Cainozoic Research, 3(1-2), pp. 127-134, December 2004
In: Donovan, S.K. (ed.). *The Mid-Cainozoic White Limestone Group of Jamaica*

Brachiopods of the White Limestone Group, Jamaica

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Received 28 May 2002; revised version accepted 1 May 2003

The brachiopod fauna of the White Limestone Group of Jamaica includes seven rhynchonelliform species, two from the Eocene Swanswick Formation and five from the Miocene Montpelier Formation. Despite the small numbers of species and specimens available, the shelf-edge fauna associated with bioclastic limestone in the Swanswick Formation, with *Hercothyris* and *Probolarina*, contrasts with that from the chalk facies of the Montpelier Formation, dominated by *Argyrotheca*, *Terebratulina* and *Tichosina*. Both faunas have links with coeval assemblages from the adjacent island of Cuba.

KEY WORDS: Brachiopoda, distribution, ecology, White Limestone Group, Jamaica.

Introduction

Seven brachiopod taxa have been described and illustrated from the White Limestone Group of Jamaica (Harper, 1993; Harper *et al.*, 1997; Harper & Portell, 2002). Despite the stratigraphic range, geographic extent and the spectrum of palaeoenvironments associated with the group, brachiopods have only been reported from two, in many respects, contrasting localities. The Swanswick Formation at Beecher Town (Figure 1A, B), parish of St Ann (Donovan *et al.*, 1989) exposes a foraminiferan bioclastic limestone and has yielded over twenty species of echinoids (Donovan, 1994) together with species of the brachiopods *Hercothyris* and *Probolarina*? The Miocene chalk facies at Duncans (Figure 1A, C), parish of Trelawny (Harper *et al.*, 1997), includes species of *Tichosina*, *Platidia*?, *Argyrotheca* (two) and *Terebratulina*. The Swanswick Formation fauna probably developed on a shelf-edge situation whereas that from the Montpelier Formation occupied a more bathyal position.

History of research

Brachiopods are a relatively recent addition to the diverse faunal lists of the White Limestone biota. Harper & Donovan (1990, p. 28, fig. 3) were first to note and illustrate *Hercothyris* sp. cf. *H. semiradiata* Cooper, 1979, from the Eocene Swanswick Formation at Beecher Town, based on the previous record of a ribbed brachiopod by Donovan *et al.* (1989, p. 6). The Swanswick fauna was later supplemented by the description of *Probolarina*? sp. from the same locality (Harper, 1993, p. 106). A more diverse and abundant fauna, in relative terms, has since been described from the younger, deeper-water chalk facies of the Miocene Montpelier Formation at Duncans (Harper *et al.*, 1997; Harper & Portell, 2002). The Duncans fauna now includes *Tichosina* sp. cf. *T. guppyi* Cooper, 1979, *Platidia*? sp., *Argyrotheca* sp. aff. *A. anomala* Cooper, 1979, *Argyrotheca plana* Cooper, 1979, and *Terebratulina* sp. cf. *T. palmeri* Cooper, 1979. The geographic and stratigraphic distribution, throughout the Caribbean region, of the majority of White Limestone taxa has been summarised in Harper (2002); as a whole, the White Limestone faunas show closest links with assemblages of the same age on the adjacent island of Cuba (Cooper, 1979). The Duncans Quarry brachiopods are reposited in the Invertebrate Paleontology Division of the Florida Museum of Natural History, University of Florida, Gainesville, Florida (UF); those from Beecher Town are in The Natural History Museum, London (BMNH BC).

