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HOLOPLANKTONIC MOLLUSCA (GASTROPODA: HETEROPODA AND THECOSOMATA) FROM THE PLIOCENE BOWDEN BEDS, JAMAICA

ARIE W. JANSSEN
XEWKIJA (GOZO), MALTA

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Three Heteropoda and 14 Euthecosomata ('Pteropoda') species are recorded from the Pliocene (Piacenzian) of Bowden, Jamaica. Two Heteropoda, four species of Limacinidae and *Clio* aff. *braidensis* (Bellardi, 1873) have not been recorded previously from Bowden. Systematic descriptions are followed by a brief discussion on the age of the assemblage. Lectotypes are designated for *Cavolinia ventricosa* (Guppy, 1882) and *Diacria digitata* (Guppy, 1882).

Key words — Bowden, Jamaica, Heteropoda, Thecosomata, Pteropoda, Pliocene, systematics, biostratigraphy.

A.W. Janssen, Nationaal Natuurhistorisch Museum, P.O. Box 9517, NL-2300 RA Leiden, The Netherlands; or: 12, Triq il-Hamrija, Xewkija VCT 110, Gozo, Malta.

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INTRODUCTION

The classic and renowned shell bed of Bowden (Jamaica) has been the subject of numerous publications. Various authors have described the molluscan faunas from this deposit, from the nineteenth century onwards, culminating in W.P. Woodring's monographs (1925, 1928). Woodring (1928, p. 113ff) mentioned the following seven species of holoplanktonic gastropods from Bowden:

Pteropoda Thecosomata
Cavolinia telemus (Linné)
Cavolinia ventricosa (Guppy)
Cavolinia digitata (Guppy)
Cavolinia vendryesiana (Guppy)
Diacria bisulcata Gabb

Pectinibranchiata Heteropoda
Atlanta (Atlanta) diamesa Woodring
Atlanta (Atlantidea) lissa Woodring

The pteropods were discussed in detail by Collins (1934, p. 155), who listed the following nine species and also mentioned one heteropod, *Atlanta* sp. (Collins, 1934, p. 146):

Cavolinia telemus (Linné)
Cavolinia ventricosa (Guppy)
Cavolinia digitata (Guppy)
Cavolinia vendryesiana (Guppy)
Diacria bisulcata Gabb
Cleodora bowdenensis Collins
Styliola sulcifera Gabb
Creseis acicula Rang
Bowdenatheca jamaicensis Collins

In addition to the genus *Bowdenatheca* and its type species, *B. jamaicensis*, *Cleodora bowdenensis* was erected by Collins (1934), who distinguished an 'upper' and a 'lower' zone, the latter being the main shell bed from which Woodring's molluscan material originated. The three last-mentioned species in the above list came from the lower zone, all others from the upper zone.

The bulk of the material studied for this paper is in shell preservation and originates from sediments yielding abundant benthic molluscan material, although a part of the samples show distinct signs of aragonite dissolution. It is assumed that most of the material comes from the main

shell bed, or from layers very close to it.

The present revision of the Bowden holoplanktonic Mollusca comprises three species of Heteropoda and fourteen pteropod species.

MATERIAL, METHODS AND LOCALITIES

Material studied for the present paper was largely (samples 1-1 to 1-6) collected at the Bowden shell bed type locality. For geographic and lithostratigraphic data on this locality, reference is made to Zans *et al.* (1963), Robinson (1969) and Pickerill *et al.* (1998). Details of the various samples, as known to the author, are given below.

Reference to material listed in the systematic part below includes only sample numbers as defined here, specifying the number of specimens, and followed by registration number (for example: sample 1-1/12 specimens, RGM 396 006).

Bowden shell bed, Sample 1-1. — Material collected in 1975 by Dr Jan P. Krijnen, housed in the RGM collections. The locality is indicated as 'Bowden, road cut exposure, gully fill'. The material includes a large sample of benthic molluscs. The holoplanktonics discussed herein were recovered from sediment infill of larger gastropod shells. Contrary to most other samples, the present sample yielded molluscan material in excellent preservation, with hardly any aragonite dissolution. The quality of the specimens is very good and only this sample yielded small specimens, such as limacinids. Sample 1-1 is therefore considered to represent the most complete holoplanktonic molluscan assemblage, in which the species occur in almost natural ratios.

A single specimen (RGM 396 032) in this sample, a large shell of *Cavolinia tridentata*, is stated to have come from 'a higher level.' This specimen has suffered from aragonite dissolution, being preserved as an internal mould with shell remains only.

Bowden shell bed, Sample 1-2. — Material housed in the Naturhistorisches Museum Basel (NMB, Switzerland) with the following label: Jamaica, SE coast; Port Morant, Bowden Fm, leg. Jooss and Strasser, 1931; don. Trinidad leaseholds.

C.H. Jooss and Strasser originally sampled five localities (partly indicated B.1 to B.5) within the Bowden Formation. However, detailed geographical data are lacking. All five localities are assumed to be situated east of Port Morant, in an area not larger than 200 m^2. This is NMB locality 10635.

Bowden shell bed, Sample 1-3. — Material housed in the Naturhistorisches Museum Basel (NMB locality 11146), carrying the following label: PJ 778. Jamaica, Bowden Shop, Bowden shell bed. Bowden Formation. Outcrop opened by bulldozer. 1:50,000 sheet N; 1:12,500 sheet 235. Same locality as PJ 464 (NMB locality 10831), PJ 669 (NMB locality 11036), PJ 743 (NMB locality 11110). Leg. E. Robinson, Myrtle Haase, Alfred Rose, Richard de Souza and P. Jung, 12 May 1969.

This sample comprises only a single specimen of *Cavolinia digitata*.

Bowden shell bed, Sample 1-4. — Material housed in the Florida Museum of Natural History, Gainesville (Florida, U.S.A.). Data are as follows: Bowden (XJ002), Jamaica, St Thomas parish. Pliocene, Bowden Formation, *in situ*. Coll. Roger Portell, 28 May 1990. The material comprises nine samples of Euthecosomata, apparently picked from washing residues. Finer fractions from the same sample received on loan appeared to yield no holoplanktonic molluscs.

Bowden shell bed, Sample 1-5. — Material collected by S.K. Donovan, donated to the RGM collections in September 1995. Label stating: Pliocene Bowden shell bed, SE Jamaica. The specimens were picked from washing residues, five species occur. Most, if not all, of this material is from unit 2 of the Bowden shell bed *sensu* Pickerill *et al.* (1998).

Bowden shell bed, Sample 1-6. — On the author's request, S.K. Donovan and R.W. Portell collected a quantity of larger benthic gastropod shells at the Bowden type locality, in order to recover holoplanktonics from their sediment contents, as for sample 1-1. The sample was collected in February 1996 and subsequently donated to the RGM. Unfortunately, almost all specimens appeared to have been collected from a level of advanced decalcification. Most shells were partly to completely dissolved, and sediment infill had become indurated, forming internal moulds. Still, a careful inspection of this material by breaking up the moulds and study under the microscope, yielded quite a number of holoplanktonics, but exclusively larger species. Ten species are represented in this material.

Bowden Formation, Sample 2-1. — Sediment sample collected by S.K. Donovan, subsequently donated to the RGM collections, September 1995, labelled: Bowden Formation, from coastal section, stratigraphically above the shell bed.

The sediment is decalcified to a high degree and the few fossils are represented as moulds and casts, stained dark reddish brown. Identification of the material is difficult because of poor preservation. Four species could be recognised.

ABBREVIATIONS

The following abbreviations are used:

NMB Naturhistorisches Museum, Geology Department, Basel (Switzerland).

RGM Nationaal Natuurhistorisch Museum (Palaeontology Department, Cainozoic Mollusca), Leiden, The Netherlands (formerly Rijksmuseum van Geologie en Mineralogie).
SMF Senckenberg Museum, Frankfurt am Main (Germany).
UF Florida Museum of Natural History, University of Florida, Gainesville (U.S.A.).
USNM National Museum of Natural History, Smithsonian Institution, Department of Paleobiology, Washington D.C. (U.S.A.).

AGE OF THE BOWDEN SHELL BED

In the classic literature on the Bowden shell bed the age of these deposits is mostly considered to be Miocene. Recent research, however, has demonstrated them to be of a younger age.

Aubry (1993) and Berggren (1993) discussed the biostratigraphy of Neogene deposits in eastern Jamaica in detail, using calcareous nannofossils and planktonic foraminifera, respectively. Berggren's results are incorporated in Aubry's paper.

Lithostratigraphically, the typical Bowden shell bed belongs to the Lower Coastal Group, Bowden Formation. At the type locality only the upper part of the formation is present or exposed. The famous Bowden shell bed is at the base of the section.

Samples from the Bowden type section (Aubry, 1993, p. 152) yielded limited nannoplankton assemblages, of low diversity and poor preservation, and could not be assigned to zone. Other nearby outcrops, however, yielded better material and without exception could all be correlated with nannoplankton zone NN16. In terms of planktonic foraminiferal biostratigraphy the Bowden Formation belongs to zones PL3 to PL5, which means 'early late Piacenzian' (Aubry, 1993, p. 158). Reference is made to Ferrero Mortara & Pavia (in press) for a revised interpretation of the chronostratigraphical indication 'Piacenzian'.

