1 **Late Pleistocene pteropods, heteropods and planktonic foraminifera from the**
2 **Caribbean Sea, Mediterranean Sea and Indian Ocean.**

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18

19 **Abstract**

20

21 Pteropods and heteropods (holoplanktonic gastropods) are an important component
22 of the modern oceans; however, detailed information on their distribution in the fossil
23 record is often based on poorly preserved specimens. This study presents the
24 micropaleontological analysis of three exceptionally well-preserved Late Pleistocene
25 marine sediment cores from the eastern Caribbean Sea, western Mediterranean Sea
26 and the Indian Ocean. This study presents the first stratigraphical record of
27 heteropods in the Caribbean Sea and extends the known zonation of pteropods in
28 the Mediterranean Sea. Distributions of pteropods, heteropods and planktonic
29 foraminifera are presented with abundance and species richness data, as well as
30 stratigraphical dates inferred from the oxygen isotope stratigraphy, argon-argon
31 dating and biostratigraphy. The findings of this study greatly improve our
32 understanding of holoplanktonic gastropod stratigraphy and ecology. Results reveal
33 that the geographical range of heteropods, thought to be restricted to sub-tropical
34 warm waters, may be much greater, including waters of sub-polar temperature.
35 Heteropods were also found to be surprisingly abundant, potentially representing a
36 more important part of the ocean food web than previously thought. Analysis
37 revealed two species of holoplanktonic gastropod that are previously undescribed
38 and indicate that the pteropod *Heliconoides mermuysi* (Cahuzac and Janssen,
39 2010), known exclusively from the Moulin de Cabanes (Miocene), may have lived in

the Caribbean Sea and Indian Ocean as recently as 4 kyr ago. These findings highlight the urgent need for increased research on holoplanktonic gastropods. The threat that current climate change and ocean acidification poses, particularly to the delicately shelled forms, means that some species may become extinct before they have even been fully 'discovered'.

INTRODUCTION

Pteropods and heteropods are planktonic gastropods, which have evolved wings from the foot structure that characterises animals in the class Gastropoda. These wings are uniquely adapted to enable the animals to live their entire lives as a planktonic form (Bé and Gilmer, 1977) and they are, therefore, termed holoplanktonic. Pteropods are a common component of the water column throughout the world's oceans (Bé and Gilmer, 1977) and consist of two orders; the shell-less gymnosomes and the shell-bearing thecosomes. These two orders are now considered to be less closely related than originally thought (Lalli and Gilmer, 1989) despite superficial similarities, although, the term pteropod is still widely used. This study focuses on the order Thecosomata, which is made up of shelled species in the suborders Euthecosomata and Pseudothecosomata. The Heteropoda, more recently known as the superfamily Pterotracheoidea, are less well-known. They consist of three families: one shelled, the Atlantidae, one with reduced shells, the Carinariidae, and one shell-less, the Pterotracheidae. Representatives of all three families, including larval shells of the Pterotracheidae, were found during this study. At present, the distribution and abundances of heteropods are not known in detail. Available information suggests that they are found in moderate to low abundances primarily in tropical and sub-tropical warm water regions (Thiriot-Quiévreux, 1973; Lalli and Gilmer, 1989; Seapy, 2011). However, the results of this study indicate that heteropods can also reside in sub-polar waters, since they were found to be abundant in sediments from glacial periods in the geological past.

Shells produced by pteropods and heteropods are formed of aragonite, a polymorph of calcium carbonate, which is particularly susceptible to dissolution (50% more susceptible than calcite). Consequently, in over 98% of the oceans, all of the aragonite shells produced are dissolved while sinking through the water column or during early sedimentation (Byrne *et al.,* 1984; Fabry, 1990). The fossil record of pteropod and heteropod shells is, therefore, restricted to sediments in shallow water that is supersaturated with respect to aragonite. The known stratigraphical range of

pteropod shells extends from the Recent to the Paleogene (Lokho and Kumar, 2008; Janssen and Peijnenburg, 2013), with the first known occurrence in the latest Paleocene of Europe (Janssen and King, 1988) and North America (Janssen *et al.,* 2007). The fossil record of heteropods is less well-known, however, the stratigraphical range is known to extend from the Recent to the Jurassic (Janssen and Peijnenburg, 2013).

Holoplanktonic gastropod shells are rarely used in biostratigraphy because of their susceptibility to dissolution. However, the sensitivity of living holoplanktonic gastropods to changes in environmental conditions makes them extremely valuable both for stratigraphical correlation and paleoenvironmental reconstructions. This study aims to improve the use of holoplanktonic gastropods in biostratigraphy by documenting their stratigraphical distributions throughout three Late Pleistocene sediment cores from the Caribbean Sea, the Mediterranean Sea and the Indian Ocean. In particular, the results of this study extend the known zonation of pteropods in the Mediterranean Sea, both spatially and stratigraphically, allowing a detailed paleoenvironmental reconstruction. Results also contribute to a greater understanding of holoplanktonic gastropod ecology and taxonomy.

METHODOLOGY

Sampling sites

For this study, three core sites situated well above the Aragonite Lysocline (ALy) were chosen to reduce the effects of post-depositional dissolution (Gerhardt and Henrich, 2001; Sabine *et al.,* 2002; Schneider *et al.,* 2007). All three cores show exceptional preservation, indicated by surface sediment assemblages of planktonic foraminifera and holoplanktonic gastropods, which are comparable to those in the overlying waters. This implies that specimens have not been affected by dissolution or transportation, retaining an accurate representation of the abundance and species richness of the overlying waters. Low fragmentation of planktonic foraminifera tests and extremely well preserved pteropod shells also indicate little to no post-depositional dissolution.

Core CAR-MON 2 was collected to the south-west of Montserrat (16°27.699'N, 62°38.077'W, water depth 1102 m) in the Lesser Antilles volcanic arc (Fig. 1) and was sampled at 5 cm (~2.2 kyr) intervals. Oxygen isotope stratigraphy (Fig. 2) and

114   additional data for CAR-MON 2 has previously been published by Le Friant *et al.*
115   (2008), Messenger *et al.* (2010) and Wall-Palmer *et al.* (2012, 2013). Core B5-1 was
116   collected to the south-east of the Balearic island of Mallorca (39°14.942'N,
117   03°25.052'E, water depth 1519 m) in the western Mediterranean Sea (Fig. 1). B5-1
118   was sampled for microfossil analysis at 10 cm (~2.7 kyr) intervals and oxygen
119   isotope stratigraphy at 5 cm intervals (Fig. 3). The stratigraphy of B5-1, based on
120   oxygen isotope stratigraphy and biozonation of planktonic foraminifera (Fig. 4), is
121   reported in this study. Indian Ocean Hole 716B was collected by the Ocean Drilling
122   Program, from a shallow site (Site 716, 04°56.0'N, 73°17.0'E, water depth 533 m) on
123   the Chagos-Laccadive Ridge within the Maldives Islands (Fig. 1). Of the cores
124   collected at Site 716, this study is based on the upper 13 m of Hole B, which was
125   recognised by Droxler *et al.* (1990) to contain abundant holoplanktonic gastropods.
126   Oxygen isotope stratigraphy (Fig. 5) for Hole 716B has been previously published by
127   Backman *et al.* (1988) and Droxler *et al.* (1990). Hole 716B was sampled at a low
128   resolution at points corresponding to major changes in climate, which were identified
129   with the use of oxygen isotope stratigraphy (Backman *et al.,* 1988).
130
131   **Microfossil analysis**
132
133   No chemicals were used during sample processing. Dried samples were gently
134   disaggregated, weighed and re-hydrated using deionised water (pH 7.89). Each
135   sample was then washed over a 63 µm sieve, filtered and air dried. Dried samples
136   were then weighed to calculate the amount of <63 µm sediment that had been
137   removed during washing. Counts of planktonic foraminifera and holoplanktonic
138   gastropods were made from two size fractions, 150–500 µm and >500 µm, in order
139   to provide representatives of both small and large species. Results from the two
140   fractions have been combined for all subsequent data analysis. For each sample,
141   just over 300 (or until the sample was exhausted) planktonic foraminifera and just
142   over 300 (or until the sample was exhausted) holoplanktonic gastropod specimens
143   were counted and identified from both size fractions. Only whole specimens and
144   fragments retaining the proloculus or protoconch were counted to avoid the distortion
145   produced by several fragments of the same specimen. Samples were weighed
146   before and after analysis to calculate the overall abundance of microfossils
147   (specimens per gram of sediment).
148
149   The identification of planktonic foraminifera was made using the taxonomic reviews
150   by Bé (1977), Saito *et al.* (1981) and Kennett and Srinivasan (1983). The

151 identification of pteropod species was made using the keys published by Bé and
152 Gilmer (1977), Van der Spoel (1976) and Janssen (2012), with additional information
153 from Tesch (1946, 1949). Identification of heteropods was made using Tesch (1949),
154 Thiriot-Quiévreux (1973), Seapy (1990)Janssen (2012) and the online guide
155 compiled by Seapy (2011). Counts of microfossils are expressed as a percentage
156 (relative abundance) of the total number of specimens, separately for planktonic
157 foraminifera and holoplanktonic gastropods.

