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A BRIEF REVIEW OF THE BENTHIC MOLLUSCA OF THE BOWDEN SHELL BED, SOUTHEAST JAMAICA

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Since Woodring documented c. 600 taxa of molluscs from the Pliocene Bowden shell bed, only a further 10 nominal species have been added to this fauna. The terrestrial gastropod *Parachondria (Parachondria) augustae* (Adams, 1849) is recorded from the Bowden shell bed for the first time. The trace fossil *Teredolites longissimus* Kelly & Bromley, 1984, produced by teredinid bivalves boring in wood, has not been figured hitherto from this shell bed. Apart from bivalves, gastropods and scaphopods, the fauna also includes cephalopods (teuthoid statoliths) and chitons (disarticulated valves representing at least three species).

This fauna formed a focus for early attempts at Lyellian chronostratigraphy in the tropical western Atlantic. However, faunal turnovers created by late Cenozoic extinctions and radiations led to the deposit being dated as Miocene (or Oligocene) on the basis of molluscan data alone.

Key words — Bowden shell bed, Pliocene, Mollusca, bivalves, gastropods, scaphopods, cephalopods, chitons.

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INTRODUCTION

The macropalaeontological aspect of the Bowden shell bed that is best known is undoubtedly its diverse fauna of molluscs, recorded in the monographic studies of Woodring (1925, 1928). The purpose of the present, brief paper is not to supersede these studies. Rather, it is intended as a supplement to Woodring's monographs, reviewing advances in the molluscan palaeontology of the Bowden shell bed since the 1920s and bringing it 'up to date'. The principal features of our paper are a historical review of molluscan research on this deposit, a discussion of the utility of the fauna in answering regional problems and the documentation of those species added to the fauna over the past 70 years. This paper is mainly concerned with the terrestrial and benthic marine molluscs; holoplanktic molluscs are considered in detail elsewhere in this volume (Janssen, 1998).

The specimens illustrated herein are deposited in the Florida Museum of Natural History, Gainesville (UF) and the Natural History Museum, London (BMNH). The bibliographies of Kinghorn (1977) and Mikkelsen *et al.* (1993) were particularly valuable in researching the present paper.

HISTORY OF RESEARCH

In Matley's (1923) bibliography of the geology of the island, there is reference to Patrick Browne's *The Civil and Natural History of Jamaica* (1756), which contains '... an history of the natural productions, including the various sorts of native fossils ...'. Indeed, this is so, but to our disappointment the diligent Dr Browne was referring to rocks and minerals, and not the petrified remains of extinct organisms. Even if Browne had been interested in cataloguing the island's fossils, as he so ably did with its living fauna and flora, it would have been difficult to determine or attribute the true location of a fossilised Bowden deposit as his maps clearly label Port Morant Bay as Port Maria! Nevertheless, this rich volume characterises the need for the early colonists of Jamaica to take stock of their unfamiliar surroundings, and to understand their significance for industry, trade and general knowledge. One prize, the Bowden shell beds, had to wait a further century before being discovered.

One author alone is principally responsible for putting the molluscan fauna of the Bowden shell bed firmly on both the palaeontological and malacological maps of Jamaica, namely Wendell P. Woodring, who contributed the two familiar monographs describing the bivalves and scaphopods (1925), and gastropods (1928). However, it is wrong to begin a history of collecting or describing fossil molluscs from Bowden with Woodring. His monographic studies relied totally on the collections of other workers who had amassed fossils from the Bowden shell bed, and had begun to interpret their significance, many years earlier (Woodring, 1925, pp. 9-12).

The first formal studies of the Bowden molluscan fauna appear to have been undertaken by J. Carrick Moore (1863), who examined a collection of shells deposited by Lucas Barrett in the British Museum in 1862. Barrett, in his role as first Director of the Geological Survey of Jamaica, discovered the beds in 1859 (Chubb, 1962). It seems apparent that Barrett had intended to work on the fauna himself, but tragically died in a diving accident before he could do so. Moore presented his own findings on Barrett's collection to the Geological Society of London, where he detailed a list of 71 molluscan species and noted that 12 were still extant in the waters around Jamaica. Shortly afterwards, R.J. Lechmere Guppy began to study the collections in more detail, taking time to figure the shells, describe them and erect new species as he saw fit. Like Moore, Guppy delivered his results to the Geological Society (1866a), but his analysis of the fauna was much more thorough. On the basis of his faunistic and comparative approach he strived to put the Bowden fauna into the context of a wider Caribbean and, indeed, global geology (Guppy, 1866a, b, 1867, 1873, 1874, 1875, 1882; Guppy & Dall, 1896).