Systematic palaeontology

The taxonomic data for the White Limestone taxa are documented below in conventional systematic order. However, illustrations of the taxa are presented in three

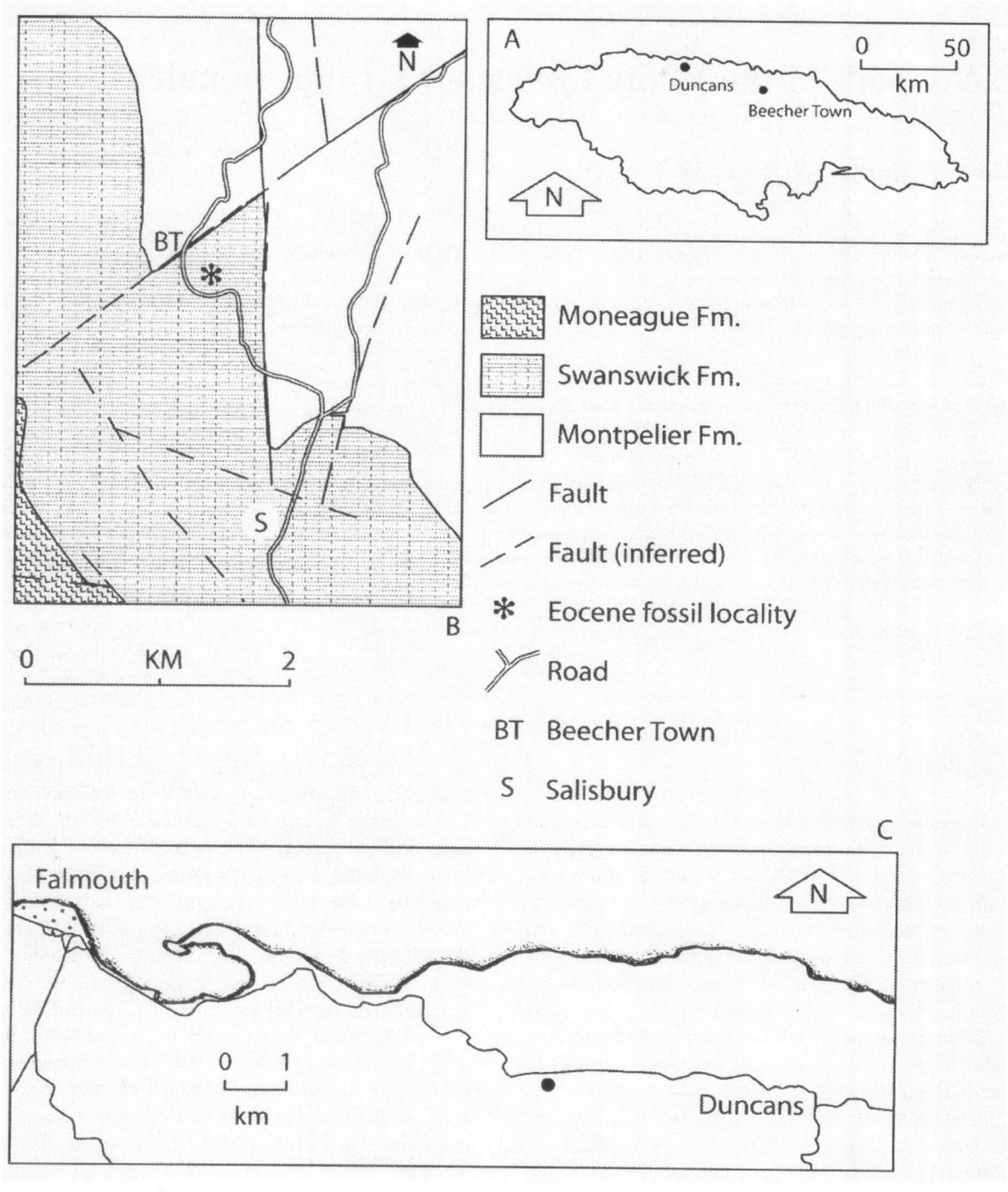

Figure 1. Position of localities within the Swanswick (B) and Montpelier (C) formations, together with their locations within the island of Jamaica (A).

figures, emphasising the co-occurrence of species within the Swanswick Formation (Figure 2) and the Montpelier Formation (Figures 3, 4).

Order Rhynchonellida Kuhn, 1949
Superfamily Rhynchonelloidea Gray, 1840
Family Basiliolidae Cooper, 1959
Genus *Probolarina* Cooper, 1988

Type species — *Rhynchonella holmesii* Dall, 1903, from the Castle Hayne Formation (Eocene), North Carolina (USA), by original designation.