158

159 **Stable isotope analysis and stratigraphical framework for B5-1**

160

161 Stable isotope analysis of core B5-1 were carried out at the Natural Environment
162 Research Council (NERC) Isotope Geosciences Laboratory, British Geological
163 Survey, Keyworth. Ten specimens of *Globigerinoides ruber* (d'Orbigny, 1839) of size
164 250 µm to 355 µm were analysed from each sample at 5 cm intervals, using a GV
165 IsoPrime mass spectrometer plus Multiprep device. Isotope values ($\delta^{18}O$) are
166 reported as per mille (‰) deviations of the isotopic ratios ($^{18}O/^{16}O$) calculated to the
167 VPDB scale using a within-run laboratory standard calibrated against NBS standards
168 ($\delta^{13}C$ were analysed but are not reported here). Analytical reproducibility of the
169 standard calcite (KCM) is <0.1‰ for $\delta^{18}O$. The isotope profile produced is
170 comparable to published data for sediments in the area (Weldeab *et al.,* 2003).
171 Marine $\delta^{18}O$ data are used as a proxy for global ice volume and data can, therefore,
172 be compared globally. By comparing the $\delta^{18}O$ record within core B5-1 to a globally
173 standardised record, such as the LR04 stack (Lisiecki and Raymo, 2005), glacial and
174 interglacial periods, termed Marine Isotope Stages (MIS), can be identified, dating
175 certain parts of the core. The $\delta^{18}O$ data show that B5-1 contains a marine isotope
176 record extending back to MIS 6. Alignment of the MIS (Fig. 4) was achieved by
177 comparison to the $\delta^{18}O$ record published by Weldeab *et al.* (2003) for site SL87 (Fig.
178 4), approximately 60 km south east of B5-1 and the LR04 stack (Lisiecki and Raymo,
179 2005).

180

181 Planktonic foraminifera distributions within B5-1 were also used to date parts of the
182 core and refine the position of MIS boundaries. The down-core distributions of
183 several key species reflect the bio-events identified by Pujol and Vergnaud-Grazzini
184 (1989) and Pérez-Folgado *et al.* (2003) in the Mediterranean Sea (Fig. 4). These
185 events indicate several minor climatic episodes, providing additional dating points
186 throughout the upper 190 cm of the core.

Statistical analysis

Cluster analysis was carried out for Mediterranean Sea core B5-1, where changes in species composition appear to be strongly influenced by changes in climate. Cluster analysis has been used in this study to identify whether apparent warm and cold water assemblages are significantly different from one another. Cluster analysis was carried out using the Paleontological Statistics package (PAST). The Paired-Group algorithm and Euclidian similarity measure were used.

RESULTS

The Caribbean Sea

The assemblage of planktonic foraminifera and holoplanktonic gastropods in the surface sediments of CAR-MON 2 is comparable to that of the overlying waters and this sedimentary record is, therefore, useful in reconstructing the paleoenvironmental conditions at this site. The similarity between surface sediment microfossil content and living assemblages in the Caribbean Sea has previously been demonstrated by Wells (1975), who found that euthecosome pteropods deposited in the surface sediments close to Barbados accurately reflect the species composition and relative abundances of the overlying waters. All species of pteropod found in the surface waters of the Western Caribbean Sea (Wells, 1975, 1976; Parra-Flores, 2009) are present in CAR-MON 2 sediments. The majority are represented within the surface 1 cm of sediment. The distribution of living shelled heteropods is not well documented and no published data from the Caribbean Sea were found. It is assumed that, like the shelled pteropods, the living assemblage of heteropods is well represented within the surface sediments of CAR-MON 2. No extensive studies have been made of the modern living planktonic foraminifera assemblage of the Caribbean Sea. More generally, Bé and Tolderlund (1971) described the distribution of living planktonic foraminifera in the surface waters of the Atlantic. This study includes species distribution maps, which allow the living planktonic foraminifera assemblage of the Lesser Antilles to be inferred. All species included in the maps of Bé and Tolderlund (1971) for the Lesser Antilles are present within the surface sediments of CAR-MON 2 with one exception, *Hastigerina pelagica* (d'Orbigny, 1839)*,* which is absent from the entire core. However, Bé and Tolderlund (1971) only found *H. pelagica* to be present within the surface waters in low numbers (0.1–4.9 %) and it may, therefore

224 not have been present in the waters overlying this site. Although there appear to be
225 several species present within the surface sediments of CAR-MON 2 that were not
226 found by Bé and Tolderlund (1971), these are mainly recently described species. For
227 example, *Globigerinoides trilobus* (Reuss, 1850) would have been included within the
228 counts of *Globigerinoides sacculifer* (Brady, 1877) by Bé and Tolderlund (1971), but
229 has now been identified as a separate species.

230

231 Due to the low latitude location of the Caribbean Sea, and the consequent low
232 variation in surface water temperature across glacial and interglacial periods, CAR-
233 MON 2 shows that very little change in species composition and species richness
234 (28–47 species) occurred over the last 250 kyr (Fig. 2). The lack of significant
235 synchronous changes between oxygen isotope data and the relative abundances of
236 temperature sensitive species (Fig. 2) supports this observation. The overall
237 abundance (specimens per gram of sediment) of holoplanktonic gastropods and
238 planktonic foraminifera shows greater variation, but does not change synchronously
239 with oxygen isotope data, suggesting that factors such as nutrient availability have
240 produced the fluctuations in overall abundance. Foster (2008) reconstructs the range
241 in temperature from the last glacial maximum at MIS 2.2 to the last interglacial
242 maximum at MIS 5.5 as being between 25.7 and 29.1°C. Schmidt *et al.* (2006) show
243 a comparable reconstruction for Caribbean surface water, finding temperatures
244 between 2.1–2.7°C colder than the present during the last three glacial maxima. The
245 species assemblage throughout CAR-MON 2 is composed of warm water sub-
246 tropical species of planktonic foraminifera and holoplanktonic gastropods. Dominant
247 planktonic foraminifera species include *G. ruber, G. sacculifer* (including *G. trilobus*)
248 and *Neogloboquadrina dutertrei* (d'Orbigny, 1839)*. Other common species include
249 *Globigerinella siphonifera* (d'Orbigny, 1839), *Globigerinoides conglobatus* (Brady,
250 1879)*, Globigerinita glutinata* (Egger, 1893) and *Globorotalia truncatulinoides*
251 (d'Orbigny, 1839)*. The pteropod genera *Heliconoides* and *Limacina* dominate the
252 assemblage of holoplanktonic gastropods. The most abundant species is
253 *Heliconoides inflatus* (d'Orbigny, 1834), which comprises up to 68% of the
254 holoplanktonic gastropod population. Other common and often abundant species of
255 pteropod include *Creseis clava* (Rang, 1828)*, Creseis virgula* (Rang, 1828)*, Limacina
256 *bulimoides* (d'Orbigny, 1834)*, Limacina trochiformis* (d'Orbigny, 1834) and *Styliola
257 subula* (Quoy and Gaimard, 1827)*. The dominant heteropod genus is *Atlanta,* with
258 the most abundant species being *Atlanta peronii* Lesueur, 1817 and *Atlanta
259 selvagensis* de Vera and Seapy, 2006. Other common and often abundant heteropod

species include *Firoloida desmarestia* Lesueur, 1817 and *Carinaria lamarckii* Blainville, 1817.

The Mediterranean Sea

The surface sediments of B5-1 contain a comparable assemblage of planktonic foraminifera and holoplanktonic gastropods to that of the overlying waters. In agreement with the distribution of living pteropods in the western Mediterranean Sea (Bé and Gilmer, 1977), the surface sediments of B5-1 contain a single extremely abundant pteropod species (*H. inflatus*), with many more present in low numbers. Limited data on modern Mediterranean heteropod species (Richter, 1968; Thiriot-Quiévreux, 1973) indicate that the surface sediments of B5-1 contain six out of the seven species which live in the overlying waters. There are also some species that were found within the surface sediments of B5-1 that are not recognised from the Mediterranean Sea. These include *Atlanta rosea* Gray, 1850 and *A. selvagensis*, which are found in tropical and sub-tropical waters of the Atlantic and Indian oceans. This is partly due to the improved recognition of species, since *A. selvagensis* was not described until 2006 (de Vera and Seapy, 2006) and specimens previously identified as *Atlanta inflata* Gray, 1850 are now thought to belong to the species *A. selvagensis* in the Atlantic Ocean. Planktonic foraminifera within the surface sediments of B5-1 are also representative of the assemblages found in overlying waters (Bé, 1977; Pujol and Verhaud-Grazzini, 1995; Parker, 2002). However, several of the species (including *Globorotalia hirsuta* (d'Orbigny, 1839)*, Globigerina falconensis* Blow, 1959*, H. pelagica* and *G. glutinata*) which Bé (1977) described as being dominant, are not found in the surface sediments of B5-1. All but one species of planktonic foraminifera, *G. siphonifera*, found within the surface sediments of B5-1 are recorded from the Mediterranean Sea. This suggests that the sediments at this site have not been affected by post-depositional dissolution, allowing the microfossil assemblage to be used in reconstructing paleoenvironmental conditions.

Climatic events within the Mediterranean Sea tend to be amplified due to the semi-enclosed nature of the basin (Pérez-Folgado *et al.,* 2003). Considerable variations in species composition therefore occur across glacial and interglacial periods. These variations have been used by several authors to reconstruct the past climate of the central and eastern Mediterranean Sea (Chen, 1968; Herman, 1971; Jorissen *et al.,* 1993; Capotondi *et al.,* 1999; Sbaffi *et al*., 2001; Janssen, 2012), the Tyrrhenian Sea (Carboni and Esu, 1987; Biekart, 1989; Asioli *et al.,* 1999; Buccheri *et al.,* 2002), the

297 Adriatic Sea (Jorissen *et al.,* 1993; Asioli *et al.,* 1999) and more generally the entire
298 Mediterranean Sea (Hayes *et al.,* 2005).