SYSTEMATIC PALAEONTOLOGY

Symbols used in the lists of synonyms in this chapter are those of Richter (1948):

1881 (in Roman) cited reference contributes to the knowledge of the taxon;
* first valid introduction of the taxon; responsibility for the identification is accepted by the present author;
(no symbol) responsibility for the identification is not accepted by the present author, but there is no reason for doubt;
? in the opinion of the present author there is reason to doubt the identification;
v the original material of this reference was studied by the present author.

ORDER HETEROPODA

Family Atlantidae Wiegman & Ruthe
Genus *Atlanta* Lesueur

Type species — *Atlanta peroni* Lesueur.

Atlanta diamesa Woodring, 1928
Pl. 1, Fig. 1a-c

v* 1928 *Atlanta (Atlanta) diamesa*, new species, Woodring, p. 133, figs 23-25.

Type material — Holotype (USNM 369335) and two poorly preserved paratypes from 'Bowden, Jamaica' (Aldrich/Johns Hopkins Collection).

Description — The shell has a distinct lenticular shape with originally a double-walled peripheral flange, that is broken for the greater part. The height/width ratio is *c.* 0.29. The number of whorls is *c.* 4½. The protoconch has no sharp boundary with the teleoconch and is partly damaged or covered with sediment. Still, it can be seen that the first whorls together form a gently elevated cone in the centre of the shell, lying in a shallow depression and therefore invisible in side view. Apparently, the initial whorls are relatively higher than the ultimate whorls. No surface ornament is visible on the protoconch whorls. On the last part of the body whorl there is a weak indication of more or less radially situated knobs, of which *c.* 4 are visible (Pl. 1, Fig. 1a).

On the base of the shell only the last two whorls are visible. There is a narrow umbilicus. Both on the upper and lower shell wall spiral striation is absent. Only growth lines are visible, which demonstrate a wide forward curve, with the strongest point of curvature in the peripheral half, touching the upper suture almost under a right angle and becoming almost parallel to the periphery on the opposite side.

The aperture is elongated heart-shaped, hardly or not indented by the penultimate whorl.

Material — Apart from the type material, just a fragmentary specimen is available: sample 1-1/1 fragment, RGM 396 006 (Pl. 1, fig. 2a-b).

Discussion — *Atlanta diamesa* seems to be closely related to the Recent *A. peroni* (Lesueur, 1817). However, in the latter the early whorls are tighter and more elevated, which characteristics no doubt indicate a juvenile shell distinctly differing from that of the present species.

The late Miocene (?) *A. cordiformis* Gabb from the Dominican Republic (Janssen, in press) differs in several respects, especially in form and ornament of the early whorls. It seems to be closely related to the Recent *A. inflata* Souleyet (Janssen, in press).

Collins (1934, p. 146) referred to a shell of *Atlanta*, collected in 1932 from a roadside exposure, *c.* 50 feet above the base of the Bowden hill, accompanied by several pteropod species. The present whereabouts of this specimen is unknown.

The juvenile and poorly preserved paratypes, as well as the fragment discussed here, cannot be assigned to this species with any certainty.

Genus *Oxygyrus* Benson

Type species — Oxygyrus keraudrenii (Lesueur).

Oxygyrus keraudrenii (Lesueur, 1817)
Pl. 1, Fig. 3a-b

* 1817 Atlante de Keraudren, *A. Keraudrenii*, Lesueur, p. 391.

Additional synonymy — Reference is made to the exhaustive synonymy of this predominantly Recent species by van der Spoel (1976, p. 137).

Description — Shell *c.* 1½ times wider than high, involute. The early whorls, inclusive of the protoconch, are invisible. Only slightly more than the body whorl is exposed, and the shell is deeply umbilicated both above and below. The whorls are very convex. At the aperture the width of the whorl is *c.* 2½ times that of the preceding whorl (apical view). The apertural margin is broken. The shape of the aperture is almost circular, slightly higher than wide and slightly indented by the preceding whorl.

The surface of the shell is covered with *c.* 20-22 spiral lines that are wavy or demonstrate a very clear zigzag structure. On the periphery of the body whorl these spirals leave a zone free of ornament, on which only growth lines are faint. Just behind the aperture the spiral ornament stops quite abruptly on a slightly thickened set of growth lines. In front of this point the shell surface is smooth.

The growth lines are distinct near the aperture and describe a backward curve close to the upper suture followed by a somewhat wider forward curve above the peripheral belt, on which they strongly curve backwards again. On the base of the shell the shape of the growth lines is similar. It appears that the shell must have been deeply sinuated in early growth stages.

In the only available specimen the aperture is irregularly broken, but at the upper and lower suture the shell material is still present over a short distance. From Recent specimens it is known that the shell material of fully-grown specimens is cartilagenous, and therefore it seems probable that the specimen at hand is in fact complete or almost complete.

Material — Sample 1-1/1 specimen, RGM 396 005.

Discussion — According to van der Spoel (1976, p. 138), the fully-grown shell is cartilagenous, covering the calcareous early whorls that become absorbed in adult specimens. Thus, as no dissolution is visible in the present specimen, it most probably is not a fully grown specimen from which the cartilagenous material has disappeared, but still a juvenile. Other specimens of this species, as known from the Mediterranean Pliocene (RGM collections), are always much smaller and never reach the stage in which the spiral ornament is completed, as in the specimen at hand.

Further fossil occurrences of this species are known from the early Pliocene of northern Italy. In the Recent fauna this species is widely distributed in the tropics and subtropics.

Genus *Protatlanta* Tesch
(= *Atlantidea* Pilsbry, objective synonym)

Type species — Atlanta souleyeti Smith, by monotypy.

Protatlanta lissa (Woodring, 1928)
Pl. 1, Figs 4a-b, 5a-c

v* 1928 *Atlanta (Atlantidea) lissa*, new species, Woodring, p. 134, pl. 2, figs 26, 27.

Type material — Holotype (USNM 369336) and paratype from 'Bowden, Jamaica' (Aldrich/Johns Hopkins Collection). The holotype is a juvenile specimen, illustrated in Woodring (1928), with a rather damaged aperture and worn surface, partly covered with glue. The paratype is more than double the size of the holotype, but barely more than an internal mould on which shell remnants are present.

Description — Shell dextral, planispiral, slightly more than twice as wide as high when adult, relatively higher in juvenile specimens. The protoconch and early teleoconch whorls are only partly preserved in the holotype. The number of protoconch whorls is difficult to estimate because of incompleteness and sediment adhering to the shell. The complete shell of the holotype at least has 4 whorls, probably *c.* 5, which means that the fully grown shell has *c.* 5½ whorls. The early whorls form a depressed cone that is excentric and positioned somewhat obliquely with respect to the body whorl. At least the last protoconch whorl has a very thin spiral thread running over the middle of the whorl.

There is slightly more than one rapidly expanding teleoconch whorl. The aperture is distinctly wider than high (damaged in the holotype); at the columellar side it is only slightly indented by the preceding whorl. The base of the shell has a similar, slightly convex shape as the apical side of the shell. The umbilicus is narrow, occupying *c.* 1/6 of total shell diameter. The base of the last protoconch whorl is visible in the umbilicus, its surface is devoid of ornament (only visible in the paratype).

The surface of the teleoconch in all available specimens is poorly preserved, but strongly curved forward growth lines are visible under slanting light. No spiral ornament is visible, except for two distinct spiral lines on the periphery that together enclose a kind of belt on the periphery on which the growth lines curve strongly backward. However, this peripheral belt in not distinctly visible in the type material.

Material — Type material as specified above, and sample 1-

6/1 specimen, RGM 396 007.

Discussion—The few specimens from the Bowden Beds, admittedly rather damaged, closely resemble the late Miocene *Protatlanta rotundata* (Gabb) known from the Dominican Republic (Janssen, in press, pl. 1, figs 3, 4), the only differences being the slightly flatter shell and the absence of spiral ornament in the Jamaican specimen. The protoconch of *P. lissa* has a similar oblique position, but seems to be less ornamented.

Another Miocene specimen from the Langhian of Italy is illustrated by Janssen (1995, pl. 1, fig. 3). This specimen, an internal mould, seems to have a higher protoconch than the Caribbean species, but the height/width ratio of the shell is similar.

A further interpretation of these *Protatlanta* specimens has to be deferred until more material is available, especially from the Caribbean. Some more material is waiting to be described from various Miocene and Pliocene localities in the Mediterranean.

ORDER THECOSOMATA

Suborder Euthecosomata
Family Limacinidae Gray
Genus *Limacina* Bosc (= *Spiratella* de Blainville)

Type species — *Clio helicina* Phipps.

Limacina bulimoides (d'Orbigny, 1836)
Pl. 1, Figs 6-8

* 1836 *Atlanta (Heliconoides) bulimoides*, d'Orb. — d'Orbigny, p. 179, pl. 12, figs 36-38.

Additional synonymy — See van der Spoel (1967, p. 53, fig. 21).

Description — In the available material from Bowden the larger specimens are all more or less broken and deformed, frequently with their apices depressed, and only some juvenile shells are complete and undistorted. They agree in all respects with material of the Recent *L. bulimoides*, both from Atlantic and Pacific localities. A juvenile and an adult Recent shell are illustrated here (Pl. 1, Figs 9, 10) to demonstrate this conspecificity. However, none of the Bowden shells has a fully grown apertural margin. For a description of Recent specimens, the reader is referred to the relevant literature, as specified above.