Subsequently, the Bowden molluscan fauna started to attract the attention of other collectors and curators (Dall, 1890-1903; Cockerell, 1894; Pilsbry, 1911). Thus, by the time Woodring came to take an interest in the fauna (Woodring, 1916, 1917), he had the opportunity to consult extensive collections in the United States National Museum, the Johns Hopkins University, the Philadelphia Academy of Natural Sciences, and the British Museum (Natural History), as well as the private collections of amateurs and professionals (Hill, 1899; Woodring, 1925). Furthermore, he could enter ongoing debates on the significance of the deposit which had already attracted the attention of other molluscan biologists (see, for example, Pilsbry, 1911) and geologists interpreting the region's history (see 'Literature list for Miocene mollusks from tropical America' in Woodring, 1928, pp. 42-48).

Woodring (1925, pp. 8, 9; 1928, pp. 39-41) considered that the Bowden fauna was Miocene in age, although it is now recognised to be Pliocene (Banner & Blow, 1965; Robinson, 1967, 1969; Bolli & Premoli Silva, 1973; Stanley & Campbell, 1981). Woodring's work (1925, 1928) has remained an important reference for both malacologists and palaeontologists. His careful comparative work, with each species discussed with reference to previously published taxa, enabled newly collected material to be quickly classified in a working taxonomy. Woodring did not restrict himself to faunistic listings, but, like Guppy, endeavoured to use the fauna to shed light on the palaeontology and palaeoecology of the Caribbean region (Woodring, 1929). In later years, Woodring turned to understanding endemism in fossil Caribbean faunas and determined that, of the 630 molluscan species he recognised from Bowden, 55% were considered to be endemic at that time (Woodring, 1965). At this time Woodring still had no firm geologic date in mind for the Bowden shell beds, but continued to discuss them as though they were Miocene, even though he recognised that the shell bed was an exceptional deposit when compared to other Miocene faunas.

Shortly before Woodring's second monograph (1928) went to press, Hodson *et al.* (1927) and Palmer (1927) described a few other shells from the Bowden beds, but overall these added little to the known list of fossil molluscs. Since Woodring, few molluscan taxa have been added to the fauna from the beds (see Table 1), although interestingly, greater attention has been paid to the rarer taxa and to revising taxonomic nomenclature (see, for example, Nicol, 1953; Clarke & Fitch, 1975, 1979; Jung, 1989; Goodfriend, 1992, 1993).

REGIONAL SIGNIFICANCE

Almost as soon as it was discovered, the Bowden shell bed became the subject of an attempt to date it, in terms of the European Tertiary, by Lyellian percentages (for a discussion of Lyell's concept of a statistical chronostratigraphy, see Rudwick, 1978). Lucas Barrett discovered the Bowden shell bed in 1859 and tried to date this, and other late Cenozoic deposits of eastern Jamaica, by determination of their included proportions of extant molluscs (Chubb, 1962). This may have been the first such research programme in the tropical western Atlantic. However, it was Barrett's determination to investigate fully the Recent molluscs for comparative purposes that led to his untimely death in 1862 (see Donovan, 1998).

Barrett considered the Bowden shell bed to be Miocene (Chubb, 1962, p. 27). Subsequent estimates, using Lyellian percentages both directly and indirectly (that is, by comparison with other, similar faunas), have varied between Oligocene (Dall, 1890-1903, pp. 1580-1588) and middle Miocene (Woodring, 1925, pp. 8, 9; 1928, pp. 105-108). Such a large fauna was a major data point in regional analyses, such as Woodring's 'middle Miocene Caribbean province' (1965). However, the evidence of planktic microfossils from the Bowden shell bed has now shown it to be Pliocene in age. This disparity between the two biostratigraphic methods is due to a major turnover in molluscan taxa of the tropical western Atlantic since the early Pliocene, giving the fauna of the Bowden shell bed and coeval deposits an anomalously low percentage of taxa that are still extant (Stanley & Campbell, 1981). This event has been referred to as a 'regional mass extinction' (= regional extinction *sensu* Donovan, 1989); it is now recognised that these extinctions began about 2.4 million years ago and were compensated for by speciation and migration into the region (Allmon *et al.*, 1993; Jackson *et al.*, 1993; Vermeij, 1993).