299

300 Throughout B5-1, species richness changes synchronously with the oxygen isotope
301 data (Fig. 3), suggesting a strong link to water temperature. Core B5-1 contains two
302 distinct planktonic assemblages, which divide the core into four major zones (Zone C
303 is further subdivided into five sub-zones), two of which (Zones B and A) have been
304 previously recognised (Herman, 1971; Carboni and Esu, 1987; Jorissen *et al.,* 1993;
305 Capotondi *et al.,* 1999; Sbaffi *et al.,* 2001; Buccheri *et al.,* 2002). These zones
306 coincide with the MIS and are characterised by a homogenous set of species
307 preferring either sub-polar cold water or sub-tropical warm water (Fig. 3). The distinct
308 assemblages can be identified using cluster analysis (Fig. 6) which shows that the
309 holoplanktonic gastropod and planktonic foraminifera assemblage of samples
310 present within cold water Zones D, C(iv), C(ii) and B is approximately 97% different
311 to the assemblage of samples within warm water Zones C(v), C(iii), C(i) and A. There
312 are four samples, 50, 240, 270 and 490 cm, which appear to be present in the
313 incorrect cluster. However, these samples all contain a slightly different assemblage
314 from other samples within their zone. For example, samples 50 and 490 show a
315 sudden reduction in cold water species and an increase in warm water species,
316 representing a very short warm fluctuation in the otherwise cold Zone B. Therefore,
317 instead of occurring in the cold water cluster, they are placed in the warm water
318 cluster.

319

320 ***Zone D (490–476 cm) ~133–130 ka***
321 Zone D occurs within MIS 6 and is a known cool period, with a high global ice
322 volume. The species present during this period are representative of a sub-polar
323 assemblage similar to that of the modern North Atlantic (Bé and Gilmer, 1977; Bé,
324 1977). It is very similar in composition to Zone B (Fig. 3), with high numbers (25–73%
325 of holoplanktonic gastropods) of the sub-polar pteropod species *Limacina retroversa*
326 (Fleming, 1823) and low numbers of *H. inflatus* (18–38%). Cluster analysis shows
327 that, at 490 cm, there is a fluctuation in the dominant species of pteropod (Figs 4 and
328 5), indicating a comparable composition to warmer zones. The presence of some
329 warm water transitional species also suggests that this is the late transition from a
330 colder period, which was not recovered in the core. The dominant species of
331 planktonic foraminifera and pteropods during this period suggest an annual sea
332 surface temperature range of 12–16°C (Bé and Tolderlund, 1971; Bé and Gilmer,
333 1977).

Zone C (475–226 cm) 130–71 ka

This is a zone mainly composed of warm sub-tropical to tropical planktonic species. It spans the whole of MIS 5 and contains alternating warm periods with short term cooler periods. It signifies a gradual warming from the boundary of MIS 6 throughout MIS 5. The overall species composition of Zone C is similar to that of the modern western Mediterranean Sea (Fig. 3).

Sub-Zone C (v) (475–446 cm)

This is a short warm period, occurring during MIS 5.5, characterised by an increase in the abundance of *H. inflatus* (77–94%) and a coinciding decrease in the abundance of *L. retroversa* (1–8%). It is similar in species composition to Zone C(i) and C(iii). Cold water species do not disappear, but remain in lower numbers. Dominant planktonic foraminifera and pteropod species during this period suggest an annual sea surface temperature range of 16–19°C (Bé and Tolderlund, 1971; Bé and Gilmer, 1977). However, since MIS 5.5 was the last interglacial maximum and shows the greatest oxygen isotope excursion, dominant fauna should indicate the highest temperature within the core. Bardaji *et al.* (2009) estimate mean annual sea surface temperature at MIS 5.5 to be 23–24°C and never below 19–21°C during the winter.

Sub-zone C (iv) (445–416 cm)

This is a short cooler period, occurring during MIS 5.4 and is characterised by a sharp peak in *L. retroversa* (from 8% at 450 cm to 85% at 420 cm) and a coinciding reduction in the abundance of *H. inflatus* (from 77% at 450 cm to 12% at 420 cm). The warm water species, such as *L. bulimoides* and *A. selvagensis,* do not disappear, but remain at a lower abundance, suggesting that this period is cooler but not sub-polar. *Globigerina bulloides* d'Orbigny, 1826, a dominant species of planktonic foraminifera in sub-polar provinces (Bé, 1977), is also present, but in low numbers. Dominant planktonic foraminifera and pteropod species during this period suggest an annual sea surface temperature range of 12–16°C (Bé and Tolderlund, 1971; Bé and Gilmer, 1977).

Sub-zones C (iii) 415–366 cm; ii) 365–356 cm; i) 355–226 cm

This section is characterised by a relatively high abundance (up to 44% of planktonic foraminifera) of the sub-tropical planktonic foraminifera *Orbulina universa* d'Orbigny, 1839. In common with Zone A, it contains a higher abundance of the pteropod *H. inflatus* (average 24%), the heteropod *A. selvagensis* (average 24%) and the

planktonic foraminifera *Globorotalia inflata* (d'Orbigny, 1839, 8–28%) and a generally low abundance of the sub-polar pteropod *L. retroversa* (variable between 2–72%). During Sub-Zone C(iii), dominant planktonic foraminifera and pteropod species suggest an annual sea surface temperature range of 19–21°C (Bé and Tolderlund, 1971; Bé and Gilmer, 1977). With exception to this, there is a very short cooler period between 365 and 356 cm (Sub-Zone C(ii)) with a higher abundance of *L. retroversa*. During Sub-Zone C (ii) the temperature decreased to between 12–16°C. The surface water then warmed again during Sub-Zone C(i) to between 17–19°C (Bé and Tolderlund, 1971; Bé and Gilmer, 1977). Cluster analysis shows that there is also some temperature fluctuation during Zone C(i), indicating that samples 240 and 270 cm reflect a cold water assemblage (Fig. 6). In both samples, this is due to increased numbers of *L. retroversa* coinciding with decreased numbers of *H. inflatus* (Fig. 3). Pteropod species *L. bulimoides* and *C. virgula* return to Zone C with an increase in the abundance of *Diacria trispinosa* (Blainville, 1821), a warm water cosmopolitan species of pteropod. The climate switched to reflect a sub-polar assemblage (Zone B) at the MIS 5/4 boundary (71 kyr, 230 cm).

Zone B (225–36 cm) 71 –14 ka

This cool period indicates a major turning point in the climate, with steady cooling throughout MIS 4, 3 and 2, towards the Last Glacial Maximum (MIS 2.2). This is a zone of sub-polar species similar to that of the modern North Atlantic (Bé and Gilmer, 1977; Bé, 1977). It is characterised by a very high abundance of the sub-polar pteropod *L. retroversa* (up to 100%, with an average of 79% of holoplanktonic gastropods) and the sub-polar planktonic foraminifera *G. bulloides* (average 48% of planktonic foraminifera). There are also higher abundances of the planktonic foraminifera *Globorotalia scitula* (Brady, 1882, 10%) and *G. glutinata* (9%), which occupy a range of habitats from sub-polar to equatorial (Fig. 3). The abundance of the heteropod *A. rosea,* which is only known from warm waters, fluctuates throughout this zone. It is interesting to note that peaks in the occurrence of *A. rosea* occur when the abundance of *L. retroversa* reduces and may therefore signify temperature fluctuations in this sub-polar zone. However, cluster analysis only indicates that one sample (50 cm) contains an assemblage comparable to the warm water zones (Fig. 6). Dominant planktonic foraminifera and pteropod species during this period suggest an annual sea surface temperature range of 7–10°C (Bé and Tolderlund, 1971; Bé and Gilmer, 1977). This is in agreement with temperature reconstruction data published by Sbaffi *et al.* (2001) and Hayes *et al.* (2005).

408   Zone B is comparable to Zone 3 described by Biekart (1989) in a deep sea core from
409   the Tyrrhenian Sea. Biekart (1989) found similar abundances of *L. retroversa*, but
410   much higher abundances of *D. trispinosa*, which are only present in this section of
411   B5-1 in low numbers (maximum 13%). Chen (1968) also recorded this period of
412   abundant *L. retroversa* in a core collected south of the island of Crete. This zone has
413   also been detected in cores throughout the eastern Mediterranean Sea and in the
414   Balearic Sea (Herman, 1971), in the Tyrrhenian Sea (Carboni and Esu, 1987;
415   Jorissen *et al.,* 1993; Buccheri *et al.,* 2002) and the Adriatic Sea (Jorissen *et al.,*
416   1993). Capotondi *et al.* (1999) and Sbaffi *et al.* (2001) have expanded on the work of
417   Jorissen *et al.* (1993), splitting the previous 'Zone 3' into more detailed zones. At the
418   top and bottom of Zone B (225 cm to 140 cm and 50 cm to 36 cm) an increased
419   abundance of the transitional species *Clio pyramidata* Linnaeus, 1767 and *G. inflata*
420   signifies the transition between warm and cold periods. Many authors consider the
421   upper transitional period (50 cm to 36 cm) as a distinct zone (Carboni and Esu, 1989;
422   Jorissen *et al.,* 1993; Buccheri *et al.,* 2002), characterised by an increase in
423   transitional and warmer water species. Capotondi *et al.* (1999) and Sbaffi *et al.*
424   (2001) also subdivide this period into smaller bio-zones.
425

