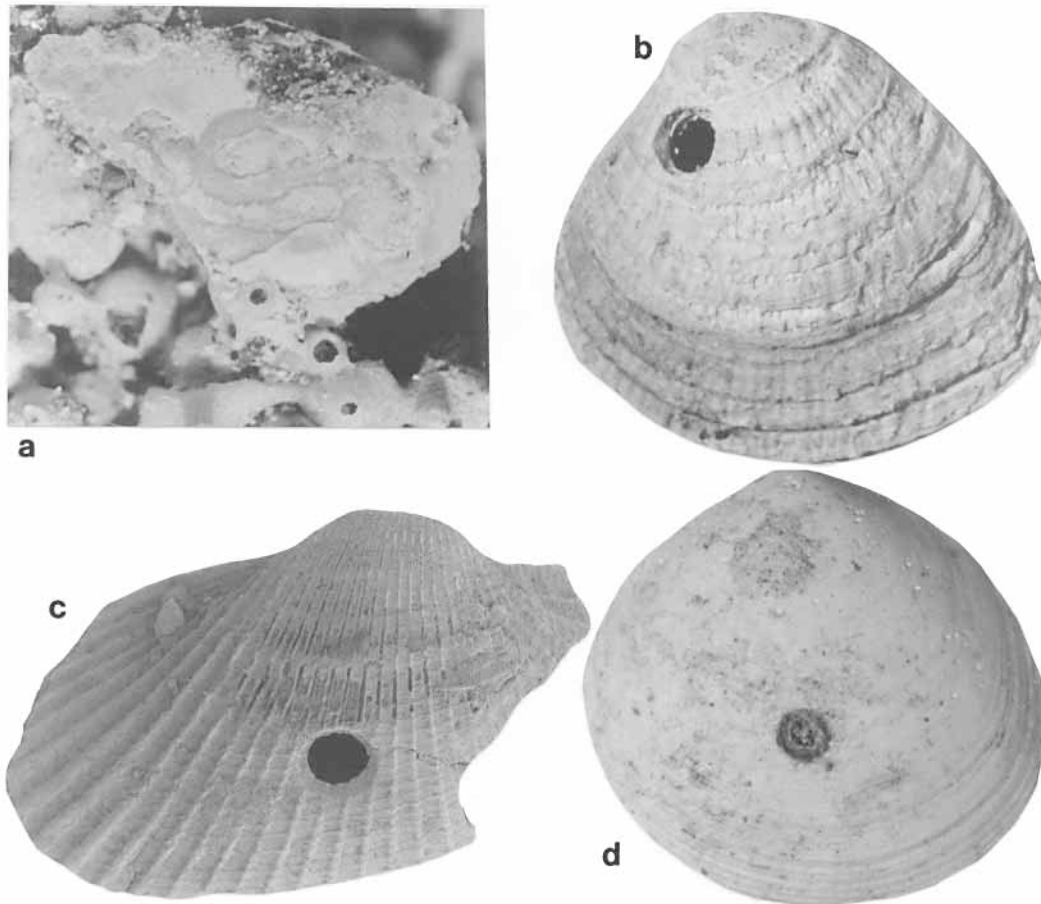


FIG. 9. a. *Meandropolydora* cf. *sulcans* Voight within an indeterminate ostracoid shell fragment from unit 3. Specimen NBMG 10124; $\times 7.5$. b. *Oichnus simplex* Bromley within valve of the mollusc *Chione cancellata* Linnaeus. Specimen NBMG 10125; $\times 2.4$. c. *Oichnus paraboloides* Bromley within valve of the mollusc *Anadara lienosa floridana* (Conrad); $\times 1.5$. d. *O. simplex* with a flattened, but perforated, base within valve of the mollusc *Diplodonta nucleiformis* Wagner. Specimen NBMG 10126; $\times 4$. All specimens from unit 3.

CONCLUDING REMARKS

As previously noted, the Port Morant Formation also crops out on the western side and northern end of Port Morant Harbour, as well as in the exposures considered herein. In the former locations, however, the sequence comprises unfossiliferous red conglomerates and cross-bedded sandstones interpreted to have been deposited in alluvial fan/fluvial environments (Donovan et al., 1995). The succession studied herein, however, is undoubtedly marine in origin as evidenced by the nature of both its contained faunas and ichnofau-

nas. Indeed, Donovan et al. (1995, p. 30) suggested that it represented a back-barrier or lagoonal sequence, a conclusion with which we concur.