BIVALVES AND GASTROPODS

Relative abundances — Although much has been written of the molluscan diversity of the Bowden shell bed, little is known of the relative abundances of taxa. Herein we tabulate the relative abundancies of bivalve shells from a rich bulk sample of poorly lithified sediment from (mainly) unit 2 of Pickerill *et al.* (1998) (Table 2 herein). Of the 21 nominal species whose valves represent at least 1% of the fauna (that is, 15 or more valves), four are arcids, three are lucinids, three are nuculanids and two are corbulids; other species represent nine families. Lucinids (15 species), arcids (11 species), tellinids (9 species) and nuculanids (8 species) show the greatest diversity within the sample; the only two nominal species of *Corbula* are represented by 239 valves and three shells.

Teridinid tubes — Small fragments of irregular, calcareous tubes which reach 5 mm maximum diameter, and the most extensive fragments of which reach 5 mm long by 2 mm diameter (Pl. 1, Fig. 4), occur rarely in the Bowden shell bed and were reported by Woodring (1925, p. 195). These tubes are referable to the ichnogenus *Teredolites* Leymerie (see discussion of the ichnogeneric assignment of such tubes in Savrda & Smith, 1996) and are interpreted as the calcareous linings of tubes bored into wood by teredinid bivalves such as *Teredo* Linné. The tubes are irregular and changed course frequently (Pl. 1, Fig. 5), at least in the short fragments that are preserved, and they have numerous internal partitions, a feature characteristic of *Teredolites longissimus* Kelly & Bromley, 1984 (Pl. 1, Fig. 6; compare with Savrda & Smith, 1996, fig. 4). No trace of the actual bivalve shells has been found associated with the tubes, although Woodring (1925, pl. 26, figs 16-18) did illustrate shells which he attributed, doubtfully, to the wood-boring genera *Martesia* Sowerby and *Xylophaga*? Turton. *Teredolites* from the Bowden shell bed are composed of fibrous calcite, with the fibres at right angles to the external surface of the tubes (Pl. 1, Fig. 6, left). Rarely, they also show striations on the external surface which could possibly be traces of the original wood fibres, but no clear evidence of cellular structure has been recognised. Pickerill *et al.* (1996, p. 227, fig. 5c, d) recorded densely crowded *Teredolites longissimus* from a float block derived from higher in the Bowden Formation. Other molluscan trace fossils in the Bowden shell bed are discussed by Pickerill & Donovan (1998).

Land snails — The importance of the small fauna of land snails from the Bowden shell bed is that it is the only pre-Quaternary deposit bearing terrestrial molluscs known from Jamaica. Goodfriend (1993) reviewed the land snails previously recorded from the Pliocene of Bowden, and considered only four, with a doubtful fifth, to be truly Pliocene, another 14 species being younger 'contaminants' (see also Woodring, 1925, p. 12). To this small fauna we add a further Pliocene species, based on a single shell (BMNH PI TG 3940) assigned to *Parachondria (Parachondria) augustae* (Adams, 1849) (Fig. 1), collected from unit 2 (*sensu* Pickerill *et al.*, 1998) of the Bowden shell bed. The shell is about 19.5 mm high by 12.5 mm wide, decollate, with just over 3½ whorls remaining, and perforate with a small umbilicus 1.3 mm in maximum diameter. The whorls are moderately tumid with well-marked sutures. The sculpture consists of weak collabral and spiral ribs.

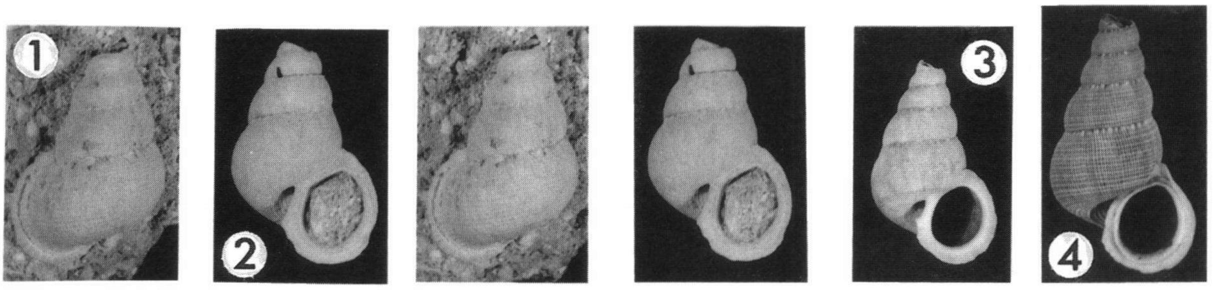

Fig. 1. *Parachondria (Parachondria)* spp. from the Pliocene and Recent of Jamaica. All figures x 1.5; 1-3 - *Parachondria (Parachondria) augustae* (Adams, 1849); BMNH PI TG 3940, Pliocene, Bowden shell bed (1, 2 - stereoscopic pairs), dorsal view of shell still partly buried in the sedimentary rock (1), anterior view of the shell after extraction (2). Note the small umbilicus, wide outer peristome which is reflected along the umbilical margin; BMNH PI TG 4226, Recent from near Bowden (3). Note the shorter reflected portion of the outer peristome adjacent to the umbilicus; 4 - *Parachondria (Parachondria) fascia* (Wood, 1828), Recent, BMNH PI TG 4227. Note the more slender and more highly sculptured shell, but the longer reflected portion of the outer peristome.