426   ***Zone A (35–0 cm depth) 14–0 ka***
427   This is a zone of sub-tropical species, which spans MIS 1 (Fig. 3) and is
428   characterised by a high abundance of the tropical pteropod *H. inflatus* (average 43%
429   of holoplanktonic gastropods) and a very low abundance of the sub-polar pteropod *L.*
430   *retroversa* (average 1%). The transitional planktonic foraminifera *G. inflata* (13–31%
431   of planktonic foraminifera) and the sub-tropical heteropod *A. selvagensis* (16–21%)
432   also increase in abundance. Zone A contains the warm water pteropods *L.*
433   *bulimoides* and *C. virgula* and the tropical planktonic foraminifera *G. siphonifera* and
434   *G. sacculifer* which are not found in Zone B. This assemblage is similar to that found
435   in Holocene sediments described from the Tyrrhenian Sea (Carboni and Esu, 1987;
436   Jorissen *et al.,* 1993; Capotondi *et al.,* 1999; Sbaffi *et al.,* 2001; Buccheri *et al.,*
437   2002), the Adriatic Sea (Jorissen *et al.,* 1993; Capotondi *et al.,* 1999), south of Sicily
438   (Capotondi *et al.,* 1999), in the western Mediterranean Sea (Pérez-Folgado *et al.,*
439   2003) and south of the island of Crete (Chen, 1968). Species present within Zone A
440   indicate a sub-tropical climate similar to that of the modern day western
441   Mediterranean Sea (Bé and Gilmer, 1977; Bé, 1977). The sea surface temperature at
442   this time, averaged over the entire Mediterranean Sea, ranged from 14–25 °C (Sbaffi
443   *et al.,* 2001). At the site of B5-1, dominant planktonic foraminifera and pteropod

444 species suggest an annual sea surface temperature range of 19–21°C (Bé and
445 Tolderlund, 1971; Bé and Gilmer, 1977).

446

447 **The Indian Ocean**

448

449 Due to drilling disturbance at the top of ODP Hole 716B, the uppermost sample at
450 this site was collected at 15–16 cm in the core. Assuming the average sedimentation
451 rate of 3.8 cmkyr^{-1} (Backman *et al.,* 1988), this sample likely represents around 4 kyr
452 before the present day. Planktonic species present in the modern overlying waters at
453 ODP Site 716 will, therefore, not be accurately represented within this sample.
454 However, many of the species of holoplanktonic gastropod found within the overlying
455 waters (Tesch, 1949; Thiriot-Quiévreux, 1973; Bé and Gilmer, 1977; Aravindakshan,
456 1977) are also found within the 15–16 cm sample. Species missing from the
457 sediments primarily appear to be the larger *Cavolinia* spp. and *Clio* spp. All pteropod
458 species found within sample 15–16 cm are recorded by Bé and Gilmer (1977) as
459 being present in the overlying waters at ODP Site 716. Fourteen of the twentyone
460 heteropod species recorded as living in the Indian Ocean were found within sample
461 15–16 cm (Tesch, 1910; Taki and Okutani, 1962; Richter, 1974; Aravindakshan,
462 1977; Seapy *et al.,* 2003). The majority of planktonic foraminifera species found in
463 the overlying waters of the Indian Ocean are present within the sample 15–16 cm.
464 Species missing from the sample are uncommon in the overlying waters, found only
465 to be 'present' (<5%) by Bé and Tolderlund (1971) and Cullen and Prell (1984).
466 These include *Candeina nitida* d'Orbigny, 1839 and *H. pelagica,* which are found
467 elsewhere in the core, and *Globigerinoides tenellus* Parker, 1958*,* which was not
468 found in the sediments of ODP Hole 716B. Several species found in the sample 15–
469 16 cm of Hole 716B were not recorded from the overlying water. This is both a factor
470 of the 4 kyr gap and also because some species are more recently described, and
471 not recognised by Bé and Tolderlund (1971) or Cullen and Prell (1984). Species
472 found in the sample 15–16 cm, but not recorded in the overlying waters include *G.*
473 *bulloides, G. trilobus, Globorotalia tumida* (Brady, 1877), *Globorotalia theyeri*
474 Fleisher, 1974 and *Sphaeroidinella dehiscens* (Parker and Jones, 1865)*.*

475

476 Similar to the Caribbean Sea, the low latitude location of ODP Hole 716B created a
477 low temperature variation across glacial and interglacial periods of the Late
478 Pleistocene. Consequently, very little change in species composition, species
479 richness (37–46 species) and overall abundance is observed throughout ODP Hole
480 716B (Fig. 5). This is supported by the lack of significant synchronous changes

481   between oxygen isotope data and the relative abundances of temperature sensitive

482   species (Fig. 5). Barrows and Juggins (2005) reconstruct the sea-surface

483   temperature at ODP Site 716 to range between 25–28°C at the Last Glacial

484   Maximum (18 cm core depth, MIS 2.2). The mean annual sea-surface temperature

485   close to ODP Site 716 at this time was 27°C, just one degree lower than that of today

486   (Barrows and Juggins, 2005). Cullen and Droxler (1990) reconstruct the sea surface

487   temperature at ODP Site 716 to be below 26°C during MIS 6–8 and suggest that any

488   variation in species abundances are more likely to be due to changes in other

489   environmental parameters, such as salinity and nutrient availability. The species

490   assemblage throughout ODP Hole 716B is composed of warm water sub-tropical

491   species of planktonic foraminifera, pteropods and heteropods, with some transitional

492   species. The dominant planktonic foraminifera species is *Globorotalia menardii*

493   (d'Orbigny, 1826)*,* making up to 39% of planktonic foraminifera. Other abundant

494   species include *G. sacculifer* (including *G. trilobus*), *N. dutertrei* and *Globoquadrina*

495   *conglomerata* (Schwager, 1866)*. G. siphonifera* and *O. universa* are also common

496   throughout the core*.* The pteropod genera *Heliconoides* and *Limacina* dominate the

497   assemblage of holoplanktonic gastropods, the most abundant species being *H.*

498   *inflatus* (up to 66% of the holoplanktonic gastropod population of Hole 716B). Other

499   common and often abundant species of pteropod include *L. trochiformis* and *Clio*

500   *convexa* (Boas, 1886)*.* The dominant heteropod genus is *Atlanta*, with common and

501   often abundant heteropod species including *A. frontieri* and *C. lamarckii.*

502

503

504   **DISCUSSION**

505

506   **The application of holoplanktonic gastropods in stratigraphy**

507

508   The results of this study demonstrate that the success of using down-core

509   distributions of holoplanktonic gastropods as biostratigraphical markers is variable.

510   Changes in temperature appear to drive changes in the assemblage composition,

511   therefore, identifying MIS boundaries using species assemblages is only possible

512   where water temperature changes considerably through time. This method proved

513   useful in the Mediterranean Sea, where amplification of the climatic changes lead to

514   substantial changes in holoplanktonic gastropod assemblage. However, in low

515   latitude locations, such as the Caribbean Sea and Indian Ocean, where temperature

516   changes are less significant, variations in species composition were not evident and

517   could not be used to identify the positions of MIS. This is, however, also true for the

assemblages of planktonic foraminifera, which are more widely used in biostratigraphy. In this study, no first or last occurrences of species were identified. Further research upon a longer record of holoplanktonic gastropods is necessary to identify these datum species, which would undoubtedly enhance their use in biostratigraphy.

Despite the variable success of using holoplanktonic gastropods for biostratigraphy, this study demonstrates their consistent use as a tool in reconstructing paleoenvironments. In particular, temperature ranges for the Mediterranean Sea were constrained by using the known temperature ranges of pteropod species combined with ranges for planktonic foraminifera. Further research into the environmental requirements of living holoplanktonic gastropods will increase their use in paleoenvironmental interpretations.

Previously undescribed species

Down-core distributions have revealed three species of holoplanktonic gastropod that are potentially previously undescribed, or that were previously assumed to be extinct. A number of specimens of the heteropod '*Atlanta* sp. D' (Plate 3, Figs 3 a–c) were found in Caribbean Sea sediments. This species appears to be previously undescribed and may, therefore, represent a new species. Further to this, pteropod specimens, thought to be *Heliconoides mermuysi,* but potentially larval shells of the benthic gastropod Architectonicidae, were found in sediments from the Caribbean Sea and Indian Ocean. The descriptions of these species can be found below. During microfossil analysis, it was also noticed that some specimens of *H. inflatus* from ODP Hole 716B showed a slightly different morphology from specimens collected in both the Caribbean Sea and the Mediterranean Sea. Although adult forms remain an overall depressed shape, the protoconch and first whorl of Indian Ocean specimens were found to be slightly raised in comparison to specimens from other locations (Fig. 7). Although this is only a slight variation of the morphology, it may indicate a new sub-species of *H. inflatus* and requires further investigation.

Limacina **sp. C [*Heliconoides mermuysi?*]**

Plate 3, Figure 1 a–c.

Diagnosis: A shell similar in size and morphology to *H. inflatus* but with whorls that inflate more gradually. The aperture is circular and the apertural margin ends in a thickened rim. The apex protrudes slightly.

Remarks: The morphology of *Limacina* sp. C is very similar to species belonging to the genus *Heliconoides,* in particular *H. mermuysi* as described by Cahuzac and Janssen (2010) exclusively from Moulin de Cabanes. However, the morphology is also similar to larval shells of the Architectonicidae. The specimens are all in good condition and are unlikely to be the result of sediment reworking. Fifteen specimens were collected in total from the >500 µm fraction throughout CAR-MON 2 and from the >500 µm and 150–500 µm of Hole 716B. The youngest specimen was collected at 10 cm core depth in CAR-MON 2, which is approximately 4 kyr.

Distribution: During this study, *Limacina* sp. C was found in the Caribbean Sea and in the Indian Ocean and showed no temperature preference through the cores.

Atlanta sp. D
Plate 4, Figure 11a–b.

Diagnosis: A relatively large, highly spired, conical shell, with up to four whorls. The whorls are flat-topped at the sutures, giving a step shape in side-on profile. The umbilicus is large and open.

