

# Fossil brachiopods from the Pleistocene of the Antilles

David A.T. Harper & Stephen K. Donovan

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Pleistocene brachiopods are poorly known from the Antillean region, but are locally common in fore-reef deposits of Jamaica (lower Pleistocene Manchioneal Formation) and Barbados (Coral Rock). Of the four species known, two are new. *Lacazella* sp. cf. *L. caribbeanensis* Cooper, an encrusting thecideidean, is known from only three valves. Other species are terebratulides. *Tichosina inconstanta* sp. nov. is a large, ventribiconvex *Tichosina* species of elongate oval to tear-drop shaped outline, variably uniplicate with a pedicle foramen of moderate diameter. It differs from the similar *Tichosina? bartletti* (Dall) in having a larger pedicle foramen and a less-marked plication. *Argyrotheca barrettiana* (Davidson) is a medium to large, usually transverse *Argyrotheca* species, multicostellate with usually eight costae and costellae, increasing by intercalation up to 21 on the largest shell. The species was originally described from the Recent of the Caribbean. *Terebratulina manchionealensis* sp. nov. is a small, elongately oval to subtriangular *Terebratulina* species with a ventral sulcus and subcarinate dorsal valve. Usually there are 6-8 ribs per 2 mm at 5 mm growth stage. The known diversity in Pleistocene brachiopods from the Antilles, only four species, is depauperate when compared to the 50+ species known from the Recent of the Caribbean Sea and the Straits of Florida. The Pliocene fauna of the region, however, is similarly lacking in diversity, but includes the same genera. The comparable Pleistocene fauna of the Mediterranean Sea includes eight species belonging to six genera, including *Lacazella*, *Argyrotheca* and *Terebratulina*; the Mediterranean *Gryphus* is an analogue for the Caribbean *Tichosina*.

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## Introduction

In his monograph of the Cretaceous and Cenozoic brachiopods of the Caribbean, Cooper (1979) described a variety of taxa, but the youngest were from the Pliocene, leaving a gap between the fossil record and the extant taxa from the same region (Cooper, 1977). However, Cooper may have been unaware that Pleistocene brachiopods had been recorded from the region previously, but as parts of monographic studies of Pleistocene molluscs from Jamaica and Barbados by Trechmann (1930, 1937). Trechmann's systematic assignments are now considered to be more or less incorrect, and his illustrations of

taxa are somewhat indistinct and of little use for modern taxonomy. Indeed, Pleistocene brachiopods had been found in Jamaica before 1862 by Lucas Barrett (see below; Long & Donovan, 2004).

A preliminary review of the Jamaican fossil Brachiopoda, including re-identification of Trechmann's Pleistocene taxa at the generic level and published 60 years after his original paper, was based on the limited material then available (Harper & Donovan, 1990), illustrated by Dr Eamon Doyle (Fig. 1). Although further papers have refined the systematics (Harper, 1993, 2002a; Harper & Donovan, 2002) and examined their palaeoecology (Harper *et al.*, 1995; Donovan & Harper, 2001, 2007), Antillean Pleistocene brachiopods have remained poorly known. Now, large new collections from a number of Trechmann's (and other) localities, made by the present authors since 1987, permit a reassessment and refinement of the systematics and relationships of the Antillean Pleistocene brachiopods, including new information concerning internal morphology and statistical comparison between and within collections.

Terminology used in the present paper follows Williams & Brunton (1997). The specimens discussed herein are deposited in The Natural History Museum, London (BMNH), the Geological Museum, University of Copenhagen (MGUH), the Florida Museum of Natural History, Gainesville (UF) and the Nationaal Natuurhistorisch Museum, Leiden (RGM). Differences in sample sizes between Jamaica and Barbados are a reflection of the more intensive field effort of the authors on the Manchioneal Formation (1987-1998) compared with the Coral Rock (1997, 2001, 2002).

### Localities and horizons

Table 1 summarises the known distribution of the common brachiopod species within each of the localities listed below. A significant part of the data from Jamaica is

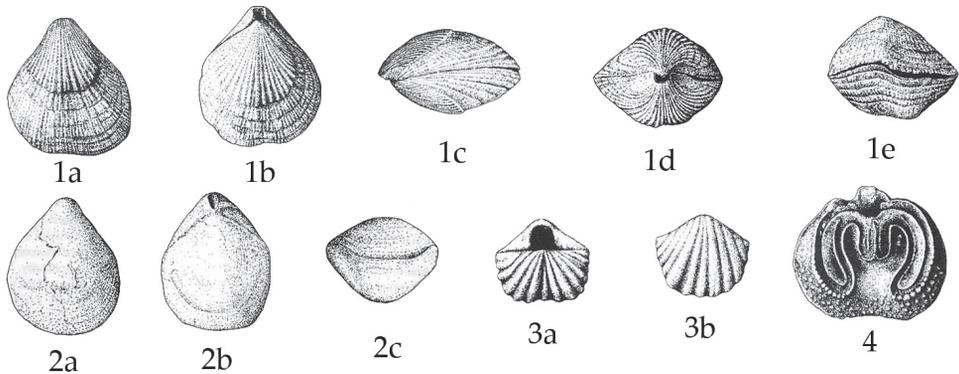


Fig. 1. Line drawings of the Pleistocene brachiopod taxa of the Antilles. 1a-e, *Terebratulina manchionealensis* sp. nov., ventral, dorsal, lateral, posterior and anterior views of conjoined valves, approximately X 2.5. 2a-c, *Tichosina inconstanta* sp. nov., ventral, dorsal and anterior views of conjoined valves, approximately X 1.6. 3a-b, *Argyrothecha barrettiana* (Davidson, 1866), dorsal and ventral views of conjoined valves, approximately X 3.3. *Lacazella caribbeanensis* Cooper, 1977, dorsal interior, approximately X 8.3. (Modified from Harper & Donovan, 1990, fig. 3).

Table 1. Distribution of brachiopods between Pleistocene localities in Jamaica and Barbados. Explanation of locality designations in text. Note 1: *Argyrotheca* sp. and *Tichosina* sp. are known from the lower Pleistocene Nancy Point Formation, Bocas del Toro, Panama (Harper & Donovan, 2002, p. 174). Note 2: *Argyrotheca* sp. is known from the lower Pleistocene Moin Formation, Limon, Costa Rica (Harper & Donovan, 2002, p. 174).

Locality/Taxon	<i>Tichosina inconstanta</i> <sup>1</sup>	<i>Argyrotheca barrettiana</i> <sup>1,2</sup>	<i>Terebratulina manchionealensis</i>
Cruikshank Bay, Jamaica (J1)	-	1	2
Manchioneal, Jamaica (J2)	123	87	11
Christmas River, Jamaica (J3)	117	14	48
San San Bay, Jamaica (J4)	-	-	2
Folly Point, Jamaica (J5)	-	1	2
N Port Maria, Jamaica (J6)	-	-	2
Whitehaven, Barbados (B1)	24	18	22
Cluffs Bay, Barbados (B2)	1	-	-
Ragged Point, Barbados (B3)	134	1	2
Arawak Cement Quarry, Barbados (B4)	-	1	-
TOTALS	399	123	91

based on collections made in association with Dr Eamon Doyle (formerly of the University of the West Indies, Mona Campus, Jamaica). The material was identified by the authors, but to date these collections have not been relocated and are presumed lost.

### *Jamaica*

Jamaica is situated at the northeastern end of the Nicaraguan Rise and is within the north Caribbean plate boundary zone (Robinson, 1994). Its rock record extends from the Lower Cretaceous to Quaternary, and is strongly faulted due to ancient and continuing tectonic activity. About two-thirds of the surface outcrop is limestone, which has been extensively karstified.

Fossil brachiopods are relatively sparse, but widely dispersed throughout the Cretaceous and Cenozoic rocks of Jamaica. Available material is assigned to eleven taxa, indicating a potential for further research. The limited previous work on the phylum was reviewed by Harper & Donovan (1990) and Harper (1993), where the early contributions of De la Beche (1827), Sawkins (1869), Cockerell (1894) and Hill (1899) were noted. The Jamaican brachiopod fauna is similar to that described from nearby Hispaniola (Logan, 1987) and from the Caribbean as a whole (Cooper, 1979).