Collabral ribs are stronger on the early whorls, but spiral ribs become of equal strength, so that the body whorl appears malleated with pits between the rounded ribs. Collabral ribs join the suture to form white nodes roughly twice as thick as the collabral ribs. These nodes are rather irregularly spaced about every fifth collabral rib. There are about 60 collabral ribs on the last half whorl, with a more obvious interruption to shell growth about every fifth rib. Sutural nodes correspond to the middles, rather than the edges, of these growth increments. About 16 spiral ribs occur on the penultimate whorl between the sutures. The aperture is flared by an outer peristome about 1 mm thick in the direction of growth and extending about 0.8 mm up the penultimate whorl. Viewed from in front (Fig. 1/2), the outer peristome is a broad, slightly concave flange attached to the penultimate whorl along the parietal margin, ascending slightly to the right and reflected back towards the umbilicus along the columellar margin. It is broadest (1.5 mm wide) at the lower end of the reflected columellar margin. The inner peristome is weakly thickened and protrudes only slightly. It has four or five growth lines visible on it. The aperture itself is pyriform in outline, slightly angled at the upper right.

Modern shells of this species (Fig. 1/3) are very similar to the Bowden specimen, but with an even weaker sculpture and usually with a slightly shorter reflected portion to the outer peristome adjacent to the umbilicus. The character of the aperture is quite similar to that of *Parachondria (P.) fascia* (Wood, 1828), but within the range of variation of *P. (P.) augustae*. Although the fossil shell is at the strong end of the range of variation of the ribbing in *P. (P.) augustae*, *P. (P.) fascia* has very much stronger sculpture and a slightly more slender shell (Fig. 1/4). At the present day, the only species of *Parachondria* living anywhere near Bowden is *P. (P.) augustae*, which suggests that its area of distribution has changed little in the last few million years.

SCAPHOPODS

The scaphopods of the Bowden shell bed were examined by Pilsbry (1911) and Woodring (1925); more recently, the Jamaican fossil Scaphopoda were reviewed by Donovan (1990). Woodring (1925, pp. 197-210, pls 27, 28) recognised 20 species from the Bowden shell bed which he assigned to *Dentalium* Linné and *Cadulus* Philippi (Pl. 1, Fig. 1). This is easily the most diverse scaphopod fauna from the fossil record of Jamaica; indeed, it is more diverse than the modern shallow-water fauna known from the island (Humfrey, 1975, pp. 294-296). Following the classification of Emerson (1962), Donovan (1990) transferred three of Woodring's smooth-shelled dentaliids to the genus *Fustiaria* Stoliczka.

CEPHALOPODS

No cephalopod macrofossils have been recorded from the Bowden shell bed, but Clarke & Fitch (1975, 1979) identified loliginid teuthoid statoliths which were referred to *Loligo valeriae* Clark & Fitch. The absence of shelled cephalopods is not surprising, as the youngest Caribbean nautiloids are Miocene (Schmidt & Jung, 1993, table 1), and extant shelled coleoids from the Caribbean Sea such as *Argonauta* spp. and *Spirula spirula* (Linné) have a patchy fossil record (see, for example, Holland, 1988).

CHITONS

There are no previous reports of chitons from the Bowden shell bed. Indeed, this group is poorly known from the fossil record of the Antillean region. The only species hitherto described, both from the Maastrichtian of Puerto Rico, are *Chiton (C.) rossi* Smith, Sohl & Yochelson, 1968, and *Lorica praecursor* (Smith, Sohl & Yochelson, 1968). This is in contrast to the extant chiton fauna of the region, which includes over 25 nominal species in more than 12 genera.

Although so far undescribed, chitons are known from two late Cenozoic units in Jamaica; the Bowden shell bed and the late Pleistocene Falmouth Formation (S.K.D. and co-workers, research in progress). Nine valves of chitons are known from the Bowden shell bed (UF 71282, 75882, 76544-76550); about half of these specimens are fragmentary. The chiton fauna represents at least three species, although further valves are desirable if specific identifications are to be made. At least two specimens are acanthochitonids on the basis of their distinctive external sculpture (for Recent examples, see Lyons, 1988). Other identifications are more tentative (for example, Pl. 1, Figs 2, 3).