Material — Sample 1-1/9 more or less defective/juvenile specimens, RGM 395 008-011.

Remarks — So far, this species was only occasionally recorded from Pleistocene deposits. This is the first record from below the Pliocene/Pleistocene boundary. In the Recent fauna this species has a wide distribution in tropical and subtropical areas.

Very similar material is available from the early Pliocene of southern France and northern Italy (RGM collections), which will be discussed in a future paper.

Limacina inflata (d'Orbigny, 1836)
Pl. 1, Fig. 12a-b

* 1836 *Atlanta (Heliconoides) inflata*, d'Orb. — d'Orbigny, p. 174, pl. 12, figs 16-19.

Additional synonymy — Reference is made to van der Spoel (1967) for extensive synonymy. Janssen (1990, in press) listed additional Cenozoic records, including data on type material and type locality.

Description — The available material is not very well preserved. Most specimens are defective, crushed or juvenile. The visible characteristics agree in general with the rich Miocene material described from Australia (Janssen, 1990, p. 15, pls 2, 3, 10), but there are minor differences.

The specimens from Bowden are somewhat more tightly coiled, resulting in a narrower body whorl (apical view). Also the Caribbean specimens, when fully grown, have half a whorl less and thus remain smaller. Finally, in the Bowden form (visible in one specimen only), the shell wall is slightly bulging at the place of the internal reinforcement. With these differences, the Bowden shells more closely resemble the Recent form of *L. inflata*.

Material — Sample 1-1/40 specimens, RGM 396 014-015.

Discussion — There might be a closer relationship between the Australian material of *L. inflata* and the European *L. miorostralis* (Kautsky) than previously thought, since in the Australian specimens (Janssen, 1990, pl. 2, figs 5-7) the internal reinforcements near the aperture do not cause an externally visible bulging of the shell wall. However, in the European species the apertural rostrum is only rarely developed and the height/width ratio is slightly lower.

Limacina sp. 1
Pl. 1, Fig. 11

Description — Only four specimens, two of them juvenile and the others strongly defective, are available. One of the juveniles is illustrated here. The shell is wider than high, but the apex clearly protrudes, much more so than in the specimen described below as *Limacina* ? sp. 2. The whorls are relatively convex and the base is perforate.

Material — Sample 1-1/4 specimens, RGM 396 916-017.

Discussion — The poor material is insufficient for a specific identification. The juveniles almost have the 'ideal' *Limacina* shape, but cannot with any confidence be assigned to any one of the taxa described. This concise description and illustration are therefore only given here to record its occurrence. An interpretation is deferred until more and better preserved specimens are available.

Limacina ? sp. 2
Pl. 1, Fig. 13a-b

Description — A single, strongly defective specimen might represent an undescribed species of *Limacina*. The shell, or rather what is left of it, has slightly more than two very flat whorls. In lateral view, the apex is hardly or not elevated; the last whorl is faintly carinated. The growth lines are very faint, but slightly directed backwards.
Material — Sample 1-1/1 defective specimen, RGM 396 018.
Remarks — At first glance this specimen resembles Recent *Limacina lesueurii* (d'Orbigny), but in that species the apex is higher, the body whorl is not angular and the growth lines are less oblique. It cannot be excluded that the present specimen is, in fact, a protoconch of a pyramidellid species, but in other such protoconchs the shell wall always is considerably thicker. In the specimen before me the shell wall agrees in thickness with Limacinidae.

Family Cavoliniidae Fischer
Subfamily Creseinae Rampal
Genus *Bowdenatheca* Collins

Type species — *Bowdenatheca jamaicensis* Collins, by monotypy.

Bowdenatheca jamaicensis Collins, 1934
Pl. 1, Figs 14a-c, 15a-c

* 1934 *Bowdenatheca jamaicensis* n. sp., Collins, p. 221, pl. 13, figs 13-15.
1959 *Bowdenatheca jamaicensis* R.L. Collins — Zilch, p. 51, fig. 171.
1980 *Bowdenatheca jamaicensis* Collins — Shibata, p. 64.
1982 *Bowdenatheca jamaicensis* (Collins) [*sic*] — Lozouet & Maestraeti, p. 184.
1982 *Bowdenatheca jamaicensis* Collins — Bernasconi & Robba, p. 218.
1983 *Bowdenatheca jamaicensis* Collins — Shibata, p. 80.
v. 1995 Creseinae sp. ? nov. — Janssen, p. 30, pl. 2, fig. 3a-d.
? 1996 *Bowdenatheca* ? sp. — Ujihara, p. 780, fig. 5/43-49.
1997 *Bowdenatheca jamaicensis* Collins, 1934 — Zorn, p. 35, pl. 4, figs 1-4.

Description — Shell vaginelliform, regularly conical in ventral view, slightly arched in lateral view. The protoconch is unknown, having apparently been shed during metamorphosis, as the opening is closed by a smooth septum. The dorso-ventral diameter of the juvenile shell is slightly more than the shell width, but towards the aperture the shell becomes flattened. The width of the aperture is almost twice the dorso-ventral diameter. The lengthwise curvature of the shell is slight and the ventral side is more strongly curved than the dorsal one, which is virtually straight. The transverse curvature of the dorsal side is stronger than that of the ventral side, which towards the aperture demonstrates a central swelling, accompanied by a very slight depression on both sides. The lateral shell parts are gradually rounded without carinae all over their length.

The growth lines are very slightly curved in apertural direction on the ventral side and much more strongly so on the dorsal side, curved in a clear V-shape on the lateral margins. It follows that the dorsal apertural margin is higher than the ventral one. Close to the aperture the growth lines are stronger and rather regularly distributed. The apertural margins are sharp, not thickened or internally reinforced.
Material — Sample 1-1/10 mainly defective or fragmentary specimens, RGM 396 019-021.
Discussion — Collins (1934, pp. 221, 222) compared his new taxon with *Vaginella*, but quite rightly concluded that it does not belong to that genus, because of differences in the apertural structures and by the absence of lateral carinae. He found a closer resemblance to *Vaginella undulata* (Gabb) and *V. caribbeana* Collins, which, together with his *Bowdenatheca jamaicensis*, he suggested to 'belong to a distinct, but closely related group.' *Vaginella undulata* and *V. caribbeana* have recently been reassigned to the genus *Edithinella* by Janssen (1995, p. 124), but *B. jamaicensis* demonstrates several differences and is not considered to belong in *Edithinella*. The main differences are the absence of transverse undulations on the dorsal side of *B. jamaicensis*, the absence of more or less distinctly developed lateral grooves, and the fact that the juvenile shell is shed. In addition, species of *Edithinella* have a widened and reinforced aperture when fully grown.

However, assignment to the Creseinae, as proposed herein, and also by Zorn (1997), has not been substantiated yet either. Especially the dorso-ventral flattening of the shell is rather unusual in that subfamily, but for the time being it seems to be the best solution. The taxonomic position of the species should be reconsidered when its protoconch is found.

This species is now known to occur also in the Messinian and early Pliocene of the Mediterranean (Janssen, 1995; Zorn, 1997). It is not yet known from deposits younger than the Bowden Beds. A Pliocene Japanese occurrence of a closely related, if not identical, form was recorded by Ujihara (1996) (see synonymy list).

Genus *Creseis* Rang

Type species — *Creseis acicula* Rang.

Creseis acicula ? (Rang, 1828)

* 1828 *Cleodora (Creseis) acicula* N., Rang, p. 318, pl. 17, fig. 6.

Additional synonymy — An extensive synonymy (mainly fossil occurrences) may be found in Janssen (in press).
Description — Elongated conical shell fragments, very slowly increasing in shell diameter and with a very thin shell wall.
Material — Sample 1-1/11 fragments, RGM 396 022.
Remarks — The available fragments closely resemble the well-known *Creseis acicula*, but lack the final proof of the

protoconchs, which were not found. Therefore, it cannot be excluded that these fragments belong to organisms other than Thecosomata. The same appears to hold true for specimens recorded from Bowden by Collins (1934, p. 208).

Genus *Styliola* Gray

Type species — *Styliola subula* (Quoy & Gaimard).

Styliola subula (Quoy & Gaimard, 1827)

* 1827 Cléodore alène, *Cleodora subula*, Quoy & Gaimard, p. 233, pl. 8D, figs 1-3.

Additional synonymy — For further synonymy see Janssen (1990, 1995, in press).
Description — The reader is referred to the relevant literature on the Recent occurrences of this well-known species (for example, van der Spoel, 1967). Fossil material was described and discussed in detail by Janssen (1990).
Material — Sample 1-1/65 specimens, RGM 396 023; sample 1-2/1 specimen, NMB H 17789; sample 1-6/5 specimens, RGM 396 024; sample 2-1/1 defective specimen, RGM 396 025.
Discussion — The synonymy of *Styliola sulcifera* Gabb, 1873, described from the Pliocene of Santo Domingo, was discussed by Janssen (1990, p. 34; in press, pl. 3, fig. 7). Janssen (1995, p. 30) gave the stratigraphical range of *Styliola subula* as middle Miocene to Recent, but in the meantime the species has been found to occur already in late Oligocene sediments of the North Sea Basin, and probably also of southwest France.

Subfamily Clioinae van der Spoel
Genus *Clio* Linné

Type species — *Clio pyramidata* Linné.