The Manchioneal Formation of eastern Jamaica, mainly exposed in the parish of Portland, is a sequence of bedded, often nodular limestones that were deposited on the island shelf in the early Pleistocene and are interpreted as fore reef deposits (Robinson, 1967, 1969a, b; Kohl, 1992; Harper *et al.*, 1995). The first account of brachiopods from the Manchioneal Formation was by Trechmann (1930, pp. 213-214, pl. 12, figs. 1-4), who recognised *Terebratula* cf. *cubensis* Pourtales, *Terebratula* cf. *bartletti* Dall, *Terebratula* sp., *Terebratula*(?) sp. and *Terebratulina caput-serpentis* Linné. Other groups that have been documented from the Manchioneal Formation (excluding the Old Pera beds; Robinson, 1969a, b) include benthic foraminiferans (Kohl, 1992), benthic molluscs (Trechmann,

1930), crinoids (Donovan, 1995), echinoids (Donovan & Embden, 1996; Donovan & Portell, 1996) and trace fossils (Donovan *et al.*, 2001; Donovan & Harper, 2007); scleractinian corals and barnacles are also present. This unit has yielded, to date, the largest and most diverse assemblage of fossil brachiopods from Jamaica. The following brachiopod localities are known from the Manchioneal Formation (Fig. 2); all are in the parish of Portland unless stated otherwise.

*Locality J1 - Cruikshank Bay, parish of St. Thomas* (NGR 809 396) – Roadside exposure along the main A4 east coast road, just south of the bridge over the Horse Savanna River and from nearby tracks.

*Locality J2 - Manchioneal* (NGR 799 413) – The type section is exposed as a vertical cliff immediately adjacent to the main A4 east coast road and to the north in coastal exposure. This section was discussed by Trechmann (1930, p. 203), Robinson (1969a, pp. 129-130; 1969b, pp. 12-14) and Donovan *et al.* (1995), and was figured by Donovan *et al.* (1990, fig. 2D). The present authors have collected shells from clean vertical faces and rare landslides, the latter providing the majority of our specimens of Jamaican *Tichosina*.

*Locality J3 - Christmas River* (NGR 798 421) – Cliffs and associated fallen blocks of the Manchioneal Formation are well-exposed adjacent to the mouth of the Christmas River,

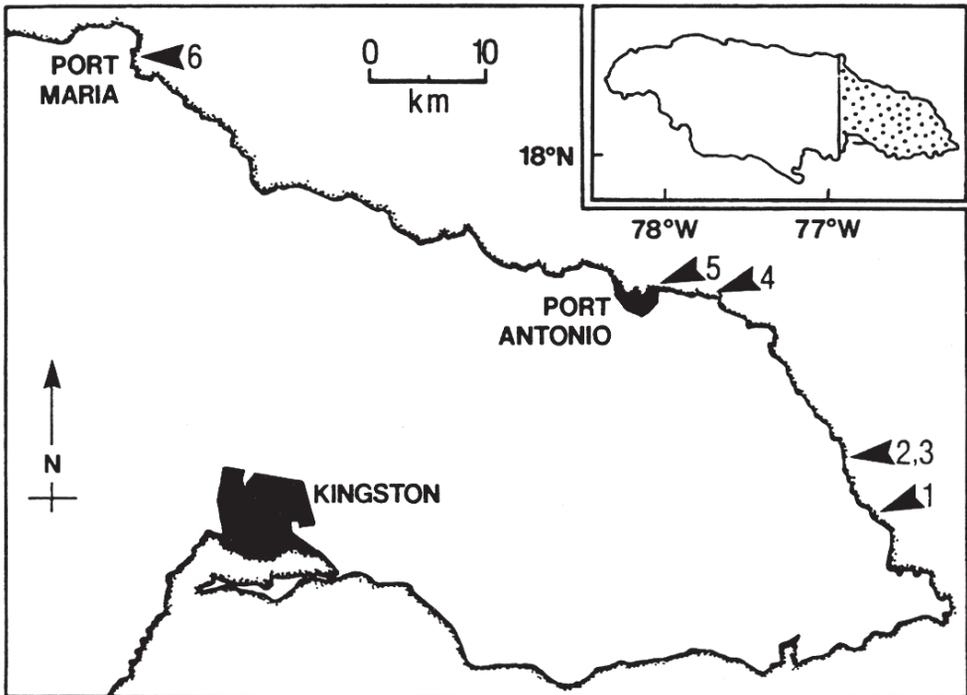


Fig. 2. Outline map of eastern Jamaica, showing the main towns and city (after Donovan & Embden, 1996, fig. 1). Key to fossil localities considered herein: (J)1 = Cruikshank Bay; (J)2 = Manchioneal; (J)3 = Christmas River; (J)4 = San San Bay; (J)5 = Folly Point, Port Antonio; (J)6 = north of Port Maria. Inset is an outline map of Jamaica showing the area of the main map (stippled).

as is the contact with the underlying Bowden Formation. This is interpreted as the deepest water depositional setting of the formation, based on the presence of stalked crinoids that indicate a palaeodepth of over 150 m (Donovan, 1995). Brachiopods were collected both *in situ* and from lithified fallen boulders.

*Locality J4 - San San Bay* (NGR 588 663) – This section in the Navy Island Member, originally described by Robinson (1969b, pp. 7-9), is now concealed by a retaining wall. This locality has also yielded isocrinids (Donovan, 1989).

*Locality J5 - Folly Point, Port Antonio* (NGR 745 466) – Folly Point protects the eastern side of the east harbour at Port Antonio. Robinson (1969b, p. 10) considered the section on the eastern coast of Folly Point to be a ‘paratype’ section for the Navy Island Member, as access to the type section can be difficult; the present authors have not examined the Folly Point section. The contacts with the underlying Bowden Formation and overlying Falmouth Formation are apparent.

*Locality J6 - North of Port Maria, parish of St. Mary* (NGR 587 543) – A spectacular coastal exposure that outcrops beneath the ruins of the Tropic Wind Hotel. A measured section through this exposure was figured by Cant (1971, p. 64-66, fig. 13).

### *Barbados*

Barbados is located in the southeast of the Antillean region, about 2000 km from Jamaica. It differs from islands of the Lesser Antilles in lying away from the convex side of the island arc and in having a sedimentary, not volcanic, origin, being situated at the summit of the Lesser Antillean accretionary prism (Speed, 1994; Machel, 1999; Donovan with Harper, 2005). The allochthonous Tertiary rocks of the accretionary prism underlie the entire island, but only form about 10 per cent of its outcrop, which is largely limited to the Scotland District in the northeast of Barbados. These deposits have yielded rare micromorphic brachiopods (Harper, 2002b). The remaining 90 percent of the island’s outcrop consists of autochthonous Pleistocene reef limestones that occur as three principal terraces, distinguished topographically as the Upper (oldest), Middle and Lower (youngest) Coral Rock (Poole & Barker, 1983; for a discussion of the historical development of ideas on the age and genesis of these limestones, see Donovan & Harper, 2002). The age of these units is Pleistocene; Trechmann considered the fauna of the basal Coral Rock to have a “pre-Pleistocene aspect” (1937, p. 358; see also 1958, p. 433; Donovan, 2003). These terraces are constructional reef features that preserve the original coral zonation of the reef structure (e.g., Mesolella, 1967; Mesolella *et al.*, 1970). They represent the product of reef growth during the complex interaction of tectonic uplift and fluctuations of sea level during the Pleistocene. Apart from brachiopods, the fauna includes benthic foraminiferans, bryozoans, benthic molluscs (Trechmann, 1937; Jung, 1968), echinoids and astropectinid asteroids (Donovan, 2000), the boring *Entobia* isp. (produced by clionid sponges) in some molluscs, and rarer pteropods, crabs (Collins & Morris, 1976) and arcoscalpellid barnacle plates. The following brachiopod localities are known from the Coral Rock (Fig. 3).