Remarks: This species is similar in form to *Atlanta inclinata* but has flat-topped whorls. Specimens found are assumed to be juvenile forms as no specimens with a large final whorl, typical of the Atlantidae, were found. Thirteen specimens were collected from the 150–500 µm fraction and six from the >500 µm fraction of CAR-MON 2. The most recent specimen was found at 40 cm core depth, which equates to around 17 kyr.

Distribution: *Atlanta* sp. D was only found in the Caribbean Sea during this study. This species appears to have a preference for warm climates, all specimens except three (150–500 µm: 570 and 575 cm; >500 µm: 60 cm) were found during interglacial periods.

Extended geographical range of heteropods

591   Down-core distributions of heteropods suggest that their environmental requirements
592   are much broader than previously thought. All species of heteropods in the modern
593   oceans are assumed to be restricted to sub-tropical warm waters (Thiriot-Quiévreux,
594   1973; Van der Spoel 1976). However, this study shows that, during cold, glacial
595   periods in the Mediterranean Sea, up to 29% of the holoplanktonic gastropod
596   assemblage was made up of heteropods. This indicates that extant species of
597   heteropod are able to live in cold sub-polar water. This finding has implications for
598   future research, particularly regarding ocean acidification in the modern oceans,
599   which is predicted to affect aragonitic shelled gastropods in polar and sub-polar
600   waters as soon as 2016 (Steinacher *et al.*, 2009).

601

602   Results also highlight the importance of heteropods to the ocean food web.
603   Heteropods are not well studied and poor sampling techniques have led to an
604   underestimation of their numbers in our oceans. Heteropods have large eyes and the
605   ability to swim (Lalli and Gilmer, 1989), which allows them to avoid collection in
606   plankton nets (Seapy, 1990). The results of this study show that heteropod shells
607   often make up a large proportion of the holoplanktonic gastropod assemblage of
608   sediments (up to 32% in the Caribbean Sea and Indian Ocean and up to 69% in the
609   Mediterranean Sea), which suggests that they are an important component of the
610   ocean food web.

611

612   **CONCLUSIONS**

613

614   The results of this study provide new information on the distribution, taxonomy and
615   ecology of holoplanktonic gastropods and planktonic foraminifera through the Late
616   Pleistocene. In all cores analysed, comparison of core top sediments to modern-day
617   overlying waters, suggests that microfossils present within the sediments are
618   representative of the species richness and relative abundances of the overlying
619   waters at the time of deposition. These data provide the first information on both
620   fossil and modern heteropods in the Caribbean Sea, as well as providing an
621   extended and enhanced distribution of holoplanktonic gastropods and planktonic
622   foraminifera in the Mediterranean Sea and Indian Ocean. The success of using
623   holoplanktonic gastropods in biostratigraphy was found to be variable and generally
624   only of use in locations that had experienced considerable changes in temperature
625   over time. However, their application to paleoenvironmental reconstructions was
626   found to be consistently valuable, often improving upon the use of planktonic
627   foraminifera to calculate a range of temperature. More research into the first and last

628 occurrences of a long holoplanktonic gastropod record would greatly improve their
629 use in biostratigraphy.

630

631 The revelation that heteropods have a wider geographical range and make up a
632 larger proportion of the ocean food web, as well as the discovery of potential new
633 species and a pteropod species only recognised from the Miocene, highlights the
634 surprisingly poor understanding that we still have of holoplanktonic gastropod
635 ecology and taxonomy. Much further research is required in this field and would be
636 timely, since the threat from climate change and ocean acidification in the modern
637 oceans, means that some species may become extinct before they have even been
638 fully 'discovered'.

639

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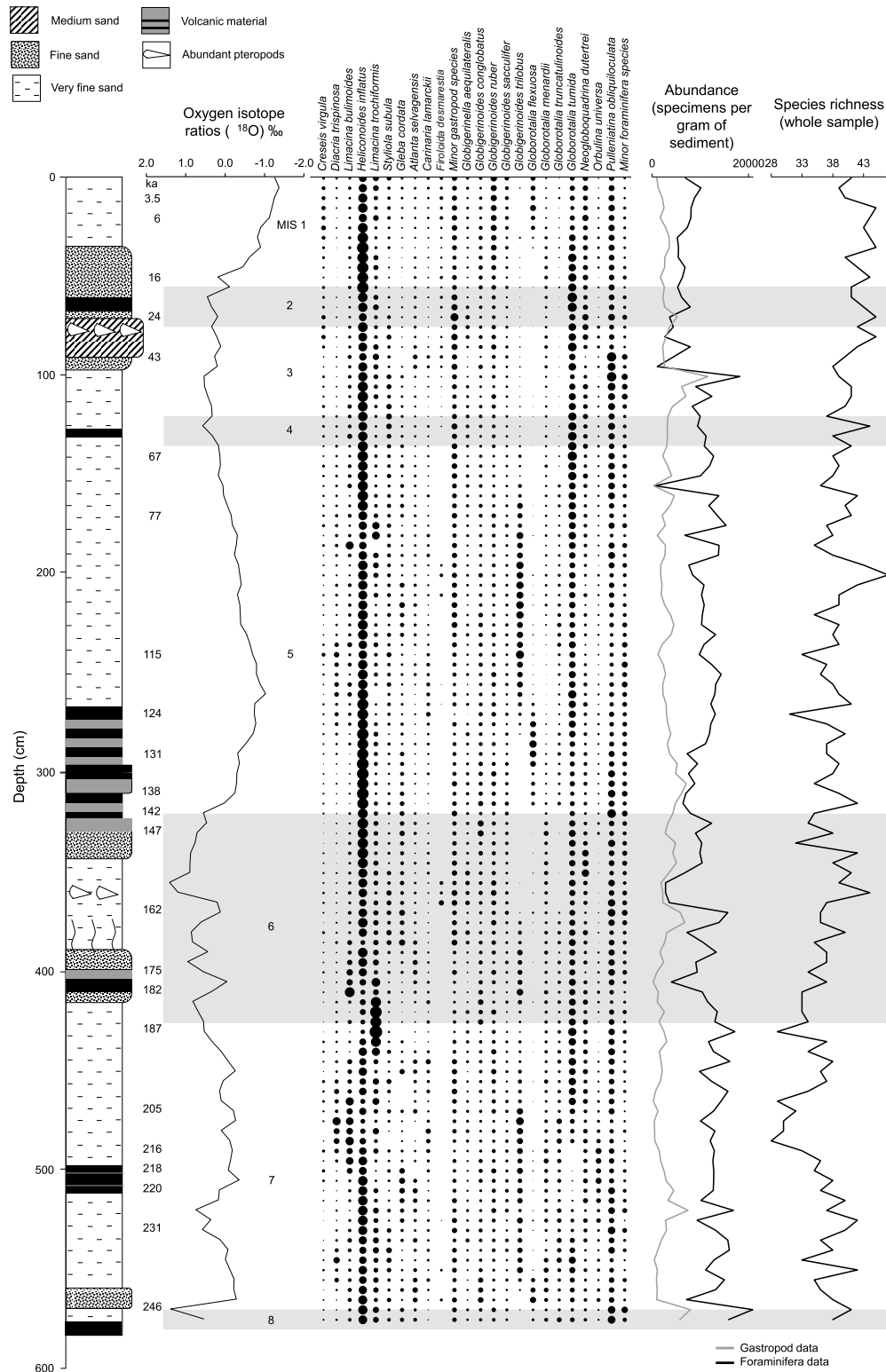
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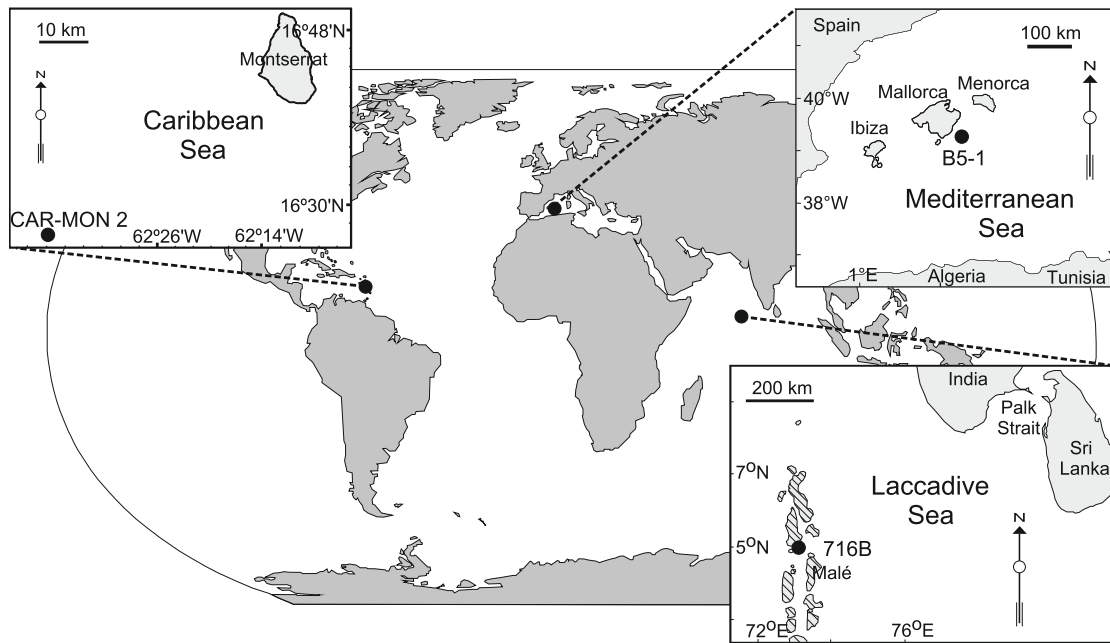
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920   Figure 1. Location of core sites: CAR-MON 2 south-west of Montserrat in the Lesser