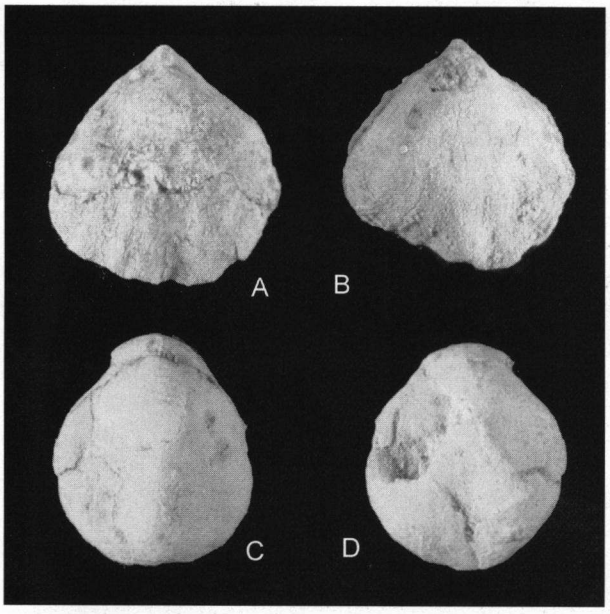

Figure 2. Brachiopods from the Eocene Swanswick Formation, Beecher Town, parish of St Ann, Jamaica; A, B - *Probolarina*? sp., dorsal and ventral views of a conjoined pair, BMNH BC1003, both x 4; C, D - *Hercothyris* sp. cf. *H. semiradiata* Cooper, 1979, dorsal and ventral views of a conjoined pair, BMNH BC1004, both x 2.

***Probolarina*? sp.**
Figure 2A, B

1989 Ribbed brachiopod — Donovan *et al.*, p. 6.
1990 Ribbed brachiopod nov.? — Harper & Donovan, p. 28.
1993 *Probolarina*? sp. — Harper, p. 106, figs 4.15, 4.16.

Material — One poorly preserved conjoined pair of valves, BMNH BC1003, from the Swanswick Formation (Middle Eocene), Beecher Town, parish of St Ann.

Discussion — This small, unequally biconvex species is characterised by a low, rounded median fold, a hypothyridid pedicle foramen and an ornament of at least six, rounded costae developed on the anterior halves of both valves. On the basis of its shape and style of ornament, Harper (1993, p. 106) compared the species with *Probolarina transversa* Cooper, 1988, from the Eocene Santee Formation of South Carolina, although the material available did not warrant a confident assignment to either an established genus or species. It is the only fossil rhynchonellide known from Jamaica to date.

Order Terebratulida Waagen, 1883
Suborder Terebratulina Waagen, 1883
Superfamily Terebratuloidea Gray, 1840
Family Terebratulidae Gray, 1840
Genus *Tichosina* Cooper, 1977

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

Tichosina* sp. cf. *T. guppyi Cooper, 1979
Figure 4A, B

cf. 1979 *Tichosina guppyi* Cooper, p. 10, pl. 2, figs. 11-16.
1997 *Tichosina* sp. cf. *T. guppyi* Cooper — Harper *et al.*, p. 118, fig. 2A, B.
2002 *Tichosina* sp. cf. *T. guppyi* Cooper — Harper & Portell, p. 257.

Material — One conjoined pair of valves crushed and fractured, UF 38966, together with a few shell fragments from the Montpelier Formation (Lower Miocene), Duncans Quarry, parish of Trelawny.

Discussion — *Tichosina* sp. cf. *T. guppyi* Cooper, 1977, is by far the largest brachiopod taxon recovered from the Montpelier Formation. These smooth, ventriconvex valves, although crushed and fractured, were assigned to *T.* sp. cf. *T. guppyi* Cooper by Harper *et al.* (1997) on the basis of the outline and profiles of the shells. *Tichosina guppyi sensu stricto* was initially described by Cooper (1979) from a similar white marly facies within the Miocene Yumuri Limestone of the province of Habana (Cuba). A few additional fragments of the Jamaican species have been collected, subsequent to the first report of the species at Duncans, but none adds materially to the existing knowledge of this taxon (Harper & Portell, 2002).