Clio pyramidata Linné, 1767 f. **lanceolata** (Lesueur, 1813)

* 1813 Hyale lancéolée (*Hyalaea lanceolata*), Lesueur, p. 284, pl. 5, fig. 3A, B.

Additional synonymy — For an extensive synonymy of predominantly Recent occurrences, see van der Spoel (1967, p. 68); for fossil occurrences, see Janssen (1995, in press).
Description — See van der Spoel (1967, p. 68).
Material — Sample 1-1/1 protoconch, RGM 396 026; sample 1-4/1 defective specimen, UF 68907; sample 1-5/2 defective specimens RGM 396 027; sample 1-6/1 specimen, RGM 396 028.
Discussion — *Clio bowdenensis* (Collins, 1934) was synonymised with the present form by Robba (1977, p. 600). Janssen (in press, pl. 3, fig. 15) illustrated the holotype.

Clio aff. **braidensis** (Bellardi, 1873)
Pl. 1, Figs 16a-d, 17a-d

*v 1873 *Balantium (Flabellulum) braidense* Bell. — Bellardi, p. 32, pl. 3, fig. 12.

Additional synonymy — For further synonymy, reference is made to Janssen (1995, pp. 62, 63).
Description — Only three specimens are available, one of which preserves the protoconch. The shell is triangular, apical angle initially *c.* 30°, but rapidly widening in apertural direction at a short distance from the apex, from there on enclosing an angle of almost 75°. Side lines are therefore concave in the apical part of the shell, straight towards the aperture and distinctly squarish in transverse section. The shell has a lengthwise curvature, especially in the apical part. In lateral view it is visible that the carinae bend slightly in opposite directions, giving the shell an elegant shape. The protoconch is spherical, with a sharp distal spine, clearly separated from the teleoconch and connected by a slight constriction of the shell.

The ventral side of the shell is much flatter than the dorsal side, with a flat central rib, occupying almost one third of the shell width. The lateral fields are virtually flat. The dorsal side is convex with a swelling in the centre, on which (very vaguely) a tripartition is visible: two narrow riblets and a wider central one. Lateral fields are concave. A narrow marginal zone is present. Under slanting light a transverse ornament may be seen on the lateral fields, consisting of widely separated and curved undulations.
Material — Sample 1-1/3 specimens, RGM 396 029-031.
Discussion — The Bowden specimens differ from those from the early Pliocene, North Italian specimens in several respects. The lengthwise curvature of the shell has not been observed yet in the Italian material. The central elevation of the dorsal side of the Bowden specimens is slightly stronger, but its tripartition is only very vaguely indicated. The same is true for the transverse ornament, which in the Bowden shells is exclusively traceable under slanting light and only on the dorsal side. Also, their apical angle is slightly wider and reaches almost 75°, instead of 70° as in Italian *C. braidensis*. Still, the general appearance of the specimens is such that a close relationship with *C. braidensis* is obvious, and, in my opinion, the observed differences do not allow the introduction of a new taxon, especially so since limited material is available.

When compared to the Recent *C. cuspidata* (Bosc) (see Pl. 1, Fig. 18a-d), there is a major difference in the dorsal side, which in *C. cuspidata* has a sharp central carina, accompanied by a weaker vertical line on each side. The transverse ornament is very well developed in the Recent species, reaching the same strength as in the early Pliocene (Zanclean) *C. braidensis* from Italy. The protoconch of *C. cuspidata* closely resembles that of the Bowden specimen, demonstrating a rather close relationship.

At first view, one might suspect a closer relationship with the Miocene *C. carinata* (Audenino), the dorsal side of which

resembles *C. cuspidata* very well. However, in *C. carinata* the ventral side has a strongly different arrangement of ornament elements. Its protoconch also differs considerably (Janssen, 1995, pl. 5, figs 7, 8; pl. 6, fig. 1). In this context it seems plausible that the specimen referred to by Janssen (in press, pl. 3, fig. 12), from the Mao Formation of the Dominican Republic, might also belong to this species rather than to *C. cuspidata*.

Subfamily Cavoliniinae Fischer
Genus *Cavolinia* Abildgaard (emend. Philippi)

Type species — *Cavolinia tridentata* (Niebuhr).

Cavolinia tridentata (Niebuhr, 1775)
Pl. 2, Fig. 1

* 1775 *Anomia tridentata*, Niebuhr, p. 124.

Additional synonymy — For an extensive synonymy of this predominantly Recent species the reader is referred to van der Spoel (1967).
Description — The mainly fragmentary material available from the Bowden locality agrees in general with the Recent material of this species.
Material—Sample 1-1/1 defective specimen, 4 fragments, RGM 396 032-033; sample 1-2/1 defective specimen, 3 fragments, NMB H 17790-2; sample 1-4/1 fragment ?, UF 68903, 7 fragments, UF 68901; sample 1-6/1 defective specimen, RGM 396 035.
Remarks — One fragment in the available material, a dorsal shell plate (sample 1-2, NMB H 17792), shows traces of an oblique transverse ornament in the apical shell part (Pl. 2, Fig. 1). This is reminiscent of the early Pliocene *Cavolinia grandis* (Bellardi) from the Mediterranean (Janssen, 1995, p. 97, pl. 8, fig. 8, holotype). However, in that species the transverse ornament is also present on adapertural shell parts and is distinctly more accentuated. Therefore, the present fragment is not considered to be a last representative of *C. grandis*, but is included in *C. tridentata*, which agrees with the age of the material.

Fossil representatives of this species are known from the Pliocene of the Caribbean and the Mediterranean, whereas in the Recent fauna this species has a circumglobal distribution in the temperate to tropical zones.

Cavolinia vendryesiana (Guppy, 1873)
Pl. 2, Fig. 2a-c

* 1873 *Hyalaea (Diacria) vendryesiana* Guppy, p. 74, pl. 2, fig. 2.
1874 *Hyalaea (Diacria) Vendryesiana* — Guppy, pp. 405, 441, pl. 17, fig. 2.
1882 *Hyalea vendryesiana*, Guppy — Guppy, p. 175.
1883 *Diacria Vendryesiana*, Guppy — Fischer, p. 435.
1894 *Hyalaea (Diacria) vendryesiana*, Guppy — Cockerell, p. 118.
1903 *Cavolinia Vendryesiana* Guppy — Dall, p. 1582.
1928 *Cavolina vendryesiana* (Guppy) — Woodring, p. 115, pl. 1, figs 12, 13.
1934 *Cavolina vendryesiana* (Guppy) — Collins, p. 190, pl. 11, figs 16-18.
1943 *Cavolina vendreysiana* [*sic*] (Guppy) — Beets, p. 306.
1962 *Cavolina vendryesiana* Guppy, sp. 1873 — Glibert, p. 62.
1971 *Cavolinia* cf. *vendryesiana* (Guppy) — Jung, p. 221.
1975 *Cavolinia vendryesiana* — Grecchi, p. 228.
1982 *Cavolinia* cf. *vendryesiana* (*in* Jung, 1971) — Bernasconi & Robba, p. 215.
1982 *Cavolinia vendryesiana* (Guppy) — Bernasconi & Robba, p. 218.

Comparative remarks — This species closely resembles the Recent *C. inflexa* (Lesueur) and differs in minor points only. The dorsal side of the fossil species has an obvious reinforcing rim along the apertural margin, which is absent in *C. inflexa*. In addition, *C. inflexa* has some wide radial folds on the dorsal side, which are absent or only very vaguely indicated in *C. vendryesiana*.
Material — Sample 1-1/5 ± defective specimens, 3 fragments, RGM 396 037-038; 11 apical spines, RGM 395 036; sample 1-2/6 ± defective specimens, NMB H 17793; sample 1/4/2 specimens, UF 68905; sample 1-5/1 defective specimen, RGM 396 039; sample 1-6/1 defective specimen, RGM 396 040.
Discussion — A Recent specimen of *C. inflexa* is illustrated here for comparison (Pl. 2, Fig. 3). It has its lateral spines also more developed and bent down, which is not necessarily a specific character. Probably the two species are closely related, belong to the same lineage, and should be grouped in a separate taxon, as the differences with most other *Cavolinia* species are considerable.

This species is also known from the Pliocene (Piacenzian) of the Mediterranean area. From the Japanese Pliocene, Ujihara (1996, p. 785, fig. 7/18-30) introduced *Cavolinia vendryesiana hyugaensis*, which I consider a synonym of *C. vendryesiana*.

Cavolinia ventricosa (Guppy, 1882)
Pl. 2, Figs 4-8

*v 1882 *Hyalea ventricosa* Guppy, p. 176, pl. 7, fig. 15.
1903 *Cavolinia ventricosa* Guppy — Dall, p. 1582.
.v 1928 *Cavolina ventricosa* (Guppy) — Woodring, p. 114, pl. 1, figs 8, 9.
.v 1934 *Cavolina ventricosa* (Guppy) — Collins, p. 184, pl. 7, figs 16-18.
1960 *Covolinia* [*sic*] *ventricosa* (Guppy) — Pchelitsev & Korobkov, p. 252, fig. 710.
1970 *Cavolina (Cavolina)* cf. *C. ventricosa* (Guppy) — Woodring, p. 429, pl. 63, figs 11, 12.

1982 *Cavolinia ventricosa* (Guppy) — Bernasconi & Robba, pp. 217, 218.