*Locality B1 - Skeete’s Bay, Whitehaven* – Brachiopods have been collected from the northwest side of Skeete’s Bay, Whitehaven, parish of St. Philip, southeast Barbados (approximately 59° 27’ 00” W 13° 10’ 00” N; see also Trechmann, 1937, pp. 346, 357, text-

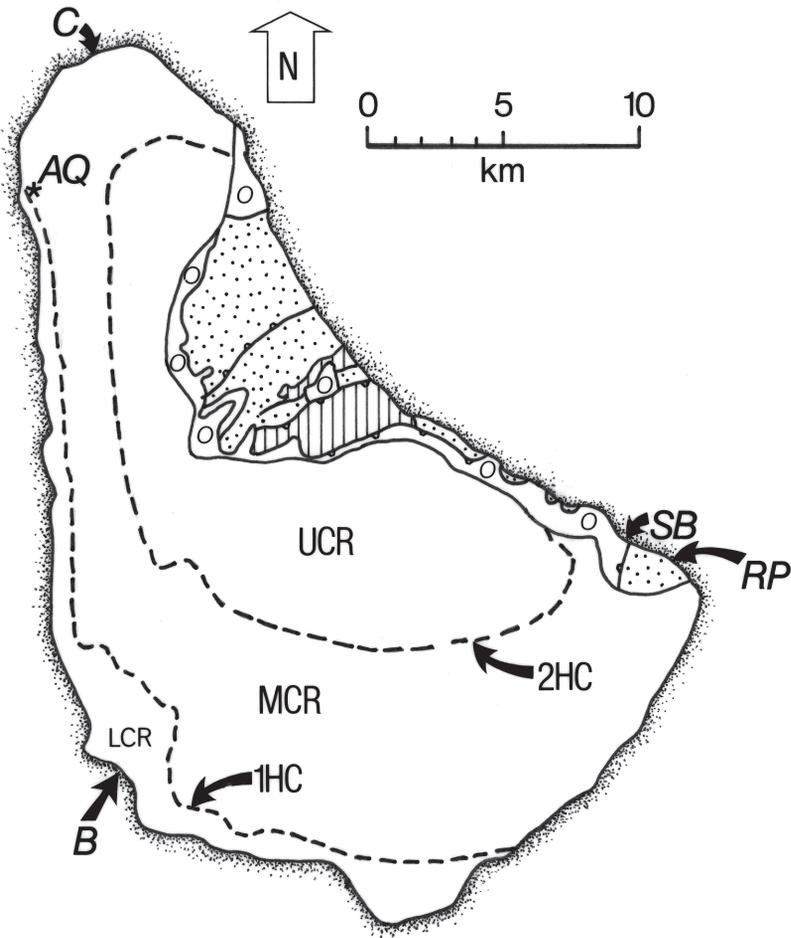


Fig. 3. Simplified geological map of Barbados (modified after Donovan with Harper, 2005, fig. 1; redrawn and modified after Speed *et al.*, 1991, fig. 2). Key to tectono- and lithostratigraphic units (for explanation, see Speed, 1994): open stipple = basal complex; vertical ruling = diapiric melange; O = Oceanic nappes; UCR = Upper Coral Rock; MCR = Middle Coral Rock; LCR = Lower Coral Rock. The First High Cliff (1HC) separates the LCR and MCR; the Second High Cliff (2HC) separates the MCR and UCR. Key to place names and brachiopod localities: AQ = Arawak Cement Quarry (B4); B = Bridgetown; C = Cluffs Bay (B2); RP = Spring Bay, south of Ragged Point (B3); SB = Skeete's Bay (B1).

fig. 3; Donovan with Harper, 2005, fig. 6). It is a coastal exposure of the basal Middle Coral Rock (484,000-127,000 years old; Poole & Barker, 1983) that rests unconformably on the Tertiary Oceanic Group; the basal position suggests a mid Pleistocene age. The brachiopods from Whitehaven were collected in August 1997 and June 2002, mainly from well-lithified float blocks on the beach and also from the lowermost 2 m of the section. The lithology, fauna and preservational style of the fossils in the Middle Coral

Rock at this locality are reminiscent of the lower Pleistocene Manchioneal Formation of Jamaica (Donovan *et al.*, 2002).

*Locality B2 - Cluffs* – Cluffs Bay, parish of St. Lucy, west of North Point and the Animal Flower showcave, is reached on a track to the coast. Care must be taken at this locality (approximately 59° 37' 48" W 13° 19' 38" N; Donovan with Harper, 2005, fig. 7), with narrow ledges perched at the unconformity between the Miocene Oceanics and the basal Middle Coral Rock. Trechmann (1937, p. 344) published a measured lithological section, and (p. 349) listed a fauna of benthic molluscs, pteropods and brachiopods from this locality that is much less diverse than that from Whitehaven; it is unclear whether this is an artefact of the easier access at the latter locality. *Tichosina* sp. cf. *T. bartletti* (Dall) (Harper, 2002a) was the only brachiopod recognised at Cluffs Bay.

*Locality B3 - Spring Bay, south of Ragged Point* – At Spring Bay, south of Ragged Point, parish of St. Philip (approximately 59° 26' 00" W 13° 09' 35" N; Donovan with Harper, 2005, fig. 6), the Tertiary/Quaternary (= Middle Coral Rock) unconformity is well-exposed (see Trechmann, 1937, p. 345). A horizon of *Tichosina* shells is exposed above the beach on the south side of the bay.

*Locality B4 - Arawak Cement Quarry* – The Arawak Cement Quarry (Lower Coral Rock), parish of St. Lucy (approximately 59° 38' 47" W 13° 17' 6" N; Donovan with Harper, 2005, fig. 7), on the west coast of northern Barbados, has yielded a single shell of *Argyrotheca* sp. This locality was not known to Trechmann (1937).

*Other localities* – Trechmann (1937, p. 349) tabulated the occurrences of molluscs and brachiopods in the basal Coral Rock. Brachiopods were recognised from seven localities. Apart from Localities B1-B3, mentioned above, Trechmann found brachiopods at Spring Hill, Caledonia, Chimborazo, and Loamfield and Hopefield (not marked on Fig. 3).

### Systematic palaeontology

*Remarks* – Despite our efforts over the past 20 years to expand the recorded fauna of fossil brachiopods from Jamaica, sample sizes of known taxa have commonly remained small. Thus, ontogenetic and size-independent intra-specific variation has been difficult to define and assess. Moreover, irrespective of the small size of samples, little information is available regarding the internal features of the majority of the described species; a number of generic assignments have thus been provisional.

An exception is the terebratulid assemblage of the Manchioneal Formation, now represented by dozens of specimens and described below. Wherever possible, species descriptions are supplemented by measurements and some statistical information; some interspecific comparisons have been effected by Principle Component Analysis (PCA). These PCA analyses have informed our taxonomic methodology concerning those species identified from both Barbados and Jamaica. It is apparent that there are differences, perhaps worthy of nominal subspecific status, between Jamaican and Barbadian samples of two of the three commoner species found in both islands. However, whereas the Manchioneal Formation has over one hundred brachiopods, the Coral Rock, with the exception of the *Tichosina* shell bed (locality B3), has yielded only tens. The latter are insufficient to permit the rigorous statistical definition of new subspecies. We therefore elect to take a conservative approach, and 'lump' the samples from Barbados and Jamaica together, but nevertheless highlight those inter-island differences that are apparent.

The following abbreviations have been used for measurements (in mm): saglv - sagittal length of ventral valve; sagld - sagittal length of dorsal valve; mwi - maximum width; hwi - hinge width; pmwi - position of maximum width; dpv - maximum depth of ventral valve; dpd - maximum depth of dorsal valve.

**Order Theceida Elliot, 1958**  
**Superfamily Thecideoidea Gray, 1840**  
**Family Thecideidae Gray, 1840**  
**Subfamily Lacazellinae Backhaus, 1959**  
**Genus *Lacazella* Munier-Chalmas, 1880**

*Type species* – *Theceida mediterranea* Risso, 1826, by original designation; from the Recent of the Mediterranean Sea.