Superfamily Terebratelloidea King, 1850
Family Platidiidae Thomson, 1927
Genus *Platidia* Costa, 1852

Type species — *Orthis anomioides* Scacchi & Philippi, 1844, a Recent species from the eastern Atlantic, by original designation.

***Platidia*? sp.**
Figure 3I, J

2002 *Platidia*? sp. — Harper & Portell, p. 257, fig. 1J, K.

Material — One conjoined pair of valves, UF 104444, from the Montpelier Formation (Lower Miocene), Duncans Quarry, parish of Trelawny.

Discussion — This minute conjoined pair of valves is characterised by the outline, profiles and lack of obvious ornament typical of *Platidia* sp. (Cooper, 1979, pl. 5, p. 17, figs 45, 46) from the Miocene of Cuba.

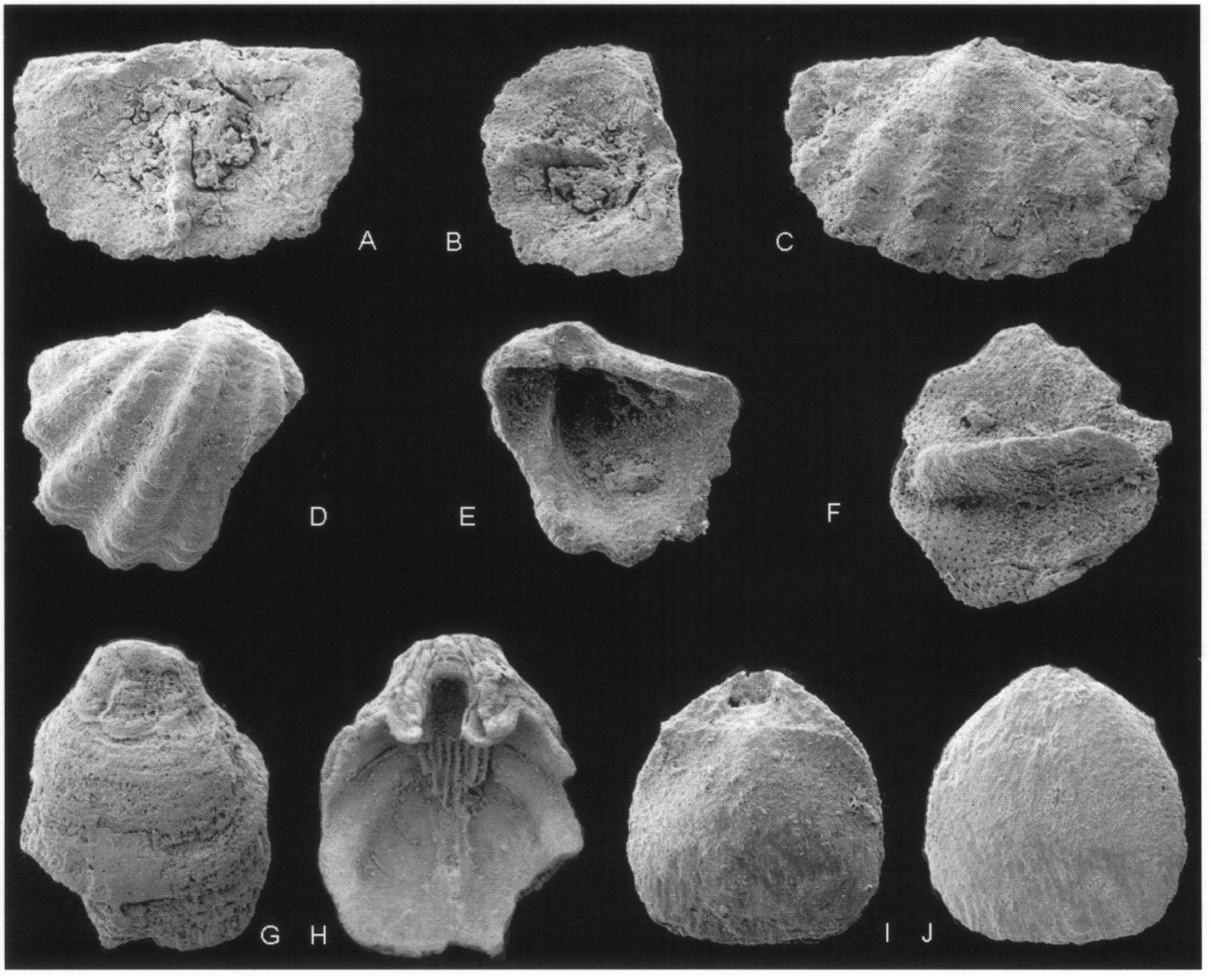

Figure 3. Brachiopods from the Lower Miocene Montpelier Formation, Duncans Quarry, parish of Trelawny, Jamaica; A-F- *Argyrotheca plana* Cooper, 1979, internal, oblique internal and external (A-C) views of a dorsal valve, UF 104449, x 29, x 21 and x 32, respectively; external and internal (D, E) views of a ventral valve, UF 103183, both x 35; internal (F) view of incomplete dorsal valve, UF 103180, x 27; G, H - *Argyrotheca* sp. cf. *A. anomala* Cooper, 1979, internal and external views of a ventral valve, UF 103181, both x 19; I, J - *Platidia*? sp., dorsal and ventral views of conjoined pair, UF 104444, both x 22.

Moreover, the development of the valve interareas is quite different from those of immature *Tichosina* which are already marked by a mesothyridid to permesothyridid pedicle foramen together with ventribiconvex shell profiles.

Family Megathyrididae Dall, 1870
Genus *Argyrotheca* Dall, 1870

Type species — *Terebratulina cuneata* Risso, 1826, a Recent species from the Mediterranean, by original designation.

Argyrotheca* sp. aff. *A. anomala Cooper, 1979
Figure 3G, H

aff. 1979 *Argyrotheca anomala* Cooper, p. 18, pl. 7, figs 31-36.