Type material — According to Collins (1934, p. 185) the two syntypes, housed in the United States National Museum, 'are partly covered with glue and cleaning is impracticable', for which reason he did not illustrate them, nor designate a lectotype. I studied these specimens some years ago; with some care both could be cleaned and they are illustrated herein (Pl. 2, Figs 4, 7). The better preserved specimen of the two (Pl. 2, Fig. 7) is here designated lectotype (USNM 115625).

Type locality — 'Jamaica'.

Description — *Cavolinia ventricosa* closely resembles the late Miocene species *C. gypsorum* (Bellardi) (see Janssen, 1995, p. 99, pl. 8, figs 9-12). As stated in that paper the dorsal shell part of *C. ventricosa* is considerably more convex, as a result of which the long apertural lip (found in a few specimens only: Pl. 2, Fig. 8c) projects horizontally, instead of obliquely as in *C. gypsorum* (compare with Janssen, in press, pl. 4, fig. 1b). The ornament of the dorsal side in *C. ventricosa* could be described as consisting of five radial ribs, but the two lateral ones are so weak that, in fact, they cannot be called ribs. Thus, the ornament comprises three ribs, of which the middle one is usually remarkably narrower than the two others. Commonly, these lateral ribs are separated on their marginal sides by a rather deeply incised furrow (Pl. 2, Fig. 7a, lectotype). The ventral side of *C. ventricosa* differs strongly from *C. gypsorum* by the absence of the two oblique furrows, so typical for *C. gypsorum*. Also, this shell part is relatively higher. Fine and regular transverse growth lines are visible in a number of specimens, but in the bulk of the material they are hardly or not preserved.

The apex of *C. ventricosa* is slightly curved in dorsal direction, but the protoconch itself is absent in all available specimens.

Material — Sample 1-1/1 specimen, 2 fragments, RGM 396 041; sample 1-2/1 specimen, NMB H 17794; sample 1-4/1 specimen, separated from UF 68904, 1 fragment, UF 68906; sample 1-5/11 ± defective specimens, RGM 396 042; sample 1-6/9 ± defective specimens, 1 fragment, RGM 396 043-044; sample 2-1/1 specimen, ?2 specimens (internal and/or external moulds), RGM 396 045-047.

Discussion — In spite of the rather close resemblance between the present taxon and *C. gypsorum*, these species are not considered to be closely related. It is assumed that the occurrence of oblique furrows on the ventral side of *C. gypsorum* must be given fairly high taxonomic value. The only other *Cavolinia* in which such furrows are found is *C.* aff. *gypsorum*, described from the late Miocene of the Dominican Republic (Janssen, in press, pl. 4, fig. 4), a form apparently also present in Pliocene deposits of Japan. Similar furrows have been observed in a single, slightly distorted specimen of *C. mexicana* (Collins, 1934) (Janssen, in press, pl. 4, fig. 8), but here these furrows may originate from an early shell injury repair.

Apart from the occurrence in Bowden 'shells that appear to belong to this species' were recorded by Collins (1934, p. 185) from two localities in Haiti.

Genus *Diacria* Gray

Type species — *Diacria trispinosa* (de Blainville).

Diacria digitata (Guppy, 1882)
Pl. 2, Figs 9a-d, 10a-d, 11a-d, 12, 13a-b, 15a-d

*v 1882 *Hyalea digitata* Guppy, pp. 175, 176, pl. 16.
1903 *Cavolinia digitata* Guppy — Dall, p. 1582.
1928 *Cavolina digatata* (Guppy) [*sic*] — Woodring, p. 114, pl. 1, figs 10, 11.
1928 *Cavolina digitata* Guppy (*pars*) — Woodring, p. 115.
.v 1934 *Cavolina digitata* (Guppy) — Collins, p. 194, pl. 11, figs 1-9.
1982 *Diacria digitata* (Guppy) — Bernasconi & Robba, pp. 218, 220.

Type material — Guppy's original material, consisting of three specimens and two fragments, survives in the Smithsonian Institution (USNM 115623). Two of these specimens are illustrated herein (Pl. 2, Figs 9, 11); the better preserved one is here designated lectotype (Pl. 2, Fig. 9), the other two are paralectotypes.

Description — A juvenile shell and the protoconch were described and illustrated by Collins (1934, pl. 11, figs 7, 8); this specimen was studied for the present paper (Pl. 2, Fig. 13a-b). It has a relatively short apical spine, the end of which is inflated to an elongate bulb with a rounded tip, resembling that of the Recent *D. quadridentata* (de Blainville). The dorsal and ventral sides are still flat, indicating a pre-metamorphosis stage; three ribs are visible on the dorsal side. The apical angle is *c.* 135°. The apertural margin is strongly curved and lateral spines project sidewards, just above mid-height of the shell.

The fully-grown shell is bilaterally symmetrical with distinctly separated dorsal and ventral sides, *c.* 1¼ times higher than wide. Both sides are convex, but the ventral side more so than the dorsal, with a distinct swelling at mid-height. The juvenile shell is shed during ontogenesis and the opening is closed with a septum. From the septum the sides curve gently to almost horizontal. At the end the lateral slits between dorsal and ventral shell parts meet the base of the shell, and there a distinct spine is present, less commonly bending slightly in apical direction, but commonly not sharply pointed. In the lectotype these spines lie at one fifth of the shell height, as in most other specimens. However, the spines less commonly lie higher, up to two fifths of the height, in which case the spines are sharper and project sidewards more strongly (Pl. 2, Fig. 15a).

The inflated ventral shell part is smooth, but for some vaguely indicated growth lines that are slightly bent in apical direction in their middle. The ventral apertural margin is straight (ventral view) and distinctly thickened. In apertural

view this lip is strongly curved.

The dorsal side of the shell is considerably flatter, higher than the ventral side and reaching beyond the ventral apertural rim. Where the ventral margin touches the dorsal one, the latter shows a distinct constriction. Three relatively strong radial ribs are present on the middle of the dorsal side, separated by furrows of the same width. Together, these ribs occupy less than one third of the shell width, leaving wide lateral fields on each side. In some specimens these lateral fields are somewhat produced and resemble wide ribs (Pl. 2, Fig. 10a). The margin of this shell part is also thickened, especially so above the point in touch with the ventral shell part. In apertural view this rim is less strongly bent than the ventral one.

Material — Sample 1-1/14 more or less defective specimens, *c.* 50 fragments, RGM 396 048-049; sample 1-2/17 specimens, 3 internal moulds, 32 fragments, NMB H 17795-7; sample 1-3/1 specimen, NMB H 17798; sample 1-4/26 specimens, 12 fragments, UF 68902, UF 68904, UF 68909; sample 1-5/46 specimens, RGM 396 050; sample 1-6/32 ± defective specimens, RGM 396 051.

Discussion — An interesting specimen of *D. digitata* was illustrated by Collins (1934, pl. 11, fig. 9). It originates from the 'Miocene' of Port-au-Prince (Haiti), which must have a more or less comparable age to the Bowden Beds (Janssen, in press). The specimen is rather poorly preserved in a slab of sediment also containing *Hyalocylis haitensis* (Collins), which I consider synonymous with *H. striata* (Rang). It has the lateral spines well developed, relatively highly situated and pointing downwards. Furthermore, this specimen, although having passed shell metamorphosis, apparently had its apical shell part preserved. A new illustration of this specimen is here presented (Pl. 2, Fig. 12).

Typical *Diacria digitata* is exclusively known from the Caribbean (Jamaica and Haiti), but related forms were recorded from the Mediterranean and from Japan. Grecchi (1982, p. 723, pl. 54, figs 1-5) introduced *Diacria digitata italica* from the Pliocene of northern Italy. This taxon differs from typical *D. digitata* by the relatively high position of the lateral spines and the more accentuated constriction of the dorsal side above the juncture with the ventral side. Also, the lateral fields next to the set of three central radial ribs in this form more commonly are swollen and could be interpreted as wide additional radial ribs. The general outline of this form therefore resembles that of *Diacria trispinosa*. A single specimen from Bowden resembles this form (Pl. 2, Fig. 15a-d), but it lacks the constriction on the dorsal apertural margin and rather seems to be an abnormal specimen of *D. digitata*.

Grecchi, still considering the Bowden Beds as Miocene, interpreted his taxon to be a 'sottospecie allocrona e allopatrica.' However, the age of the Bowden Beds being Pliocene would make *D. digitata italica* a real geographic subspecies, so far restricted to the Mediterranean.

From Japan, Shibata (1980, pp. 61, 62, pl. 3, fig. 18), Shibata & Ishigaki (1981, p. 57, figs 5, 6) and Ujihara (1996, p. 781, fig. 6/1-6) recorded *Diacria digitata* from the Pliocene. The last-mentioned author considered his material to probably represent a new subspecies, but as far as can be seen from the illustrations all specimens referred to by the Japanese authors resemble closely the Mediterranean form, especially by the relatively high position of the lateral spines.

Diacria trispinosa (de Blainville, 1821)
Pl. 2, Fig. 14

* 1821 *Hyaloea trispinosa* Lesueur — de Blainville, p. 82.
* 1873 *Diacria bisulcata* Gabb n.s. — Gabb, p. 200.