Accordingly, we interpret the boulder conglomerates of unit 1 as having formed on a transgressive and erosional flooding surface in a littoral or shallow sublittoral environment. The initial transgression was undoubtedly accompanied by erosion, but not significant reworking, of sandstone layers of the underlying Old Pera Beds, the large basal boulders and platy slabs of which we interpret as essentially in situ. In support of this, it is notable that such boul-

ders and slabs only exhibit borings of *Gastrochaenolites* cf. *cluniformis* on their sides and tops. Their lack of disturbance presumably precluded boring activities on their undersides. Indeed, Osman (1977) and Lieberman et al. (1979), amongst others, have demonstrated that boulders of comparable size are only rarely overturned and, if so, only under very severe conditions. In contrast, sandstone cobbles and boulders that overlie these platy slabs in the uppermost horizons of unit 1, and which are accompanied by bored coral and non-bored volcanic clasts of variable size and composition, exhibit evidence of considerable reworking (they are all extremely well rounded). Furthermore, many exhibit *G. cf. cluniformis* on all surfaces, suggesting relatively prolonged reworking as a mobile substrate and exposure of all surfaces to potential borers at some stage in their transport history. It is also from these uppermost boulder horizons that Donovan et al. (1994) documented an essentially in situ echinoid fauna, including *Eucidaris tribuloides* (Lamarck) and *Echinometra viridis* A. Agassiz, urchins typical of hard substrates and rocky bottoms. Interestingly, none of the boulders exhibit encrusting or nestling organisms, which are typically developed in later successional stages of cobble and boulder colonization history (Wilson, 1987). Instead, they only exhibit monoichnospecific borings, elsewhere interpreted as examples of early colonization stages of unstable substrates (Doyle et al., 1997).

We interpret the muddy and calcareous sandstones of units 2 and 3 as representing the lagoonal sediments proper. These substrates were extensively bioturbated by crustaceans, in places virtually pervasively, resulting in production of *Ophiomorpha nodosa* and, particularly, *Thalassinoides paradoxicus*. As a consequence, primary depositional fabrics are now very difficult to discern. As previously noted, cementation has variably, but generally, enhanced the preservation of these ichnotaxa. This, and the fact that bedding plane exposures are only sporadically developed and the sandstones are very poorly lithified, may explain the low diversity of soft-sediment ichnotaxa. Additionally, we would inter-

pret *Ophiomorpha* and particularly *Thalassinoides* as climax trace fossils (sensu Bromley, 1996). Such are well known in stable habitats where conditions change gradually and predictably, and dictate the final ichnofabric, previous structures being overprinted and commonly effectively destroyed by such forms (Bromley, 1996).

The conglomeratic horizons at the base of unit 3, which as noted thin and disappear southwards, are interpreted as marine (lagoonal) equivalents of the alluvial/fluvial conglomerates deposited to the north and west. In terms of clast composition they are more or less identical to these latter conglomerates which, therefore, we regard as their penultimate source. They are interpreted as having formed as isolated beaches, bars or channels (Donovan et al., 1995) on the landward side of the lagoon. A marine origin for them is supported by the presence, albeit rare, of molluscs, and by *Ophiomorpha* and *Thalassinoides* at the top of unit 2, that clearly represent a pre-omission to post-omission (sensu Bromley, 1970) suite of ichnotaxa.

The in situ scleractinian coral colonies at the base of unit 2, that we interpret as small patch reefs and isolated heads that grew in the lagoon, provided a suitable substrate for the boring mytilid *Lithophaga artillarum*. *Rocellaria (Gastrochaena) hians* also bored these corals such that they now contain examples of both *G. cf. torpedo* and *G. cf. cluniformis* (Fig. 10), several still preserving their producers. The remaining bioerosional structures are associated with two extremely fossiliferous horizons of parautochthonous shells present near the top of unit 3 (Fig. 10). The resultant ichnotaxa, a product of boring activity by polychaete annelids, sponges, and gastropods (naticids and mucricids), occur in association with several species of bivalves, particularly ostraceids, and the gastropod *Strombus gigas*. Undoubtedly, the essential pre-requisite for their development was the presence of suitable calcareous substrates and sufficient exposure time of these substrates to permit such bioerosion. As discussed by Pickerill and Donovan (1997), the latter may have been accomplished by repeated