***Lacazella* sp. cf. *L. caribbeanensis* Cooper, 1977**  
Pl. 1, fig. 1

- cf. 1864 *Thecidium mediterraneum* (Risso); Davidson, p. 21, pl. 2, fig. 5.
- cf. 1887 *Thecidium mediterraneum* (Risso); Davidson, p. 158.
- cf. 1971 *Lacazella mediteranea* (Risso); Meile & Pajaud, p. 470, pl. 1, figs. 1-4.
- cf. 1977 *Lacazella caribbeanensis* Cooper, p. 132, pl. 4, figs. 12-19.
- cf. 1979 *Lacazella caribbeanensis* Cooper; Logan, p. 75, pl. 10, figs. 9-14.
- cf. 1979 *Lacazella caribbeanensis* Cooper; Cooper, p. 28, pl. 1, figs. 2-5.
- cf. 1987 *Lacazella caribbeanensis* Cooper; Logan, p. 51, pl. 12, figs. 42-49.
- 1990 *Lacazella* sp.; Harper & Donovan, p. 29, fig. 3.
- 1993 *Lacazella* sp. cf. *L. caribbeanensis* Cooper; Harper, pp. 106-108, fig. 2.17.
- 1995 *Lacazella* sp. cf. *L. caribbeanensis* Cooper; Harper *et al.*, p. 221, fig. 2c.
- 1998 *Lacazella*; Donovan & Harper, p. 27.
- 2002a *Lacazella* sp. cf. *L. caribbeanensis*; Harper, table 12.1.
- 2002 *Lacazella* sp. cf. *L. caribbeanensis*; Harper & Donovan, p. 175.
- 2007 *Lacazella* sp. cf. *L. caribbeanensis* Cooper; Donovan & Harper, p. 60.

*Material* – A single specimen in the Lucas Barrett collection, BMNH B 21988 and a further valve in the collections of the Geological Museum, University of Copenhagen, both from Jamaica. A valve from the Middle Coral Rock of Barbados is also deposited in the Geological Museum, University of Copenhagen.

*Description and measurements* – See Harper (1993).

*Discussion* – Until further specimens of this taxon become available, little can be added to the comments made by Harper (1993). However, despite its rarity in the fossil record of Jamaica, it is worthwhile re-emphasising that extant *L. caribbeanensis* Cooper, 1977, is also known from the Tertiary of Cuba and the Dominican Republic (Cooper, 1979; Logan, 1987). Our inability to find more than one further specimen in the Manchioneal Formation, after many years of collecting, has been frustrating, but strongly indicates that this species is rare within this unit. However, it is also conceivable that our interpretation of the horizon from which it was collected may be erroneous, although we do not consider this likely. One valve of this species has also been collected from Barbados.

*Occurrence* – The label of BMNH B21988 states that this specimen is from the “newer Pliocene” of Jamaica. This is interpreted to be the Manchioneal Formation. However, in over 140 years since Barrett’s original discovery only one further specimen has been collected from Jamaica. As noted by Trechmann (1930, p. 216), “...the Manchioneal beds have been referred by most writers to the Pliocene ...”, a position with which he agreed with “... some doubt ...” and considered that “... Possibly if they were in Europe the Manchioneal [Formation] and perhaps also the Bowden [shell] beds might be placed in the Pliocene rather than the Miocene.” This was at a time when the Bowden shell beds, recognised to be older than the Manchioneal Formation, were considered to be Middle Miocene (Woodring, 1928; Trechmann, 1930, p. 200); they are now identified as Upper Pliocene (Donovan, 1998, and references therein).

*Remarks* – A printing error in Harper (2002a, table 12.1) omitted the symbol ‘J’ (for Jamaica) in the ‘Pleistocene’ column for this taxon.

**Order Terebratulida Waagen, 1883**  
**Suborder Terebratulidina Waagen, 1883**  
**Superfamily Terebratuloidea Gray, 1840**  
**Family Terebratulidae Gray, 1840**  
**Subfamily Tichosininae Cooper, 1983**  
**Genus *Tichosina* Cooper, 1977**

*Type species* – *Terebratula floridensis* Cooper, 1977, by original designation; from the Recent of the Caribbean and Gulf of Mexico.

***Tichosina inconstanta* sp. nov.**

Pl. 1, figs. 2-7; Pl. 2.

- 1930 *Terebratula* cf. *cubensis* Pourtales; Trechmann, p. 214, pl. 12, fig. 1.
- 1930 *Terebratula* cf. *bartletti* Dall; Trechmann, p. 214.
- 1930 *Terebratula* sp.; Trechmann, p. 214, pl. 12, fig. 2.
- 1937 *Liothyryna* sp. or *Gryphus* sp.; Trechmann, p. 354, pl. 122, figs. 27, 28, table.
- 1990 *Tichosina* sp.; Harper & Donovan, p. 22, fig. 3.
- 1993 *Gryphus?* sp.; Harper, p. 108, figs. 3.1, 3.2, 3.16, 3.17.
- 1993 *Tichosina* sp.; Harper, p. 108, figs. 3.3-3.15, 3.18, 3.19.
- 1995 *Tichosina* sp. cf. *bartletti* (Dall); Harper *et al.*, p. 221, fig. 2j, k.
- 1998 *Tichosina* cf. *bartletti* (Dall); Donovan & Harper, fig. 3e-i.
- 2002a *Tichosina* cf. *bartletti* (Dall); Harper, table 1.
- 2002a *Tichosina*; Harper, p. 145.
- 2002 *Tichosina* cf. *bartletti* (Dall); Harper & Donovan, p. 175.
- 2002 *Tichosina*; Harper & Donovan, pp. 175-178, fig. 16.2.
- pars* 2005 terebratulid brachiopods; Donovan with Harper, p. 24.
- 2005 *Tichosina* cf. *bartletti* (Dall); Donovan with Harper, p. 24.
- 2007 *Tichosina* sp. cf. *T. bartletti* (Dall); Donovan & Harper, p. 60.

*Holotype* – A conjoined pair, MGUH 28767 (Pl. 1, fig. 4a, b) from the Manchioneal Formation, Christmas River (J3), Jamaica.

*Type locality and horizon* – Christmas River, Manchioneal Formation (J3) (lower Pleistocene).

*Material* – About 400 shells of this species have been collected from localities on both Jamaica and Barbados.

*Derivation of name* – Name referring to the morphological variation seen in the species.

*Diagnosis* – Large, ventribiconvex *Tichosina* species of elongate oval to tear-drop shaped outline, variably uniplicate; pedicle foramen of moderate diameter.

*Description* – Large ventribiconvex valves, elongate oval to tear-drop shape outline. Maximum width over twice hinge width, occurring at about two-thirds valve length; cardinal extremities obtuse and rounded. Anterior commissure rectimarginate to sulcate; lateral commissures curved. Ventral valve almost nine-tenths as wide as long and about one-third as deep as long. Anterior profile uniformly convex; lateral profile with maximum curvature at umbo, elsewhere surface evenly curved except over anterior third where valve slopes steeply towards anterior commissure. Pedicle foramen variable, circular, oval or labiate, permesothyrid and of moderate diameter. Dorsal valve almost as wide as long and about one-fifth as deep as long. Anterior profile flatly convex with shallow, broad sulcus developing anteriorly from near mid-valve length; lateral profile convex over posterior half of valve, elsewhere surface slopes anteriorly. Ornament of variably accentuated, but subdued, concentric growth lines.

Ventral interior with small, elongate teeth and short pedicle collar. Dorsal interior with narrow loop; outer hinge plates, long and concave; flat-bladed crural bases form raised margin to outer hinge plates. Broad crura with wide transverse ribbon.