Additional synonymy — Lists of further synonyms (mainly fossil occurrences) may be found in Janssen (1995, in press).
Description — See van der Spoel (1967, p. 84, figs 76-78).
Material — Typical form: sample 1-1/21 fragments, RGM 396 052; sample 1-2/1 specimen, 9 fragments, NBM H 17799-800; sample 1-4/1 fragment, UF 68908; sample 1-5/1 specimen, 2 fragments, RGM 396 053; sample 1-6/1 defective specimen, 2 fragments, RGM 396 054-055; sample 2-1/1 specimen (external mould), RGM 396 056. *Diacria trispinosa* f. *bisulcata*: sample 1-2/7 specimens, NMB H 17801-3.
Discussion — Several specimens amongst the available material show the typical features of f. *bisulcata* Gabb. For a discussion on the status of that taxon see Janssen (in press). The Jamaica specimens likewise are small shells with a height of some 4 mm. Even under slanting light they do not show a subdivision of the wide central rib. A specimen in the NMB collection, showing the typical features quite well, is illustrated herein (Pl. 2, Fig. 14).

CONCLUSIONS

The holoplanktonic molluscan fauna of the Bowden shell bed was found to comprise three heteropod and 14 pteropod species:

Heteropoda
Atlanta diamesa Woodring, 1928
Oxygyrus keraudrenii (Lesueur, 1817)
Protatlanta lissa (Woodring, 1928)

Thecosomata
Limacina bulimoides (d'Orbigny, 1836)
Limacina inflata (d'Orbigny, 1836)
Limacina sp. 1
Limacina ? sp. 2
Bowdenatheca jamaicensis Collins, 1934
Creseis acicula? (Rang, 1828)
Styliola subula (Quoy & Gaimard, 1827)
Clio pyramidata Linné, 1767 f. *lanceolata* (Lesueur, 1813)
Clio aff. *braidensis* (Bellardi, 1873)

Cavolinia tridentata (Niebuhr, 1775)
Cavolinia vendryesiana (Guppy, 1873)
Cavolinia ventricosa (Guppy, 1882)
Diacria digitata (Guppy, 1882)
Diacria trispinosa (de Blainville, 1821)
Diacria trispinosa (de Blainville, 1821) f. *bisulcata* Gabb, 1873

Naturally, taxa identified in open nomenclature yield no indication of the age of the assemblage. *Clio* aff. *braidensis* is here assumed to be a younger evolutionary form of the early Pliocene (Zanclean) *C. braidensis*. Amongst the remaining species two (*Atlanta diamesa* and *Protatlanta lissa*) are exclusively known from Bowden, whereas several others are long ranging:

Oxygyrus keraudrenii	early Pliocene—Recent
Limacina inflata	middle Miocene—Recent
Styliola subula	late Oligocene—Recent
Clio pyramidata f. *lanceolata*	late Miocene—Recent
Diacria trispinosa	late Miocene—Recent

Bowdenatheca jamaicensis is known from the late Miocene (Messinian) and early Pliocene (Zanclean); the occurrence in Bowden might represent its youngest known appearance. *Diacria trispinosa* f. *bisulcata* was recorded from the (?) late Miocene and late early Pliocene of the Dominican Republic.

Cavolinia vendryesiana is known from the Pliocene (Piacenzian) of the Mediterranean area and of Japan. *Cavolinia ventricosa* and *Diacria digitata* have both been recorded from the 'Miocene' of Port-au-Prince (Haiti). The Port-au-Prince assemblage may in fact be younger and be comparable with the Bowden Beds, as was already suggested by Janssen (in press). One species occurring at that locality, *Hyalocylis haitensis* Collins [= *H. striata* (Rang)], is unknown from the Bowden fauna. Its known range is late Miocene to Recent; it thus does not yield any precise stratigraphic data. Forms closely related to *D. digitata* are furthermore known from the Pliocene of the Mediterranean and Japan.

The most interesting species found at Bowden, biostratigraphically speaking, is *Cavolinia tridentata*. This species is only known from Pliocene (Piacenzian) age to the Recent, its predecessor species, *C. grandis* (Bellardi) being known from the Zanclean. Its occurrence at Bowden therefore indicates that the age of the association is Piacenzian or younger. This, in fact, agrees quite well with the age assignments proposed by Aubry (1993) and Berggren (1993).

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REFERENCES

Aubry, M.-P., 1993. Calcareous nannofossil stratigraphy of the Neogene formations of eastern Jamaica. *In*: R.M. Wright & E. Robinson (eds). Biostratigraphy of Jamaica. — Geological Society of America Memoir, 182: 131-178.

Beets, C., 1943. Beiträge zur Kenntnis der angeblich oberoligocänen Mollusken-Fauna der Insel Buton, Niederländisch-Ostindien. — Leidsche Geologische Mededeelingen, 13: 256-328.

Bellardi, L., 1873. I molluschi dei terreni terziari del Piemonte e della Liguria, 1. Cephalopoda, Pteropoda, Heteropoda, Gastropoda (Muricidae et Tritonidae). — Memorie della Reale Accademia delle Scienze, Torino, (2)27: 1-264.

Berggren, W.A., 1993. Neogene planktonic foraminiferal biostratigraphy of eastern Jamaica. *In*: R.M. Wright & E. Robinson (eds). Biostratigraphy of Jamaica. — Geological Society of America Memoir, 182: 179-217.

Bernasconi, M.P. & E. Robba, 1982. The thecosomatous pteropods: a contribution towards the Cenozoic Tethyan paleobiogeography. — Bolletino della Società Paleontologica Italiana, 21: 211-222.

Blainville, M.H. de, 1821. Hyale, Hyaloea (Malacoz.). — Dictionnaire des Sciences naturelles, 22: 65-83.

Cockerell, T.D.A., 1894. A list of the Brachiopoda, Pelecypoda, Pteropoda and Nudibranchiata of Jamaica, living and fossil. — The Nautilus, 7: 103-107, 113-118.

Collins, R.L., 1934. A monograph of the American Tertiary pteropod mollusks. — Johns Hopkins University Studies in Geology, 11: 137-234.

Dall, W.H., 1903. Contributions to the Tertiary fauna of Florida, with especial reference to the Miocene silex-beds of Tampa and the Pliocene beds of the Caloosehatchie River, including in many cases a complete revision of the generic groups treated of and their American Tertiary species, 6. Concluding the work. — Transactions of the Wagner Free Institute of Science, Philadelphia, 3(6): 1219-1654.

Ferrero Mortara, E. & G. Pavia, in press. La successione marina previllafranchiana. — AIQUA, Villafranchian Meeting, June 20th-24th, 1994.

Fischer, P., 1880-1887. Manuel de conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles suivi d'un appendice sur les brachiopodes par D.P. Oehlert (1-12). Paris (Savy), xxiv + 1369 pp. [Pteropods

in part 5 (1883)].

Gabb, W.M., 1873. [Notes on the] Topography and geology of Santo Domingo. — Transactions of the American Philosophical Society, n.s., 15: 49-259.

Glibert, M., 1962. Euthyneura et Pulmonata fossiles du Cénozoique étranger des collections de l'Institut royal des Sciences naturelles de Belgique. — Mémoires de l'Institut royal des Sciences naturelles de Belgique, (2)70: 1-140.

Grecchi, G., 1975. Pteropoda fossili a Castell'Arquato. — Conchiglie, 11(11-12): 225-232.

Grecchi, G., 1982. Pteropodi pliocenici dell'Italia settentrionale. — Rivista Italiana di Paleontologia, 87(4): 703-738.

Guppy, R.J.L., 1873. On some new Tertiary fossils from Jamaica. — Proceedings of the Scientific Association of Trinidad, 2(2): 72-88. [Reprinted 1921, Bulletins of American Paleontology, 8(35): 56-72].

Guppy, R.J.L., 1874. On the West Indian Tertiary fossils. — Geological Magazine, 11: 404-411, 433-446.

Guppy, R.J.L., 1882. On the Recent and Tertiary species of *Leda* and *Nucula* found in the West Indies, with notices of West Indian shells. — Proceedings of the Scientific Association of Trinidad, 2(12): 168-180. [Reprinted 1921, Bulletins of American Paleontology, 8(35): 89-101.]

Janssen, A.W., 1990. Pteropoda (Gastropoda, Euthecosomata) from the Australian Cainozoic. — Scripta Geologica, 91 (1989): 1-76.

Janssen, A.W., 1995. Systematical revision of holoplanktonic Mollusca in the collections of the 'Dipartimento di Scienze della Terra' at Torino, Italy. — Memorie del Museo Regia di Scienze Naturali, Torino, 17: 1-233.

Janssen, A.W., in press. Neogene paleontology in the northern Dominican Republic. Holoplanktonic molluscs (Gastropoda: Heteropoda and Thecosomata). — Bulletins of American Paleontology.

Jung, P., 1971. Fossil mollusks from Carriacou, West Indies. — Bulletins of American Paleontology, 61(269): 147-262.

Lesueur, C.A., 1813. Mémoire sur quelques espèces d'animaux mollusques et radiaires recueillis dans la Méditerranée, près de Nice. — Nouveau Bulletin du Société scientifique de Philom, 3: 281-285.

Lesueur, C.A., 1817. Mémoire sur deux nouveaux genres de mollusques, Atlante et Atlas. — Journal de Physique, de Chimie et d'Histoire naturelle, Paris, 85: 390-393.

Linné, C., 1767. Systema naturae, 12th edition, 1(2). Holmiae (Laurentii Salvii): 533-1327.