921   Antilles island arc, eastern Caribbean Sea; B5-1 south-east of Mallorca in the

922   western Mediterranean Sea; ODP Site 716, Hole B on the Chagos-Laccadive Ridge,

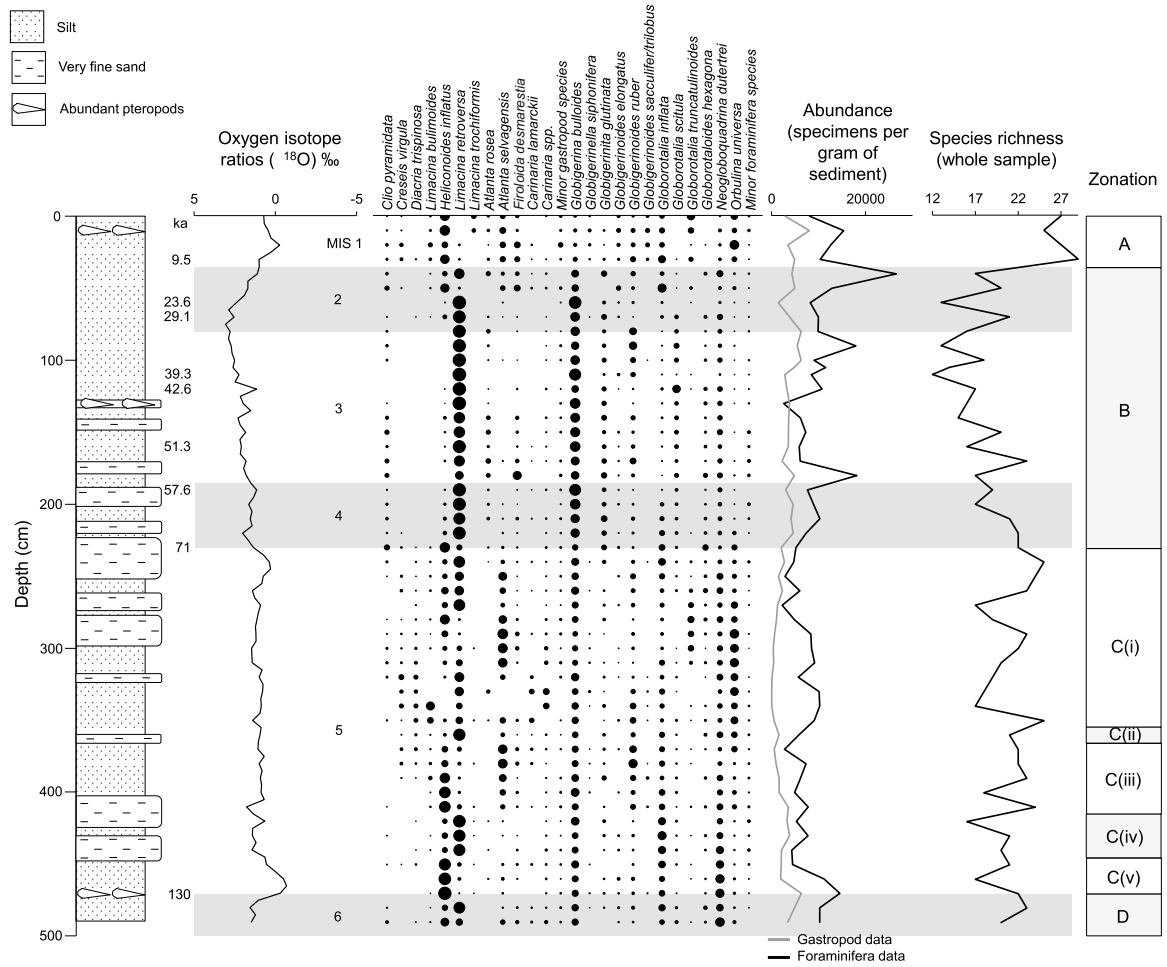923   amongst the Maldives Islands in the Indian Ocean.

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927 Figure 2. CAR-MON 2 Lithology, Oxygen isotope ratios and Marine Isotope Stages,

928 species assemblages, abundances by weight and species richness. Bubble areas

929 represent percentages, calculated separately for gastropods and planktonic

930 foraminifera. Dates from Le Friant *et al.* (2008).

Figure 3. B5-1 Lithology, Oxygen isotope ratios and Marine Isotope Stages, species assemblages, abundances by weight and species richness. Bubble areas represent percentages, calculated separately for gastropods and planktonic foraminifera. Dates from biozonation and isotope stratigraphy.
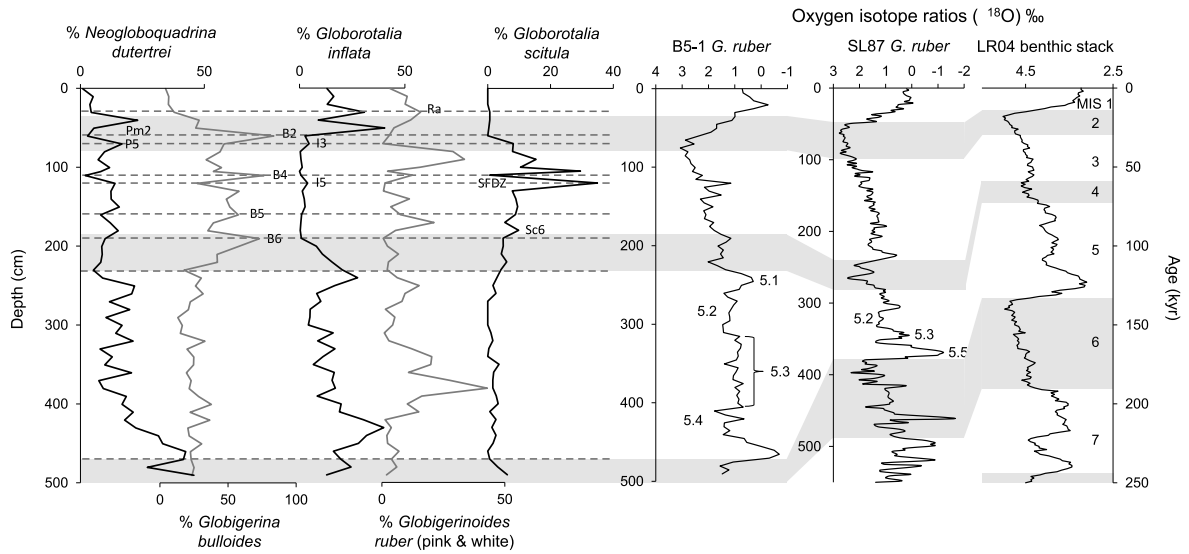
Figure 4. Stratigraphy of B5-1 with bio-events of Pujol and Vergnaud-Grazzini (1989) and Pérez-Folgado *et al.* (2003) identified within B5-1 planktonic foraminifera data. Oxygen isotope stratigraphy of B5-1 and comparison of the marine oxygen isotope records for B5-1, SL 87 (Weldeab *et al.,* 2003), approximatey 60 km south east of B5-1, and the LR04 benthic stack (Lisiecki and Raymo, 2005).

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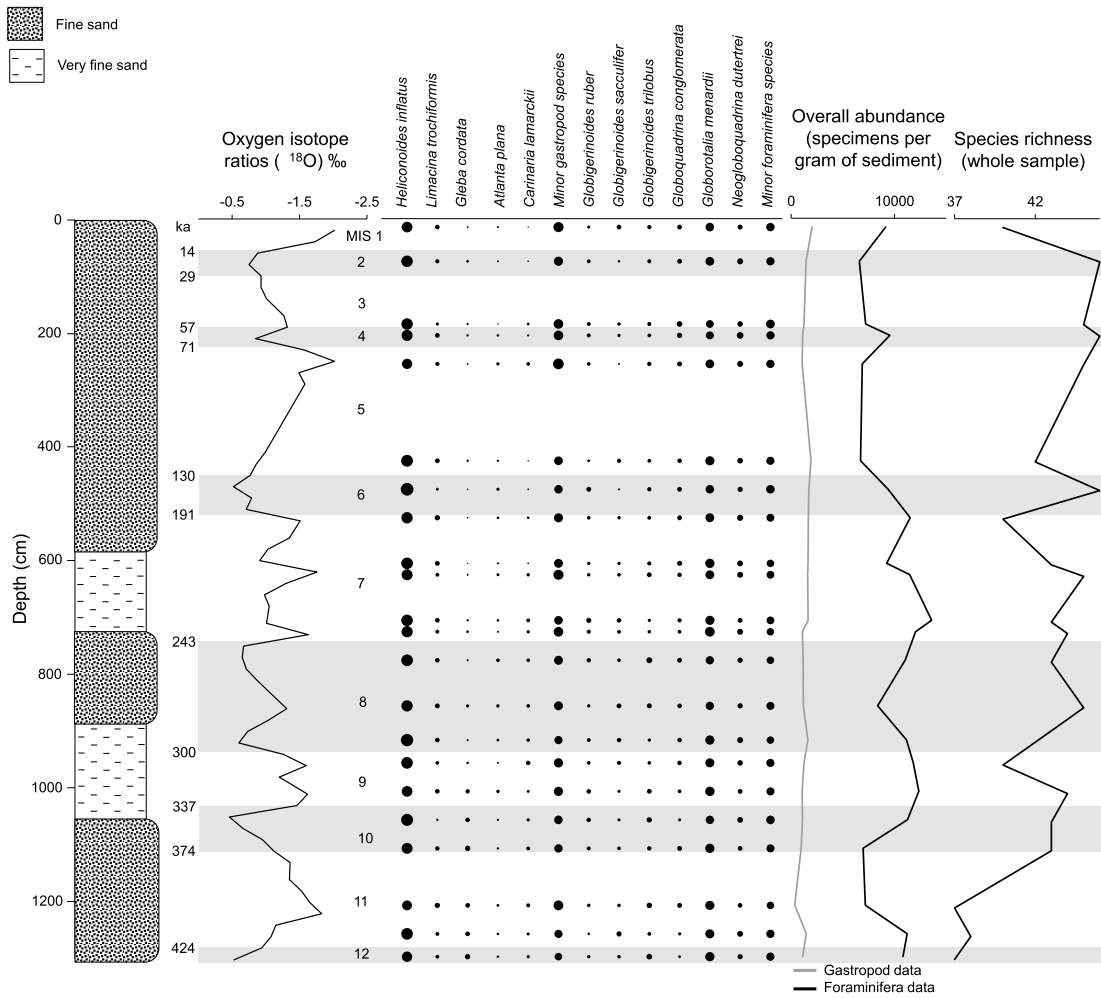
Figure 5. Hole 716B Lithology, Oxygen isotope ratios and Marine Isotope Stages, species assemblages, abundances by weight and species richness. Bubble areas represent percentages, calculated separately for gastropods and planktonic foraminifera. Dates from isotope stratigraphy (Backman *et al.,* 1988).