aff. 2002 *Argyrotheca anomala* Cooper — Harper & Portell, p. 257, fig. 1G, H.

Material — One well-preserved, disarticulated, but slightly broken ventral valve, UF 103181, from the Montpelier Formation (Lower Miocene), Duncans Quarry, parish of Trelawny.

Discussion — The material comprises a small, convex, ventral valve with an elongate, oval outline and a faintly plicate anterior commissure. The shell is essentially smooth, but modified by concentric growth bands. The ventral interior possesses a short apical plate and a low median ridge, extending anteriorly to near the commissure together with large, blunt, unsupported, cyrtomatodont teeth projected anteromedianly. Cooper (1979, p. 18)

emphasised the obsolescent costae when distinguishing his new species, *Argyrotheca anomala* Cooper, 1979, from the Middle Oligocene of the province of Matanzas (Cuba). The Jamaican material apparently entirely lacks any costae on the ventral valve surface, but is similar in outline and profile to the Cuban species; the entire absence of costae on the Jamaican shell is considered to be a more advanced condition of obsolescence and eventual loss of a radial ornament in this mid-Tertiary stock (Harper & Portell, 2002).

A number of other smooth *Argyrotheca* have been reported from adjacent regions. *Argyrotheca saltmountainensis* Toulmin, 1940, from the Upper Paleocene Salt Mountain Limestone (formerly considered Eocene, but see Bryan *et al.*, 1997) of Alabama; *A. akymatophora* Stenzel, 1940, from the Eocene of the Atlantic Coastal Plain; *A. laevis* Cooper, 1988, from the Oligocene of South Carolina; and *A. robinsoni* Donovan *et al.*, 1993, from the Eocene of Jamaica, all lack an external radial ornament and commonly co-occur with ribbed forms. The smooth condition may be a polyphyletic feature amongst the Caribbean stocks of the genus (Harper & Portell, 2002).