Lozouet, P. & P. Maestrati, 1982. Nouvelles espèces de mollusques de l'Oligocène (Stampien) pour les bassins de Paris et d'Aquitaine. — Archiv für Molluskenkunde, 112: 165-189.

Niebuhr, C., 1775. Descriptiones animalium avium, amphibiorum, piscium, insectorum, vermium; quae in itinere orientali observavit Petrus Forskål, prof. Haun. Adjuncta est materia medica Kahirina atque tabula Maris Rubri geographica. Hauniae (Möller), 164 pp.

Orbigny, A. d', 1836-1846. Voyage dans l'Amérique méridionale (le Brésil, la république orientale de l'Uruguay, la république Argentine, la Patagonie, la république du Chili, la république de Bolivia, la république du Pérou), exécuté pendant les années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833, 5(3). Mollusques. Paris (Bertrand): 49-184 (1836), atlas, 20 pls (1846).

Pchelintsev, V.F. & I.A. Korobkov, 1960. Osnovy paleontologii. Spravochnik dlya paleontologov i geologov S.S.S.R. Molljuski-Bryukhonogie (Podotryad Pteropoda). — Gosudarstv. Nauchno-Tekhn. Izdat. Liter. Geol. Okhrane Nedr., 1960: 251, 252.

Pickerill, R.K., S.F. Mitchell, S.K. Donovan & D.G. Keighley, 1998. Sedimentology and palaeoenvironment of the Pliocene Bowden Formation, southeast Jamaica. *In*: S.K. Donovan (ed). The Pliocene Bowden shell bed, southeast Jamaica. — Contributions to Tertiary and Quaternary Geology, 35: 9-27 (this volume).

Quoy, J.R.C. & J.P. Gaimard, 1827. Observations zoologiques faites à bord de l'Astrolabe, en Mai 1826, dans le détroit de Gibraltar (suite et fin). Description des genres biphore, carinaire, hyale, flèche, cléodore, anatife et briarée. — Annales des Sciences naturelles, 10: 225-239.

Rang, P.C.A.L., 1828. Notice sur quelques mollusques nouveaux appartenant au genre cléodore, et établissement et monographie du sous-genre créseis. — Annales des Sciences naturelles, 13: 302-319.

Richter, R., 1948. Einführung in die zoologische Nomenklatur durch Erläuterung der Internationalen Regeln (2nd edition). Frankfurt am Main (W. Kramer), 252 pp.

Robba, E., 1977. Pteropodi serravalliani della Langhe (Piemonte). — Rivista Italiana di Paleontologia, 83: 575-640.

Robinson, E., 1969. Geological field guide to Neogene sections in Jamaica West Indies. — Journal of the Geological Society of Jamaica, 10: 1-24.

Shibata, H., 1980. Pteropods from the early Miocene (Kurami and Saigo Groups) of the Kakegawa District and the early to middle Miocene (Yatsuo Formation) of the Yatsuo District, central Japan. — Bulletin of the Mizunami Fossil Museum, 7: 59-68 [In Japanese with English summary].

Shibata, H., 1983. Miocene pteropods from central Honshu, Japan. — Research Bulletin of the College of General Education, Nagoya University, B27: 65-86.

Shibata, H. & T. Ishigaki, 1981. Heteropodous and pteropodous biostratigraphy of Cenozoic strata of Chubu Province, Japan. — Bulletin of the Mizunami Fossil Museum, 8: 55-70 [In Japanese with English summary].

Spoel, S. van der, 1967. Euthecosomata, a group with remarkable developmental stages (Gastropoda, Pteropoda) [PhD thesis, University of Amsterdam]. Gorinchem (J. Noorduijn), 375 pp.

Spoel, S. van der, 1976. Pseudothecosomata, Gymnosomata and Heteropoda (Gastropoda). Utrecht (Bohn, Scheltema and Holkema), 484 pp.

Ujihara, A., 1996. Pteropods (Mollusca, Gastropoda) from the Pliocene Miyazaki Group, Miyazaki Prefecture, Japan. — Journal of Paleontology, 70: 771-788.

Woodring, W.P., 1925. Miocene mollusks from Bowden, Jamaica. Pelecypods and scaphopods. — Carnegie Institute of Washington, Publication 366: 1-222.

Woodring, W.P., 1928. Miocene mollusks from Bowden Jamaica. Part II. Gastropods and discussion of results. — Carnegie Institute of Washington, 385: 1-564.

Woodring, W.P., 1970. Geology and paleontology of Canal Zone and adjoining parts of Panama. Description of Tertiary mollusks (gastropods: Eulimidae, Marginellidae to Helminthoglossidae). — United States Geological Survey Professional Paper, 306D: D299-D452.

Zans, V.A., L.J. Chubb, H.R. Versey, J.B. Williams, E. Robinson & D.L. Cooke, 1963. Synopsis of the geology of Jamaica. An explanation of the 1958 provisional geological map of Jamaica. — Bulletin of the Geological Survey Department, Jamaica, 4: 1-72.

Zilch, A., 1959. Gastropoda, 2. Euthyneura, 1. Handbuch der Paläozoologie, 6: xii + 200 pp.

Zorn, I., 1997. Holoplanktonic gastropods from the Early Messinian of the Heraklion Basin (Crete, Greece). — Contributions to Tertiary and Quaternary Geology, 34(1-2): 31-45.

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PLATE 1

All specimens figured in Plates 1 and 2 are from the Pliocene Bowden shell bed, southeast Jamaica, unless stated otherwise.

Fig. 1 *Atlanta diamesa* Woodring, 1928 (**holotype**), USNM 369335, apical, frontal and umbilical views, x 12.5.

Fig. 2. *Atlanta* ? *diamesa* Woodring, 1928, sample 1-1, RGM 396 006; apical view and transverse section, x 25.

Fig. 3. *Oxygyrus keraudrenii* (Lesueur, 1817), sample 1-1, RGM 396 005; apical and right lateral view, x 25.

Fig. 4 *Protatlanta lissa* (Woodring, 1928) (**holotype**), USNM 369336; apical and frontal views, x 12.5.

Fig. 5. *Protatlanta lissa* (Woodring, 1928), sample 1-6; RGM 396 007; apical, frontal and umbilical view, x 6.

Figs 6-8. *Limacina bulimoides* (d'Orbigny, 1836), sample 1-1, RGM 396 009-011; frontal views, x 25.

Figs 9, 10. *Limacina bulimoides* (d'Orbigny, 1836), Recent, Manihiki Plateau Expedition, sample U 336b, co-ordinates 11° 33.3'S 165° 26.7' W, water depth 981-1297 m, RGM 396 012-013; frontal views, x 25.

Fig. 11. *Limacina* sp. 1, sample 1-1, RGM 396 017; frontal view, x 25.

Fig. 12. *Limacina inflata* (d'Orbigny, 1836), sample 1-1; RGM 396 015; apical view and oblique frontal view to show rostrum; x 25.

Fig. 13. *Limacina* ? sp. 2, sample 1-1; RGM 396 018; apical view and left lateral view, x 25.

Figs 14, 15. *Bowdenatheca jamaicensis* Collins, 1934, sample 1-1; RGM 396 020-021; 14 - dorsal view, right lateral view and transverse sections at aperture and apical part, and ventral view, respectively; 15 - ventral view, right lateral view and transverse section at aperture and dorsal view, x 6.

Figs 16, 17. *Clio* aff. *braidensis* (Bellardi, 1873), sample 1-1, RGM 396 029-030, 16: x 6; 17: x 12.

Fig. 18. *Clio cuspidata* (Bosc), Atlantic Ocean, E of mid-Atlantic ridge, 45° 21.3'N 27° 9.1'W, boxcore T90-10B, JGOFS Leg-IV expedition, 16th June 1990, sea depth 2,162 m; Holocene, from upper 43 cm of bottom sediment, with pteropod-rich layers throughout; RGM 396 034, dorsal, right lateral, ventral views and transverse section at aperture, x 6.