*Statistics* –

<b>Variates</b>							
saglv	sagld	mw	hinw	pmw	dpv	dpd	dpf
<b>Means</b>							
25.24	22.45	20.75	11.54	15.61	9.11	6.56	2.02
<b>Var-Covar</b>							
175.39	156.76	133.52	67.24	111.18	65.76	52.08	12.89
	141.10	120.57	59.90	99.82	58.15	46.69	11.36
		105.58	52.32	85.90	48.75	39.59	9.84
			28.77	43.91	25.65	19.94	5.18
				74.90	41.74	33.51	8.36
					29.72	20.70	4.87
<b>Sample</b>						17.65	3.83
N=35							1.14

*Discussion* – The Jamaican material was originally compared (Harper, 1993) with *Tichosina? lecta* (Guppy, 1866), first described from the Eocene of Trinidad and subsequently re-described from the type area by Cooper (1979). This species is also reported from the Miocene and Pliocene of the Dominican Republic (Logan, 1987), although that

material was relatively rare and poorly preserved. Based on data from Cooper (1979) and Logan (1987), a pooled sample of all three forms was investigated by PCA for the following variates: saglv, sagld, mwi and thickness (= dpv+dpd). Differentiation was achieved with respect of scores on the third eigenvector. The type specimens from Trinidad had higher scores (0.20, 0.42) on this eigenvector than the specimens from Jamaica and the Dominican Republic. The direction cosines of the third eigenvector (-0.69, -0.20, 0.60, 0.36) indicate the type *T.? lecta* to have relatively shorter, wider and more globose shells than those of the other two forms (Harper, 1993). However, larger samples of all three are required to confirm these apparent differences. More recent assessments of the Jamaican material (e.g., Harper *et al.*, 1995) have compared it with *T.? bartletti* (Dall, 1920), a living species from the Caribbean with a more pronounced uniplicate anterior margin (Cooper, 1977). The large samples now available of the Pleistocene form together with details of its internal features allow, first a confident assignment to *Tichosina* and second the establishment of a new species. The cardinalia of the new species have the flat-bladed crural bases that are diagnostic for the genus. The large size, elongate oval shape and variably uniplicate anterior commissure associates the Pleistocene material with only *T.? bartletti*. However, that species has a small pedicle foramen and a more marked plication.

The large samples now available from both Jamaica and Barbados indicate extreme variation in the external morphology of this species. In fact, a large specimen of this species was originally ascribed to *Gryphus?* (Harper, 1993); information on the interior of that specimen is unfortunately lacking, but it now seems more probable, in view of the large and continuous sample variation now apparent (see statistics above), that the specimen should be included within the new species. It seems unlikely that populations of two or more species have been mixed; rather, the Pleistocene form of *T. inconstanta* had a fairly plastic external shape. It is also possible that the material described from Miocene and Pliocene of the Dominican Republic (Logan, 1987) may also belong within *T. inconstanta*, but more material of the latter is required to test this.

Although a large number of specimens of *Tichosina* are known from Barbados only two have yielded a complete set of measurements. These, together with a sample of 35 specimens from Jamaica, including the conjoined valves previously assigned to *Gryphus?* sp., were subjected to a PCA interrogation of the correlation matrix based on the following variates: saglv, sagld, mw, hinw, pmw, dpv and dpd. The first two eigenvectors account for 95% of the variation. The Barbados material could not be separated on these or indeed the next two eigenvectors that accounted together for further 2% of the sample variation. With regard to the variates analysed, both samples, including *Gryphus?* sp., are considered conspecific.

*Occurrence* – This species is common on Jamaica at the type section of the Manchioneal Formation (J2) and Christmas River (J3), and occurs at Cruikshank Bay (J1) and Folly Point (J5); approximately 240 shells of this species are now known from the Jamaican localities. Additionally, eight specimens in the Lucas Barrett collection (BMNH) are from the ‘Tertiary and newer Pliocene’ of Jamaica (= Manchioneal Formation; see above). The localities on Barbados, Skeete’s Bay, Whitehaven (B1), Cluff’s Bay (B2) and Spring Bay, Ragged Point (B3) have yielded almost 160 shells; although a large number were recovered from the shell bed at Spring Bay, Ragged Point (B1), most are incomplete.

**Superfamily Cancellothyridoidea Thomson, 1926**  
**Family Cancellothyrididae Thomson, 1926**  
**Subfamily Cancellothyridinae Thomson, 1926**  
**Genus *Terebratulina* d'Orbigny, 1847**

*Type species* – *Anomia retusa* Linné, 1767, by original designation; from the Recent of Norway.

***Terebratulina manchionealensis* sp. nov.**

Pl. 1, fig. 8; Pl. 3, figs. 3-6.

- 1930 *Terebratulina caput-serpentis* Linn.; Trechmann, p. 214, pl. 12, fig. 4.  
1937 *Terebratulina caput-serpentis* Linn.; Trechmann, pl. 12, fig. 29, table.  
1937 *Terebratulina caput serpentis* Linn.; Trechmann, p. 354.  
cf. 1979 *Terebratulina?* *palmeri* Cooper sp. nov., p. 6, pl. 1, figs. 6-23, pl. 7, figs. 9-20.  
1990 *Terebratulina* sp.; Harper & Donovan, pp. 21-22.  
1993 *Terebratulina* sp. cf. *T. palmeri* Cooper; Harper, p. 113, figs 4.1-4.10, 4.17.  
1995 *Terebratulina* sp. cf. *palmeri* Cooper; Harper *et al.*, p. 221, fig. 2e-I, l, m.  
1998 *Terebratulina* cf. *palmeri* Cooper; Donovan & Harper, fig. 3a, b.  
2002a *Terebratulina* cf. *palmeri* Cooper; Harper, table 12.1  
2002a *Terebratulina* sp.; Harper, p. 145.  
2002 *Terebratulina* sp. cf. *palmeri* Cooper; Harper & Donovan, p. 175.  
2002 *Terebratulina* sp.; Harper & Donovan, p. 175-178, fig. 16.2.  
*pars* 2005 terebratulid brachiopods; Donovan with Harper, p. 24.  
2007 *Terebratulina* sp. cf. *T. palmeri* Cooper; Donovan & Harper, p. 60.

*Holotype* – A disarticulated conjoined pair, MGUH 28774a, b (Pl. 3, figs. 5, 6) from the Manchioneal Formation, Christmas River (J3), Jamaica.

*Type locality and horizon* – Christmas River, Manchioneal Formation (J3) (lower Pleistocene).

*Material* – About 90 shells of this species have been collected from localities on both Jamaica and Barbados.

*Derivation of name* – Named after the Manchioneal Formation on Jamaica from whence the majority of the Pleistocene specimens were collected.

*Diagnosis* – Small, elongately oval to subtriangular *Terebratulina* species with ventral sulcus and subcarinate dorsal valve. Usually 6-8 ribs per 2 mm at 5 mm growth stage.

*Description* – Small, dorsibiconvex valves of elongately oval to subtrigonal outline. Maximum width about twice hinge width, occurring at or near mid-valve length; cardinal extremities obtuse and rounded. Anterior commissure uniplicate. Ventral valve about nine-tenths as wide as long and about one-fifth as deep as long. Anterior profile with narrow, relatively deep median sulcus originating near prominent umbo and developing anteriorly; flanks convex medianly with steep lateral slopes. Lateral profile convex with maximum curvature at mid-valve length. Large suboval pedicle foramen

perforates shell apex. Dorsal valve about as long as wide and about one-fourth as deep as long. Anterior profile subcarinate with prominent median fold and sloping, slightly concave flanks; lateral profile uniformly convex with marked umbo. Ornament of variably accentuated costae and costellae numbering 5-8 per 2 mm at 5 mm growth stage on 1, 7, 9 and 8 valves, and arising by both bifurcation and intercalation.

Ventral interior with short pedicle collar; large, elongate teeth. Dorsal interior with small transverse cardinal process; socket ridges thin and elevated. Crural processes directed ventrally and medianly, but distal extensions either broken or obscured; anterior part of loop, concave and flattened.

*Statistics –*

<b>Variates</b>						
saglv	sagld	mw	hinw	pmw	dpv	dpd
<b>Means</b>						
6.61	5.82	5.08	3.09	4.05	1.47	1.69
<b>Var-Covar</b>						
6.07	5.67	4.65	3.23	4.50	1.22	1.33
	5.37	4.30	2.99	4.13	1.11	1.22
		3.86	2.65	3.47	0.99	1.01
			2.09	2.42	0.64	0.64
				3.65	0.86	0.98
<b>Sample</b>					0.33	0.31
N=31						0.37

*Discussion –* Initial studies of this species suggested that the distinctive outline, development of the dorsal fold and ventral sulcus together with the style and density of the radial ornament invite a close comparison with *T.? palmeri* Cooper from the Miocene of Cuba. Cooper (1979, p. 7) considered, however, that *T.? palmeri* was rather anomalous. Apart from having a subcarinate dorsal fold and narrow ventral sulcus, the species lacked a complete loop; the crural processes are directly dorsally, but only slightly medianly, obviating the possibility to unite and form a loop. This same configuration is not apparent in the few dorsal interiors available from Barbados. Both groups of species are thus no longer considered congeneric. Cooper (1979, p. 7) suggested that the loop was much more similar in orientation and structure to that of *Chilidonophora* rather than that of *Terebratulina*. The possibility of homoplasy or the reassignment of the *T.? palmeri* to the Chilidonophoridae requires further material of Cooper's species together with a rigorous phylogenetic analysis of the group.