Argyrotheca plana Cooper, 1979
Figure 3A-F

1979 *Argyrotheca plana* Cooper, p. 23, pl. 4, figs 29-49.
2002 *Argyrotheca plana* Cooper — Harper & Portell, p. 257, fig. 1A-F.

Material — Two disarticulated dorsal valves, one broken together with a slightly broken ventral valve. All three valves are well preserved, UF 103180, UF 103183 and UF 104449, from the Montpelier Formation (Lower Miocene), Duncans Quarry, parish of Trelawny.

Discussion — This minute species is characterised by planoconvex valves of transversely subquadrate outline together with a sulcate anterior commissure scalloped by the termination of strong ribs. The Jamaican material is conspecific with *A. plana* from the Miocene of the province of Mantanzas (Cuba), a transverse species with a flat to concave dorsal valve together with strong costae (Cooper, 1979, p. 23), having interiors similar to those of *A. bermudezi* Cooper, 1979, from the Miocene of the same province.

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

Type species — *Anomia retusa* Linné, 1767, a Recent species from Norwegian waters, by original designation.

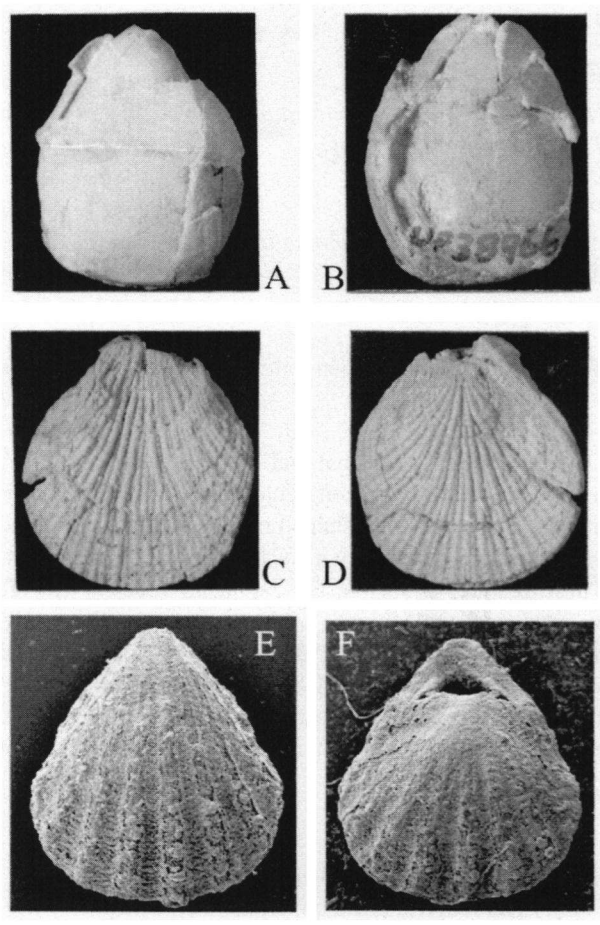

Figure 4. Brachiopods from the Lower Miocene Montpelier Formation, Duncans Quarry, parish of Trelawny, Jamaica; A, B - *Tichosina* sp. cf. *T. guppyi* Cooper, 1979, ventral and dorsal views of a conjoined pair, UF 38966, both x 2; C-F - *Terebratulina* sp. cf. *T. palmeri* Cooper, 1979, dorsal and ventral (C, D) views of a conjoined pair, UF 68661, x 4; ventral and dorsal (E, F) views of a conjoined pair, UF 103184, x 22.

Terebratulina* sp. cf. *T. palmeri Cooper, 1979
Figure 4C-F

cf. 1979 *Terebratulina? palmeri* Cooper, p. 6, pl. 1, figs 6-23; pl. 7, figs 9-20.
1990 *Terebratulina* sp. — Harper & Donovan, p. 21.
cf. 1993 *Terebratulina* sp. cf. *T. palmeri* Cooper — Harper, p. 113, figs 4.1-10, 4.17.
1997 *Terebratulina* sp. cf. *T. palmeri* Cooper — Harper *et al.*, p. 118, fig. 2C, D.
2002 *Terebratulina* sp. cf. *T. palmeri* Cooper — Harper & Portell, p. 259, fig. 1I, L.