PLATE 1

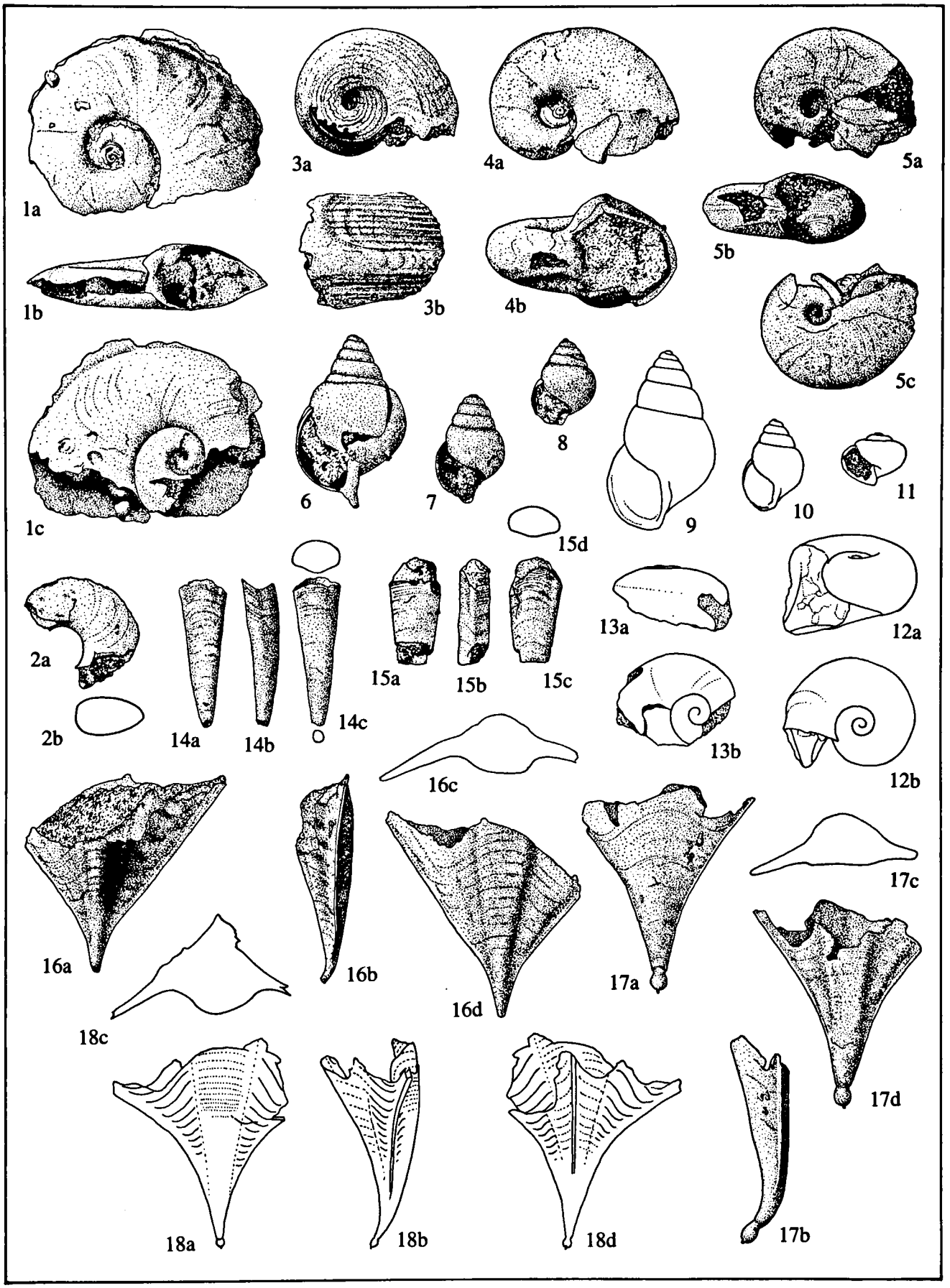
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PLATE 2

Fig. 1. *Cavolinia tridentata* (Niebuhr, 1775), sample 1-2; NMB H 17792; fragment showing dorsal shell part preserving weak transverse ornament in apical part, x 3.

Fig. 2. *Cavolinia vendryesiana* (Guppy, 1873), sample 1-1, RGM 396 038; ventral, left lateral and dorsal view, x 6.

Fig. 3. *Cavolinia inflexa* (Lesueur, 1813), Atlantic Ocean, off Morocco coast, 34° 54.5'N 7° 34.6'W, Meteor M53, sample 170 (box core), sea depth 1,478 m, 22nd March 1988; Holocene; RGM 396 430; dorsal view, x 6.

Fig. 4. *Cavolinia ventricosa* (Guppy, 1882), paralectotype; USNM 115625; dorsal, left lateral and ventral view, x 6.

Fig. 5. *Cavolinia ventricosa* (Guppy, 1882), specimen illustrated in Woodring (1928), USNM 369313; dorsal, left lateral, ventral and adapical views, x 6.

Fig. 6. *Cavolinia ventricosa* (Guppy, 1882), specimen *ex* Aldrich/Johns Hopkins University Collection, illustrated in Collins (1934), USNM 645204; dorsal, left lateral, ventral and adapical views, x 6.

Fig. 7. *Cavolinia ventricosa* (Guppy, 1882) (**lectotype**), USNM 115625; dorsal, left lateral and adapical views, x 6.

Fig. 8. *Cavolinia ventricosa* (Guppy, 1882), sample 1-6, RGM 394 044; dorsal, left lateral and ventral views, x 6.

Figs 9, 11. *Diacria digitata* (Guppy, 1882), USNM 115623; 9 - **lectotype**, 11 - **paralectotype**; adapical, dorsal, left lateral and ventral views, x 6.

Fig. 10. *Diacria digitata* (Guppy, 1882), specimen illustrated in Collins (1934, pl. 11, figs 4-6), USNM 645203; adapical, dorsal, ventral and left lateral views, x 6.

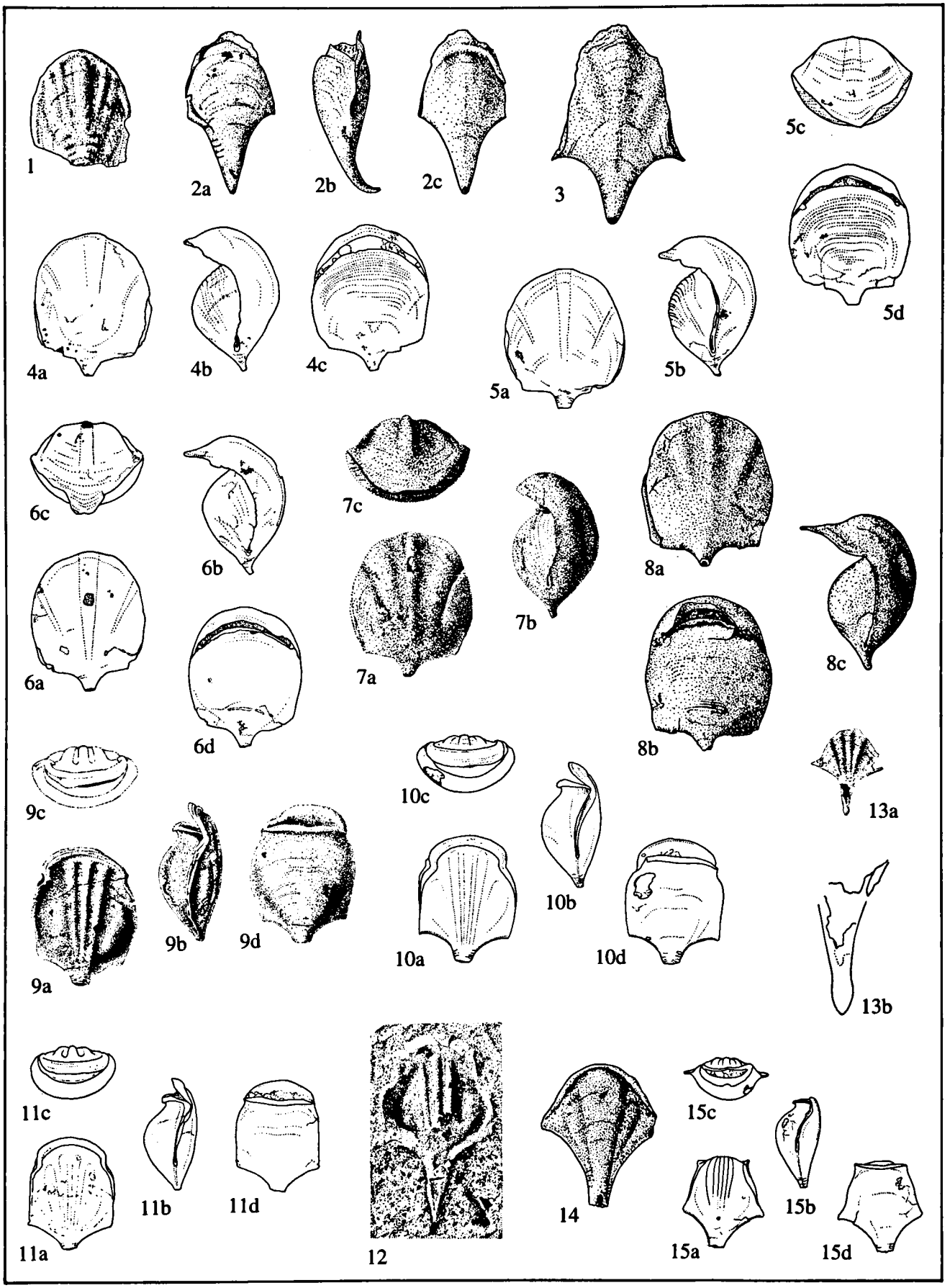
Fig. 12. *Diacria digitata* (Guppy, 1882), Port-au-Prince, near Pétionville, Haiti; illustrated in Collins (1934, pl. 11, fig. 9), USNM 371903, *ex* Woodring & Brown Collection; specimen in sediment slab, showing dorsal side, x 6.

Fig. 13. *Diacria digitata* (Guppy, 1882), juvenile, illustrated in Collins (1934, pl. 11, figs 7, 8), USNM 645207, *ex* Andrews & Lynn Collection; dorsal view (x 6) and protoconch (x 25).

Fig. 14. *Diacria trispinosa* (de Blainville, 1821) f. *bisulcata* Gabb, 1873, sample 1-2; NMB H 17802; dorsal view, x 6.

Fig. 15. *Diacria digitata* (Guppy, 1882), aberrant specimen, illustrated in Collins (1934, pl. 11, figs 1-3), USNM 645202, *ex* Aldrich/Johns Hopkins University Collection; adapical, dorsal, left lateral and ventral views, x 6.

PLATE 2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