The large sample now available indicates that there are further differences between the Pleistocene form and Cooper's species from the Miocene of Cuba. A PCA analysis of the correlation matrix, based on saglv, sagld, mwi and thickness (= dpv+dpd), of a sample of 25 specimens of the Pleistocene form together with the nine measured specimens of *T.? palmeri* presented in Cooper (1979, p. 7) suggests first the Cuban specimens are larger (higher scores on the first [size-related] eigenvector), and second the Pleistocene species is on average narrower (most Cuban specimens have lower scores on the second eigenvector that itself has a high negative loading of maximum width). Moreover, the Pleistocene species has a less-narrow ventral sulcus and less-marked carinate

dorsal valves. Although Cooper did not present numerical data for the rib density of his new species, measurements on his figured specimens suggest that the rib density of the Cuban species (usually 5 or 6 ribs per 2 mm at the 5 mm growth stage) may be less than that for the Pleistocene species.

The material obtained from the Manchioneal Formation was compared by PCA ordination with specimens of *Terebratulina* from the 'newer Pliocene' within the Lucas Barrett collection (Harper, 1993); no separation was achieved along any of the eigenvectors, thus the two samples are considered conspecific. The new large sample now available from Jamaica was also compared, using PCA, with two specimens from Barbados. Separation was achieved only on the fourth eigenvector, which accounts for only 1 % of the sample variation. The two Barbados specimens have lower scores on this axis than those of the Jamaica material; since the depth of the dorsal valve has a large negative loading on this vector, the Barbados specimens have deeper dorsal valves.

*Occurrence* – A printing error in Harper (2002a, table 12.1) omitted the symbol 'J' (for Jamaica) in the 'Pleistocene' column for this taxon. This species is common on Jamaica at Christmas River (J3), and occurs at the type section of the Manchioneal Formation (J2), Cruikshank Bay (J1), San San Bay (J4), Folly Point (J5) and Port Maria (J6); approximately 65 shells of this species are now known from the Jamaican localities. On Barbados, the species is most common at Skeete's Bay, Whitehaven (B1), but it also occurs at Spring Bay, Ragged Point (B3) together about 25 shells.

**Suborder Terebratellidina Muir-Wood, 1955**  
**Superfamily Megathyridoidea Dall, 1870**  
**Family Megathyrididae Dall, 1870**  
**Genus *Argyrotheca* Dall, 1900**

*Type species* – *Terebratula cuneata* Risso, 1826, by original designation; from the Recent of the Mediterranean Sea.

***Argyrotheca barrettiana* (Davidson, 1866)**  
 Pl. 3, figs. 1, 2.

- cf. 1866 *Argiope barrettiana* Davidson sp. nov., p. 103, pl. 12, fig. 3.
- cf. 1866 *Argiope antillarum* Crosse & Fischer sp. nov., p. 270, pl. 8, fig. 7.
- cf. 1887 *Cistella barrettiana* (Davidson); Davidson, p. 145, pl. 22, figs. 1, 2.
- cf. 1920 *Argyrotheca barrettiana* (Davidson); Dall, p. 329.
- 1930 *Terebratella*(?) sp.; Trechmann, p. 214, pl. 12, fig. 3.
- 1937 *Megathyris decollata* Chem.; Trechmann, p. 355, pl. 12, fig. 30, table.
- cf. 1977 *Argyrotheca barrettiana* (Davidson); Cooper, p. 107, pl. 22, figs. 9-21, pl. 23, figs. 6, 7, pl. 32, figs. 22-32.
- 1990 *Argyrotheca* sp.; Harper & Donovan, pp. 21-22.
- 1993 *Argyrotheca* sp. cf. *A. barrettiana* (Davidson); Harper, p. 111, figs. 2.5, 2.9, 2.11-2.16.
- 1995 *Argyrotheca* sp. cf. *barrettiana* (Davidson); Harper *et al.*, p. 221, fig. 2a, b, d, m.
- 1998 *Argyrotheca* cf. *barrettiana* (Davidson); Donovan & Harper, fig. 3c, d.
- 2002a *Argyrotheca* cf. *barrettiana* (Davidson); Harper, table 12.1.
- 2002a *Argyrotheca*; Harper, p. 145.
- 2002 *Argyrotheca* cf. *barrettiana* (Davidson); Harper & Donovan, p. 175.

- 2002 *Argyrotheca*; Harper & Donovan, pp. 176-178, fig. 16.2.  
 pars 2005 terebratulid brachiopods; Donovan with Harper, p. 24.  
 2005 *Argyrotheca* sp. cf. *A. barrettiana* (Davidson); Donovan with Harper, p. 25.  
 2007 *Argyrotheca* sp. cf. *A. barrettiana* (Davidson); Donovan & Harper, p. 60.

*Material* – One hundred and twenty shells of this species have been collected from localities on both Jamaica and Barbados.

*Diagnosis* – Medium to large, usually transverse *Argyrotheca* species; multicostellate with usually eight costae and costellae, increasing by intercalation up to 21 on the largest shell.

*Description* – Medium-sized, ventribiconvex valves of transverse to semicircular outline with maximum width either at or near hinge line or mid-valve length; cardinal extremities rounded, acute or perpendicular. Ventral valve about four-fifths as long as wide and about two-fifths as deep as long. Anterior profile with maximum convexity medianly where valve surface slightly carinate; flanks flat or weakly concave particularly near lateral margin. Lateral profile uniformly convex; umbo subdued. Ventral interarea flat to slightly curved, apsacline and about one-third valve length. Delthyrium large and open.

Dorsal valve over four-fifths as long as wide and about one-fourth as deep as long. Anterior profile with narrow sulcus originating near umbo; flanks slightly convex adjacent to sulcus, but flattened laterally. Dorsal interarea short and anacline. Ornament of strong costae and more rarely costellae; median sulcus with pair of costellae arising by internal branching within 5 mm growth stage. Four-21 ribs present on 4, 0, 1, 1, 17, 3, 6, 1, 0, 2, 0, 1, 1, 3, 0, 0, 0 and 1 valves; median costae of average thickness 0.8 mm at 5 mm growth stage. Accentuated growth lamellae numbering about 3-6 per mm at 5 mm growth stage more marked on larger valves. Valve surfaces densely punctate.

*Statistics* –

<b>Variates</b>							
saglv	sglb	mw	hinw	pmw	dpv	dpd	lia
<b>Means</b>							
4.32	3.45	5.12	4.39	1.68	1.94	0.58	1.64
<b>Var-Covar</b>							
1.84	1.66	2.46	1.35	1.29	0.77	0.36	0.46
	1.62	2.40	1.31	1.24	0.71	0.35	0.46
		3.84	2.60	1.85	1.05	0.52	0.76
			3.69	1.20	0.72	0.41	0.63
				1.14	0.60	0.27	0.35
					0.51	0.13	0.29
<b>Sample</b>						0.13	0.09
N=25							0.24

*Discussion* – The outline and profile of this species together with the style of radial ornament are most similar to those of *A. barrettiana* (Davidson), a Recent species, described from the Caribbean (Harper, 1993). The large amount of material now available

for study suggests that the Pleistocene form is, in fact, conspecific with Davidson's living species. A sample of 25 specimens from Jamaica was compared, by PCA of the correlation matrix, with two specimens from Barbados that yielded a comparable set of complete measurements. The two specimens from Barbados are separated on the third eigenvector, responsible for 2.5 % of the sample variation. Both specimens have higher positive scores on this eigenvector than those of the Jamaican sample; maximum width (mw) has high negative loading on this eigenvector indicating that the Barbados specimens are relatively narrower than those from Jamaica. The Barbados material is currently insufficient to form the basis for the new subspecies, suggested by the multivariate analysis.