Material — Two conjoined pairs. The larger is broken umbonally (UF 68661); the smaller is complete and well preserved (UF 103184). Montpelier Formation (Lower Miocene), Duncans Quarry, parish of Trelawny.

Taxon	Age	Formation	Distribution	Ecology
Probolarina? sp.	Eocene	Swanswick	Jamaica, South Carolina	small pedunculate
Hercothyris sp. cf. *H. semiradiata*	Eocene	Swanswick	Jamaica, Cuba	medium pedunculate
Tichosina sp. cf. *T. guppyi*	Miocene	Montpelier	Jamaica, Cuba	large pedunculate, possibly recumbent
Platidia? sp.	Miocene	Montpelier	Jamaica, Cuba	minute pedunculate
Argyrotheca sp. aff. *A. anomala*	Miocene	Montpelier	Jamaica, Cuba	minute pedunculate
Argyrotheca plana	Miocene	Montpelier	Jamaica, Cuba	minute pedunculate
Terebratulina sp. cf. *T. palmeri*	Miocene	Montpelier	Jamaica, Cuba	small pedunculate

Table 1. The age, distribution and ecology of the White Limestone brachiopod fauna, Jamaica.

Discussion — The original material (Harper *et al.*, 1997, p. 118) of a single, broken conjoined pair of valves (UF 68661) has a tear-drop shaped outline, a dorsal fold and ventral sulcus together with a fascicostellate ornament. These features associate the Jamaican species with *T. palmeri* from the Miocene of the provinces of Matanzas and Pinar del Río (Cuba). Additional material, assembled since 1997, comprises a well-preserved conjoined pair (UF 103184) displaying details of the pedicle foramen and the early stages of development of the ribbed ornament (Harper & Portell, 2002).

Superfamily Dallinoidea Beecher, 1893
Family Hercothyrididae Cooper, 1979
Genus *Hercothyris* Cooper, 1979

Type species — *Hercothyris borroi* Cooper, 1979, from the Eocene of Cuba, by original designation.

Hercothyris* sp. cf. *H. semiradiata Cooper, 1979
Figure 2C, D

cf. 1979 *Hercothyris semiradiata* Cooper, p. 27, plate 5, figs 24-29.
1990 *Hercothyris* sp. cf. *H. semiradiata* Cooper — Harper & Donovan, p. 21.
1993 *Hercothyris* sp. cf. *H. semiradiata* Cooper — Harper, p. 113, figs 4.11-13.

Material - One slightly damaged conjoined pair, BMNH BC1004, from the Swanswick Formation (Middle Eocene), Beecher Town, parish of St Ann.

Discussion - This medium-sized, elongate species is ventribiconvex, but is distinguished by the development of a marked uniplicate anterior commissure, a large submesothyridid pedicle foramen and a weak, costate ornament visible only on the early growth stages of the shell. The valve outline and ornament is most similar to those of *H. semiradiata* from the Eocene of the province of Camaguëy (Cuba), where this taxon is tentatively assigned (Harper, 1993).

Autecology

Models for the autecology of Cainozoic brachiopods in the Caribbean region, particularly for the Pleistocene of Jamaica (Donovan & Harper, 1998; Harper *et al.*, 1995; Harper & Donovan, 2002), have been developed from the studies of Surlyk (1972) and others on the Danish Cretaceous chalk. Regarding the White Limestone, only two species have been recorded from the Eocene Swanswick Formation (Harper, 1993). Both almost certainly were attached to small patches of hard substrate such as shells or shell fragments. However, new material (Harper & Portell, 2002) from the Miocene chalks at Duncans has expanded the diversity of that fauna from two (Harper *et al.*, 1997) to six species based on ten complete or near-complete specimens. The new material consists of a range of micromorphic valves each with clear evidence of peduncular attachment. The brachiopod biofacies resembles that of the Danish chalk, where the diverse brachiopod assemblages are dominated by micromorphic species probably attached to small patches of substrate (Surlyk, 1972) such as local hardgrounds and other shells. All six species probably were able to attach to hard substrates, although *Terebratulina* perhaps could root directly into the sediment and *Tichosina* may have been free living during later growth stages (Harper *et al.*, 1995). The two larger conjoined pairs, one each of *Terebratulina* and *Tichosina* described and figured by Harper *et al.* (1997), are both broken posteriorly, obscuring details of the umbones and pedicle openings. Both may have been broken from their substrate, while in life position, the umbonal parts of the shells proving weaker than the bond of their pedicles to the substrate.