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Bivalvia	*Venericardia bowdenensis* Hodson *et al.*, 1927*
Gastropoda	*Hemitrochus bowdenensis* Goodfriend, 1992
	Pleurodonte bernardi Kimball, 1947
	Poirieria (Pazinotus) bowdenensis E.H. Vokes, 1970
	Poteria bowdenensis Bartsch, 1942
	Strombina (Sinaxilla) naufraga Jung, 1989
	Strombus dominator delabechei von Rutsch, 1931
Cephalopoda	*Loligo valeriae* Clarke & Fitch, 1979

Table 1. Nominal species of molluscs described from the Bowden shell beds since Woodring (1925, 1928). It should be noted that Woodring's work on bivalve molluscs tended to follow many original, older and possibly incorrect nomenclatures, such that contemporary literature (such as Sheldon, 1916-1917; Palmer, 1927) listed taxa from the same collections studied by Woodring (for example, Dall, 1890-1903), but used different specific names. These works should be consulted for a full list of synonyms. * =synonymised, by Woodring (1928, p. 48), as *Cardita scabricostata* Guppy, 1866a. Further to these new species, Jung (1971) recorded *Strombus gigas* Linné, a common extant species in the Caribbean, and terrestrial *Parachondria (Parachondria) augustae* (Adams) is reported herein.

Taxon	% (valves)
Corbula (C.) sericea Dall, 1898	13.64
Palliolum guppyi (Dall, 1898)	7.98
Diplodonta (D.) homalostriata Woodring, 1925	6.72
Nuculana (Jupiteria) indigena (Dall, 1898)	6.65
Linga (Bellucina) actinus (Dall, 1903)	5.59
Arca (Ar.) yaquensis berryi Woodring, 1925	4.66
Anadara (An.) donacia (Dall, 1898)	4.59
Nuculana (Jupiteria) subcerata (Woodring, 1925)	3.59
Bathyarca hendersoni (Dall, 1898)	2.86
Nuculana (Jupiteria) peltella (Dall, 1898)	2.86
Corbula (Varicorbula) heterogena (Dall, 1898)	2.66
Crassinella guppyi (Dall *in* Guppy & Dall, 1896)	2.46
Gouldia (G.) insulare (Dall & Simpson, 1901)	1.80
Lucina (Parvilucina) limnidus? (Woodring, 1925)	1.66
Trigonocardia (T.) haitense (Sowerby, 1849)	1.60
Verticordia (V.) bowdenensis Dall, 1903	1.26
[indeterminate bivalves]	1.26
Orthoyoldia ovalis (Gabb, 1873)	1.20
Myrtaea furcata Dall, 1903	1.20
Cuspidaria (Bowdenia) distira Dall, 1903	1.13
Anadara (An.) dasia? (Woodring, 1925) + *An. (An.) wordeni* (Woodring, 1925)	1.13
Limopsis (Pectunculina) ovalis silova Woodring, 1925	1.00*

Table 2. Relative abundances of fossil bivalves in a bulk sample (unweighed) from the Bowden shell bed, collected by C.R.C.P. in 1994. Total number of species = 97 (counting indeterminate shells in any given genus or family as one species); total number of valves = 1,503, comprised of 1,411 disarticulated valves and 46 conjoined pairs; valves of 22 species present as 1% of sample or greater; * = rounded up from 0.998%.

PLATE 1

Benthic molluscs of the Bowden shell bed, Jamaica.

Fig. 1. BMNH G11024, general view of a coquinoid slab with abundant *Dentalium* sp. or spp. and associated gastropods, probably from the Bowden shell bed (after Donovan, 1990, fig. 4J); the specimen indicated by the arrow has been bored (see Pickerill & Donovan, 1998), x 2.

Figs 2, 3. UF 76544, indeterminate intermediate chiton valve; 2 - left lateral view, x 16; 3 - dorsal view, x 15.

Figs 4-6. *Teredolites longissimus* Kelly & Bromley, 1984; 4 – BMNH PX TF 21, short fragment of a narrow tube about 2 mm in diameter, x 19.5; 5 – BMNH PX TF 22, short fragment of a tube showing several changes in direction, x 22.5; 6 – BMNH PX TF 23, convex end of a rounded internal partition showing the fibrous calcite of the outer wall (left), x 35.

Figs 2-6 are scanning electron micrographs of specimens coated with 60% gold-palladium.

PLATE 1