Although Cooper redescribed *A. barrettiana* (Davidson) from the Caribbean Sea, he did not provide a modern diagnosis of the species. That is provided here.

*Occurrence* – This species is common on Jamaica at the type section of the Manchio-neal Formation (J2) and Christmas River (J3), and occurs at Cruikshank Bay (J1) and Folly Point (J5); approximately 100 shells of this species are now known from the Jamaican localities. On Barbados, the species is most common at Skeete's Bay, Whitehaven (B1), but it also occurs at Spring Bay, Ragged Point (B3) and the Arawak Cement Quarry (B4) together yielding 20 shells.

## Discussion

The living brachiopod fauna of the Caribbean Basin is relatively diverse. Cooper (1977) reported over 50 species of brachiopod assigned to some 20 genera from the Caribbean Sea and Florida Straits. Miocene horizons have yielded 25 species assigned to ten genera (Harper, 2002a). By contrast, only four taxa are, to date, known from the Pleistocene (Trechmann, 1930, 1937; Harper, 1993, Harper *et al.*, 1995; Harper & Donovan, 2002). This association is a continuation of a similarly depauperate Pliocene brachiopod fauna that, where developed, is also of low diversity, characterized by species of *Argyrotheca*, *Terebratulina*, *Tichosina* and *Lacazella* (Logan, 1987). Thus, assemblages with *Argyrotheca*, *Terebratulina*, *Tichosina* and *Lacazella* apparently continued from the underlying Pliocene in deep-water facies commonly associated with fore-reef deposits (Donovan & Harper, 1998). By comparison the Pleistocene fauna of the Mediterranean Sea was more diverse with some eight species belonging to seven genera, and including *Argyrotheca*, *Gryphus*, *Lacazella*, *Megathiris*, *Megerlia*, *Platidia* and *Terebratulina* (Logan *et al.*, 2004). Both faunas have *Argyrotheca*, *Lacazella* and *Terebratulina* in common, whereas *Gryphus* is very similar to *Tichosina*. It is possible that either a sufficient range of sedimentary environments has not yet been collected to appreciate the full range of the Pleistocene fauna or the Plio-Pleistocene interval represents a survivor fauna following local extinction events in the Caribbean Basin at the Miocene-Pliocene boundary.

Establishment of the depth and environments of depositions of the two successions is based on both faunal and sedimentological criteria. In particular, brachiopod data have already proved useful in studies of the Pleistocene rocks of Jamaica (Donovan & Harper, 1998). Modern brachiopods display a considerable depth range from the intertidal zone to abyssal depths in excess of 6 km, but with about 40 % of all living brachiopods occurring at depths between 50-400 m; the majority occupy depth bands between

100-400 m. *Tichosina* species generally occur at depths greater than 100 m in the modern Caribbean (Cooper, 1977) while *Terebratulina* is still common at depths in excess of 300 m (Logan, 1987). The faunal arguments for the depositional depths of the Manchioneal Formation on Jamaica were discussed in detail by Harper *et al.* (1995) and Donovan & Harper (1998). Low current velocities, low light intensity and substrate preferences are the main controlling factors on initial larval attachment, and thus the subsequent distributional patterns of the brachiopod animal. At low latitudes micromorphic brachiopod species would be more suited to cryptic habitats associated with reefs and other cavernous carbonate buildups (Jackson *et al.*, 1971); the strategies of larger species may be associated with deeper-water environments where larger patches of substrate are available in darker, less turbulent waters.

Asgaard & Stentoft (1984) established precise figures for the depth range of a number of brachiopod species in a more focused study of the distribution of living and dead modern brachiopods on the shelf and slope off Barbados. Species of *Argyrotheca* and *Terebratulina* preferred depths in the ranges of approximately 90-100 m and 90-140 m, respectively, whereas *Tichosina* occupied deeper water from approximately 200-250 m. Observations on both the reproductive behaviour and the associated predators of all three taxa may have also impacted on their ecological and geographical distributions. Asgaard & Stentoft (1984) noted the development of brood pouches in *Argyrotheca*, and possibly *Terebratulina*, where fertilized ova and larvae are retained within the mantle cavity of the female. When expelled, the resulting distribution of the larvae is local and patchy. This may partly explain the morphological differences apparent between the Barbadian and Jamaican *Argyrotheca* and *Terebratulina* species. Moreover, during early stages of attachment, the larvae and larval shells are commonly removed from open and accessible substrates by grazing herds of the black sea urchin, *Diadema antillarum* (Philippi). Clearly, a restricted, cryptic life style would be a considerable advantage. In this context it is significant that predatory borings are relatively rare in our collections of Pleistocene brachiopods (Donovan & Harper, 2007). Either by occupying cryptic habitats (*Argyrotheca* and *Terebratulina*) or the deep sea (*Tichosina*), predators were probably avoided.

In summary, the basal and probably deeper-water facies of both the Coral Rock of Barbados and the Manchioneal Formation of Jamaica are characterized by high dominance brachiopod faunas with abundant *Tichosina*. Stratigraphically younger units within each formation have fewer *Tichosina*, but more abundant *Argyrotheca* and *Terebratulina*. The move from large, deeper-water generalists to more micromorphic cryptic faunas may have been a reflection of adaptations in the brachiopod biofacies to increasing water turbulence, light intensities and predation pressures within a regressive sequence. Nevertheless, the shallower-water faunas were still in the range of 80-150 m water depth, implying relative uplift in this order for these parts of Barbados and Jamaica since the early Pleistocene.

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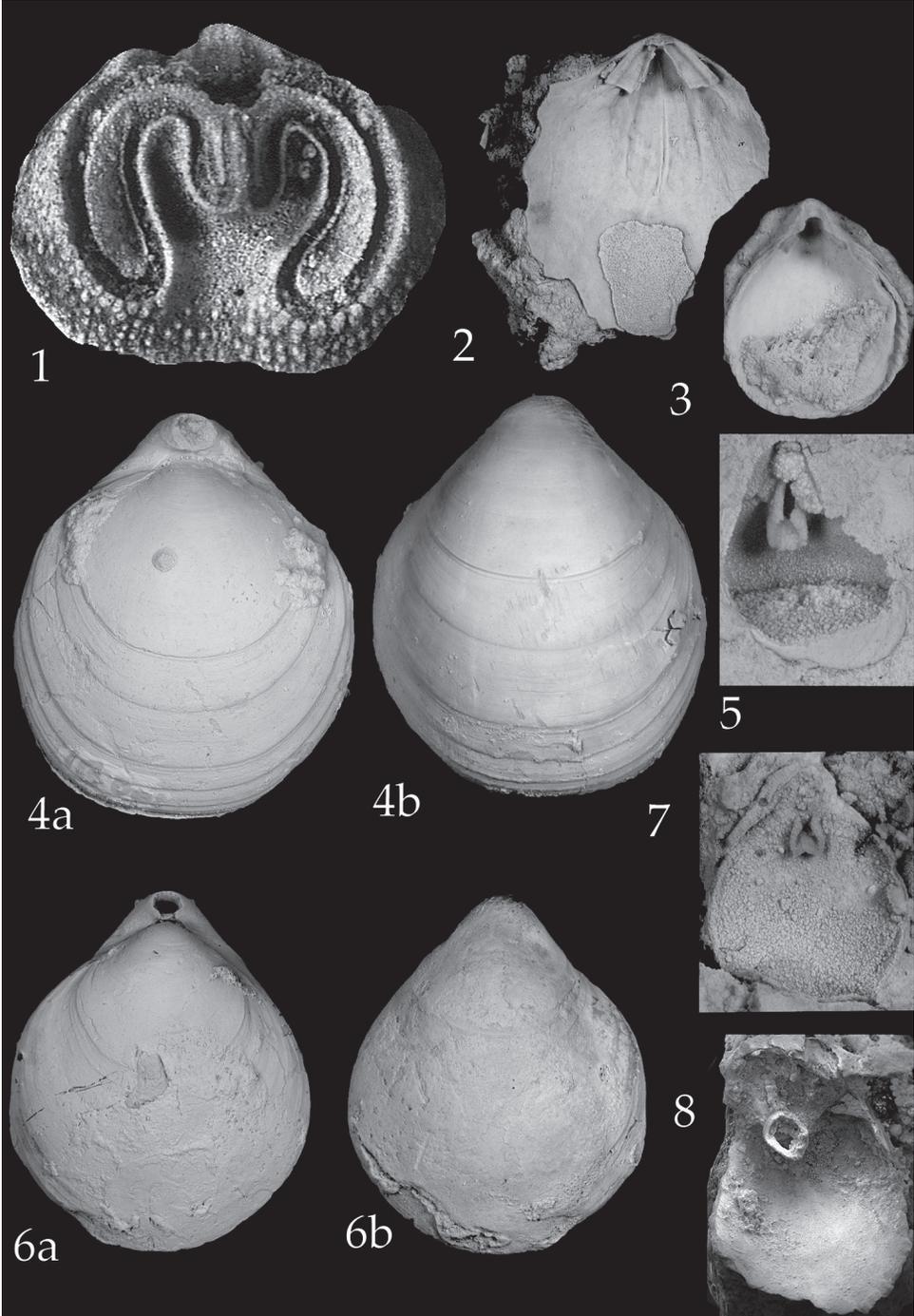
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**Plate 1**