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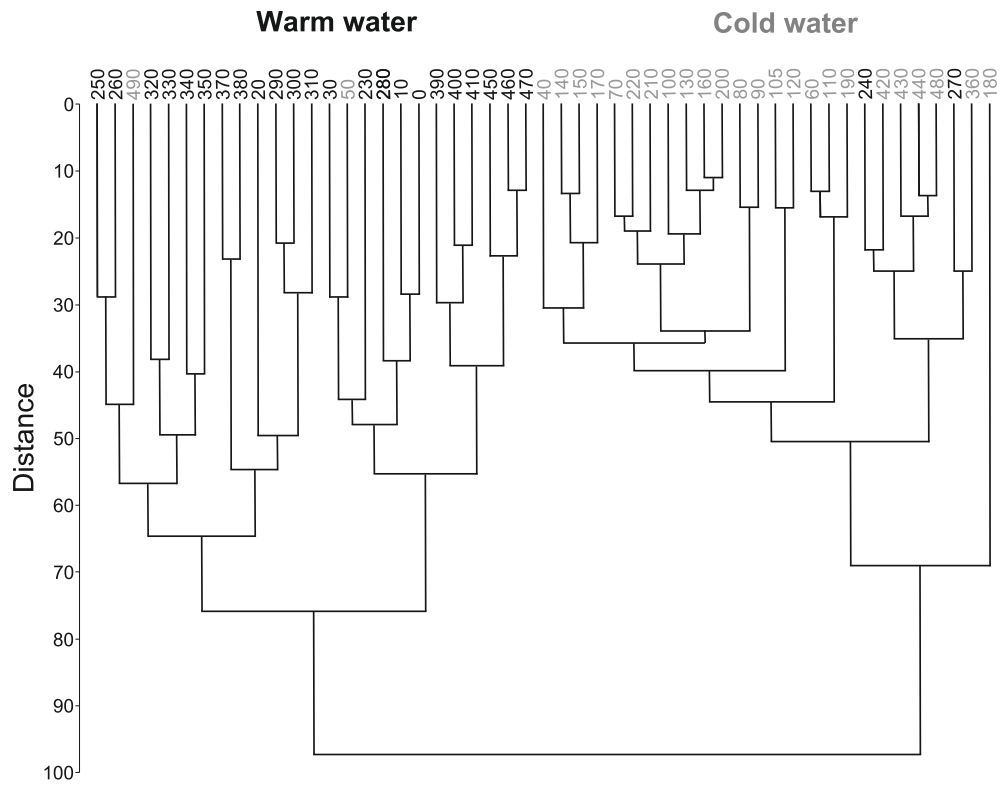
Figure 6. Cluster analysis of B5-1 samples performed using the Paleontological

Statistics package (PAST). Abundances of pteropods, heteropods and planktonic

foraminifera show two defined groups with similar assemblages, preferring either

warm or cold water.
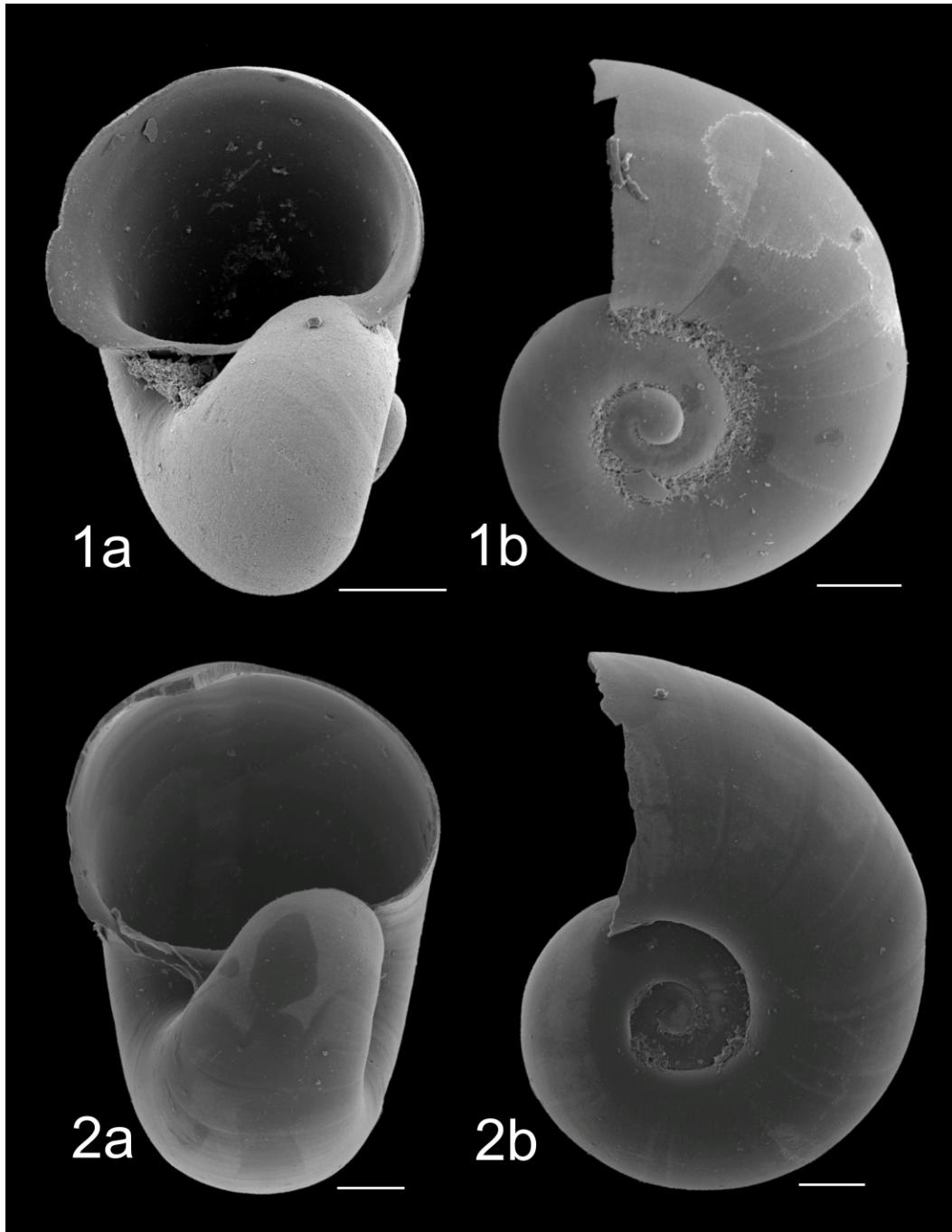
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Figure 7. Specimens of *Heliconoides inflatus* 1a) and b) from Hole 716B (15–16 cm, 150–500 µm) have a protruding protoconch; 2a) and b) from B5-1 (0–1 cm, >500 µm) have a depressed protoconch.
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20 µm