Synecology

Ager (1965, 1993) developed a unifying template for post-Palaeozoic brachiopod synecology based on the relationship of shell morphology to habitat across a spectrum of

depths and environments; this distributional model has been modified by Sandy (1995) with the addition of cold-seep chemosynthetic environments. Clearly, in view of the diversity of both habitats and taxa, together with the fact that brachiopod distributions have changed since the Mesozoic, any simplified framework is difficult to apply to more local biotas and their environments. Nevertheless, on the basis of the criteria and data presented by Ager and others, the White Limestone assemblages occur at the lower end of the depth spectrum. With the exception of *Hercothyris* and *Tichosina*, the brachiopods are micromorphic and all species were apparently pedunculate.

The Middle Eocene Swanswick Formation was deposited on the shelf edge at depths of water probably less than 200 m (Donovan, 1994). The foraminiferan bioclastic limestone contains species of the large terebratulide *Hercothyris* and the rhynchonellide *Probolarina*. Both are plicate with relatively large pedicle openings.

By contrast, the dominantly pelagic chalk facies of the Lower Miocene Montpelier Formation was deposited on a slope-basin transect, at water depths in excess of 500 m. The formation is dominated by pelagic sediments and contains small to minute, thin-shelled brachiopods. The small, thin-shelled taxa are clearly candidates for an epiplanktonic life style, but these adaptations were more probably developed for life associated with a soft chalk substrate at bathyal depths.

The brachiopod faunas from both localities are rare, in contrast with, for example, the abundant assemblages in the Miocene of Carriacou (Donovan & Harper, 2001) and the Pleistocene of Jamaica (Harper *et al.*, 1995); the latter two are located in relatively deep-water environments. The fauna of the Swanswick Formation is dominated by echinoids that may have predated sessile brachiopod larvae (Asgaard & Stentoft, 1984) whereas in the deep-water facies of the Montpelier Formation there may have been a scarcity of suitable substrates.

Distribution

The geographical distribution of the Caribbean fossil brachiopod fauna has been summarised by Harper (2002); comments regarding the distribution of the White Limestone fauna are tabulated here (Table 1). Regarding the Swanswick fauna, *Hercothyris* is represented by two species in Eocene rocks on Cuba, whereas *Probolarina* occurs in the Eocene of South Carolina. The geographical ranges of two of the Miocene Cuban species of *Argyrotheca* have been extended south into the Jamaican region, whereas a possible species of *Platidia*?, a genus with an Eocene to Pliocene range on Cuba, is reported from Jamaica for the first time. Both *Terebratulina* and *Tichosina* have long ranges in the Caribbean region; however, the Duncans Quarry material is most closely associated with coeval species from Cuba.

Acknowledgements

We thank Professor S.K. Donovan for his constant encouragement and interest; he, together with Dr Sarah Long, provided careful and helpful reviews of the manuscript. Kurt Nielsen (Geological Institute, University of Copenhagen) helped with the SEM images and Anne Haastrup Hansen (Geological Museum, University of Copenhagen) redrafted Figure 1. Barbara and Reed Toomey, Kevin Schindler and George Hecht assisted RWP in collecting matrix that yielded the Duncans brachiopods. Financial support for fieldwork, in part, was provided by the McGinty Endowment at the FLMNH, and B. and R. Toomey. DATH thanks the Carlsberg Foundation for financial support. This is University of Florida Contribution to Paleobiology 542.

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