Fig. 1. *Lacazella* sp. cf. *L. caribbeanensis* Cooper, 1977. NHM B21998, dorsal interior from the 'Tertiary' of Jamaica, Lucas Barrett collection, X 15.

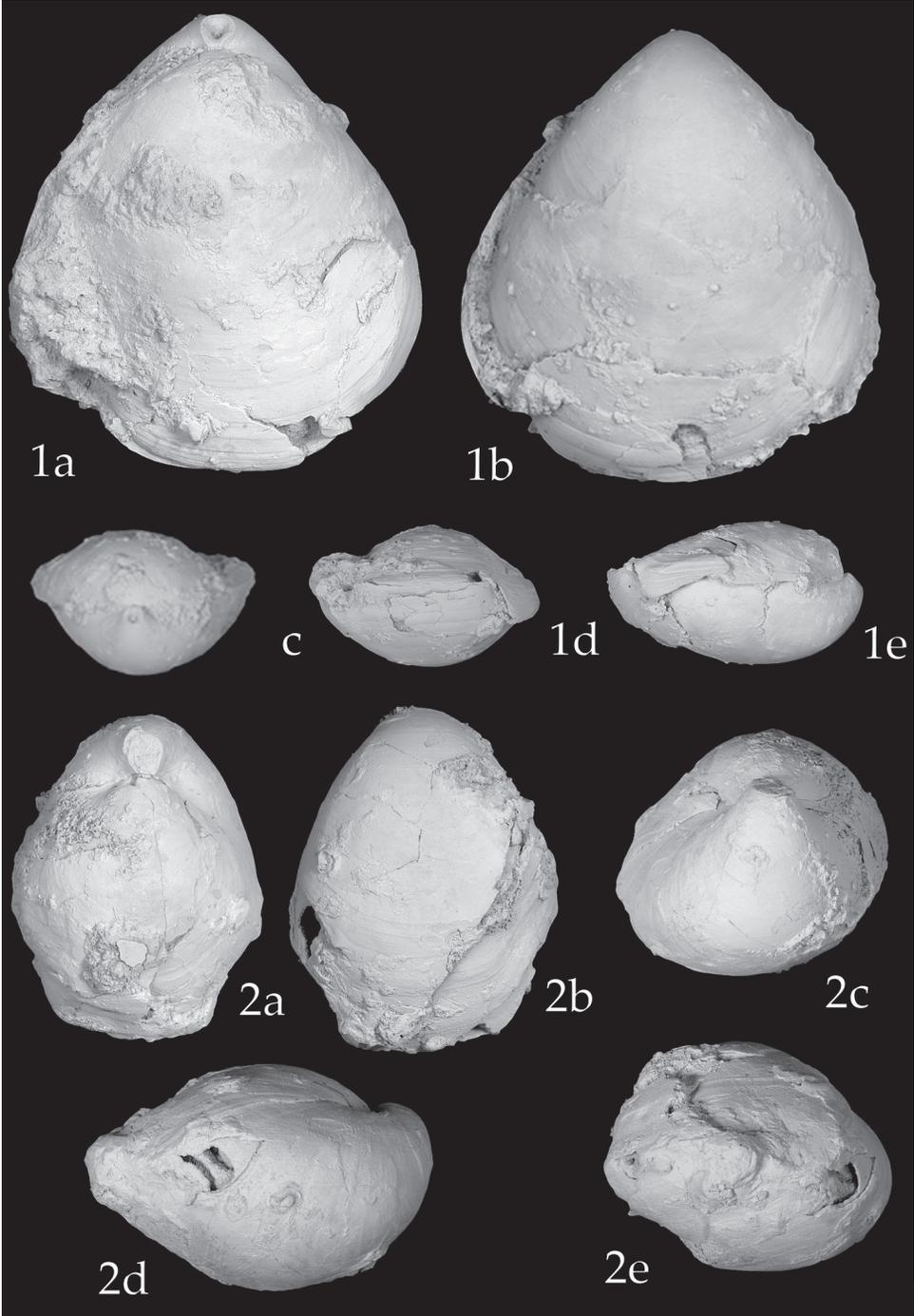
Figs. 2-7. *Tichosina inconstanta* sp. nov. (2): MGUH 28765, dorsal interior from the Manchioneal Formation, Manchioneal (J2), Jamaica, X 1.6. (3): MGUH 28766, ventral interior from the Manchioneal Formation, Manchioneal (J2), Jamaica, X 3.5. (4a, 4b): MGUH 28767, holotype, dorsal and ventral views of conjoined valves from the Manchioneal Formation, Christmas River (J3), Jamaica, X 2.2. (5): MGUH 28768, details of loop in dorsal interior from Middle Coral Rock, Spring Bay (B3), Barbados, X 2.8. (6a, 6b): MGUH 28769, dorsal and ventral views of conjoined valves from the Manchioneal Formation, Manchioneal (J2), Jamaica, X 1.3. (7): *Tichosina inconstanta* sp. nov. MGUH 28770, details of loop in dorsal interior from Middle Coral Rock, Spring Bay (B3), Barbados, X 3.

Fig. 8. *Terebratulina manchionealensis* sp. nov., MGUH 28771, SEM photograph showing details of loop in dorsal interior from Manchioneal Formation, Manchioneal (J2), Jamaica, X 4.



**Plate 2**

Figs. 1, 2. *Tichosina inconstanta* sp. nov. (1a-e) MGUH 28772, dorsal, ventral, posterior, anterior and lateral views of conjoined valves, Manchioneal Formation, Christmas River (J3), Jamaica, fig. 1a, b, X 1.2; figs. 1c-e, X 0.7. (2a-e) MGUH 28773, dorsal, ventral, posterior, lateral anterior views of conjoined valves from the Manchioneal Formation, Manchioneal (J2), Jamaica, X 1.



**Plate 3**

Figs. 1, 2. *Argyrotheca barrettiana* (Davidson, 1866). (1a, b) BMNH B21998, ventral and dorsal views of conjoined valves from the 'Tertiary' of Jamaica, X 5. (2a, b) BMNH B41835, ventral and dorsal views of conjoined valves from the 'Tertiary' of Jamaica, X 3.8.

Figs 3-6. *Terebratulina manchionealensis* sp. nov. (3a-d) NHM B22000, ventral, dorsal, posterior, anterior views of conjoined valves from the 'newer Pliocene' of Jamaica, X 3. (4a, b) NHM B22000, ventral and dorsal views of conjoined valves from the 'newer Pliocene' of Jamaica, X 3. (5a, b) MGUH 28774a, holotype, internal and external views of dorsal valve from Manchioneal Formation, Christmas River (J3), Jamaica, X 3. (6a, b) MGUH 28774b, holotype, internal and external views of ventral valve from Manchioneal Formation, Christmas River (J3), Jamaica, X 3.5. (5) and (6) are part and counterpart of a formerly conjoined pair.