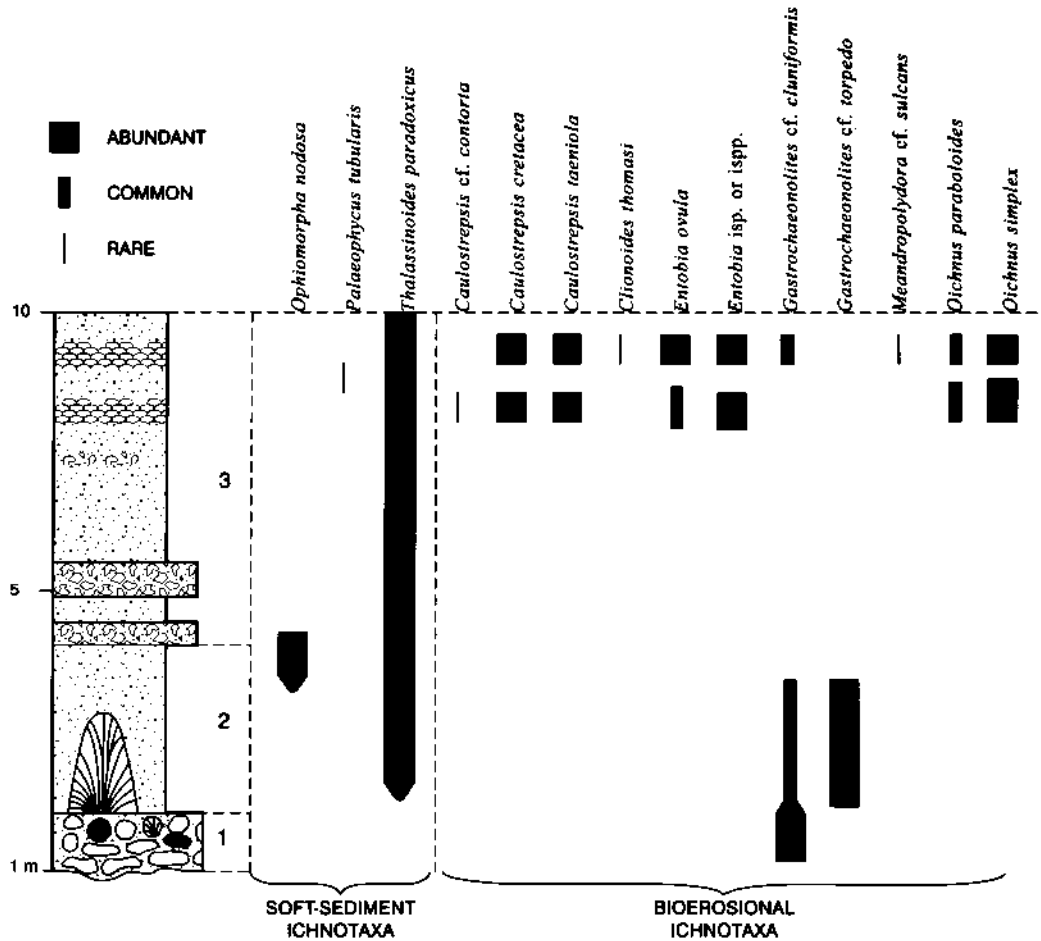


FIG. 10. Stratigraphic distribution and relative abundance of ichnotaxa in the Port Morant Formation. To the left is a schematic vertical stratigraphic section, measured from south of Pera Point, and indicating the relative thicknesses and lithologies of units 1-3 (see text for details). Note that all bioerosional ichnotaxa in unit 3 occur in association with two abundantly fossiliferous horizons toward the top of the sequence (see text for details). Rare = <10 specimens, common = 10-20 specimens and abundant = >21 specimens.

episodes of burial and exhumation of the component shells within these horizons. Notably, *G. cf. torpedo* is the only bioerosional ichnotaxon absent from these layers, presumably a consequence of the unavailability of thickened calcareous substrates required for its production, substrates only provided by corals lower in the sequence.

The present contribution is the first of its kind in one of the several Pleistocene stratigraphic units of Jamaica (see Wright and Robinson, 1993). It also represents one of the few such studies in coeval strata of the Caribbean. The only comparable studies are those by Jones and Pemberton (1988, 1989)

and Pemberton and Jones (1988) from Pleistocene lagoonal carbonates of the Ironshore Formation of Grand Cayman Island, British West Indies. These authors described both the soft-sediment ichnotaxa and *Lithophaga* borings (*G. torpedo*) from this sequence, and Jones (1994, p. 99) noted the occurrence of the borings *Entobia* and *Trypanites* Mägdefrau. Although contributions in Donovan and Jackson (1994) indicate that Pleistocene sequences are not uncommon in the Caribbean, they have attracted little ichnological research. Such future research may prove important with respect to broader conclusions on the controlling parameters on the

nature and distribution of ichnofossils produced in different environmental regimes and in varying substrates in the Pleistocene of the Caribbean.

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