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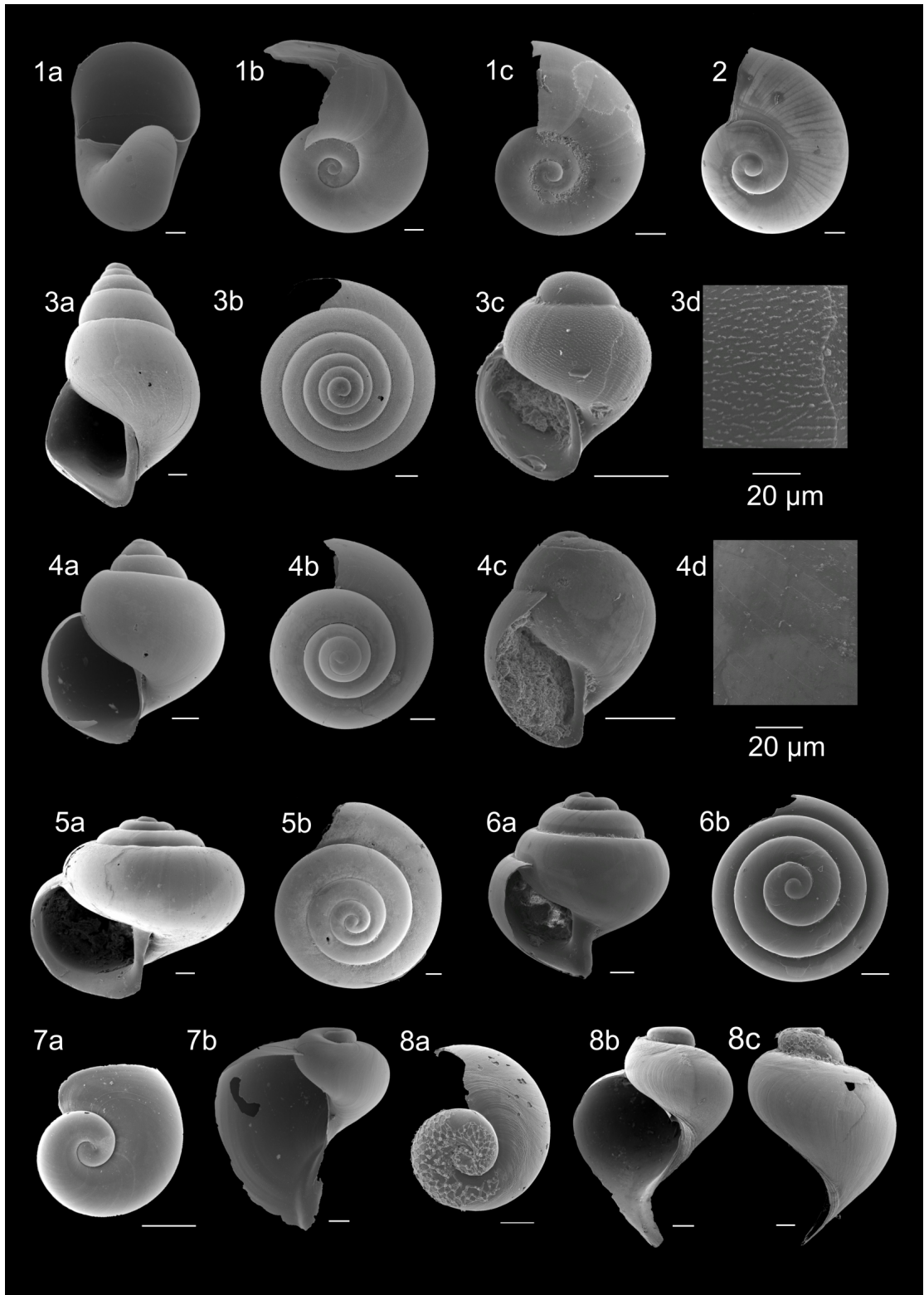
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965 **PLATE 1. FAMILY LIMACINIDAE AND PERACLIDIDAE.** All scale bars
966 represent 100 µm, except where stated otherwise. **1. *Heliconoides inflatus***
967 a) apertural view (CAR-MON 2, 70 cm); b) apical (CAR-MON 2, 70 cm); c)
968 apical view (716B, 15 cm). **2. *Limacina* sp. C** a) apical view (CAR-MON 2, 45
969 cm) **3. *Limacina bulimoides*** a) apertural view (CAR-MON 2, 80 cm); b)
970 apical view (CAR-MON 2, 70 cm); c) larval shell (B5-1, 20 cm); d) larval shell
971 surface (B5-1, 20 cm). **4. *Limacina trochiformis*** a) apertural view (CAR-
972 MON 2, 70 cm); b) apical view (CAR-MON 2, 70 cm); c) larval shell (B5-1, 0
973 cm); d) larval shell surface (B5-1, 0 cm). **5. *Limacina lesueurii*** a) apertural
974 view (CAR-MON 2, 30 cm); b) apical view (CAR-MON 2, 30 cm). **6. *Limacina***
975 ***retroversa*** a) apertural view (B5-1, 210 cm); b) apical view (B5-1, 210 cm). **7.**
976 ***Peracle moluccensis*** a) larval shell (CAR-MON 2, 365 cm); b) apertural view
977 (CAR-MON 2, 360 cm). **8. *Peracle diversa*** a) apical view (CAR-MON 2, 350
978 cm); b) apertural view (CAR-MON 2, 70 cm); c) side view (CAR-MON 2, 75
979 cm).

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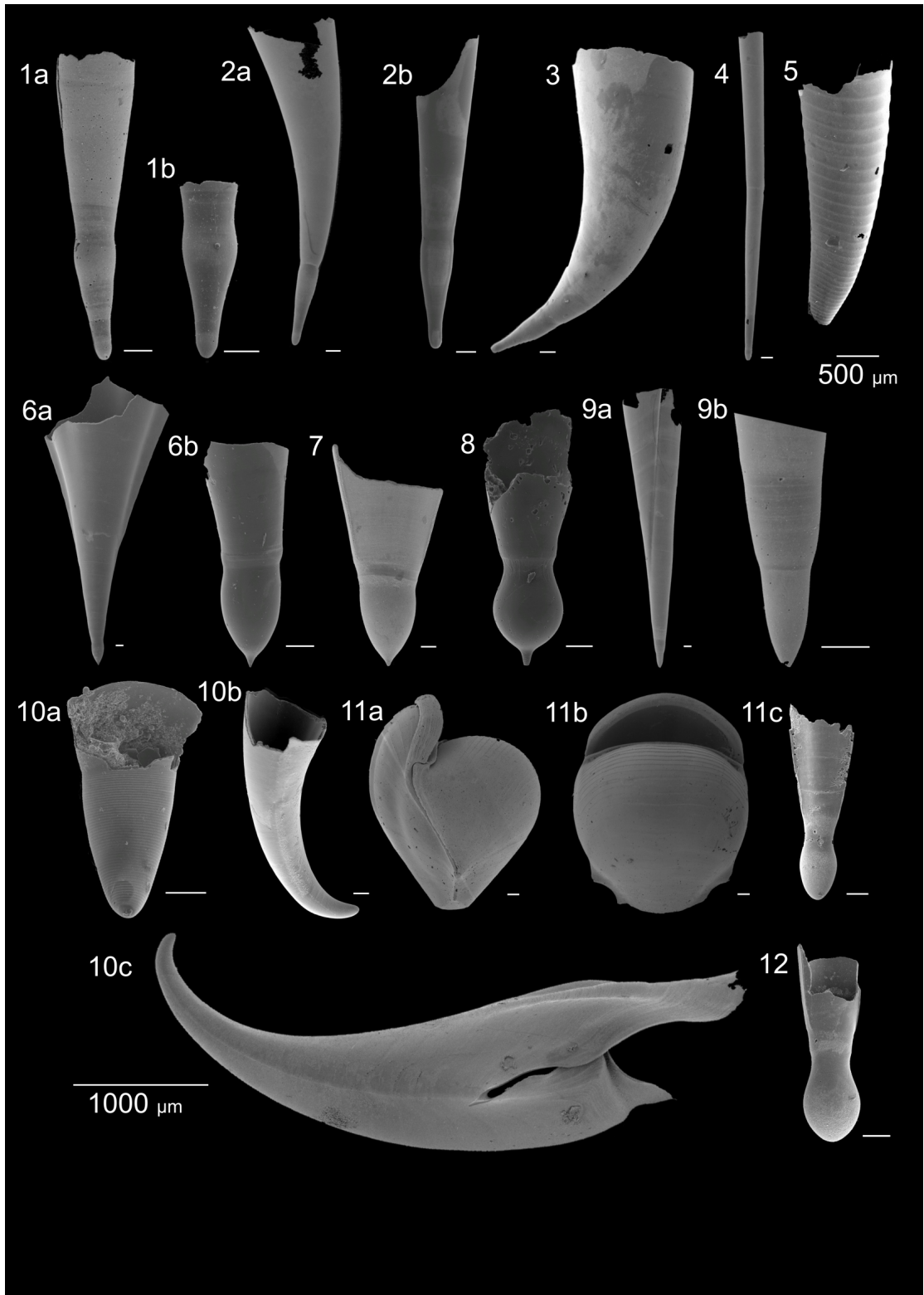
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985 **PLATE 2. FAMILY CAVOLINIIDAE.** All scale bars represent 100 μm, except
986 where stated otherwise. **1. *Creseis chierchiae*** a) adult shell (716B, 15 cm);
987 b) protoconch (716B, 15 cm). **2. *Creseis virgula*** a) adult shell (CAR-MON 2,
988 70 cm); b) protoconch B5-1, 20 cm). **3. *Creseis virgula*** adult shell (CAR-
989 MON 2, 30 cm). **4. *Creseis clava*** adult shell (CAR-MON 2, 70 cm). **5.**
990 ***Hyalocylis striata*** (CAR-MON 2, 80 cm). **6. *Clio pyramidata*** a) adult shell
991 (CAR-MON 2, 80 cm); b) protoconch (B5-1, 90 cm). **7. *Clio convexa***
992 protoconch (716B, 15 cm). **8. *Clio cuspidata*** protoconch (B5-1, 20 cm). **9.**
993 ***Styliola subula*** a) adult shell (CAR-MON 2, 80 cm); protoconch (CAR-MON
994 2, 80 cm). **10. *Cavolinia inflexa*** a) protoconch (B5-1, 20 cm); b) protoconch
995 (CAR-MON 2, 80 cm); c) adult shell (CAR-MON 2, 80 cm). **11. *Diacria***
996 ***quadridentata*** a) adult shell, side view (CAR-MON 2, 70 cm); b) apertural
997 view (CAR-MON 2, 70 cm); c) protoconch (CAR-MON 2, 20 cm). **12. *Diacria***
998 ***trispinosa*** protoconch (CAR-MON 2, 0 cm).

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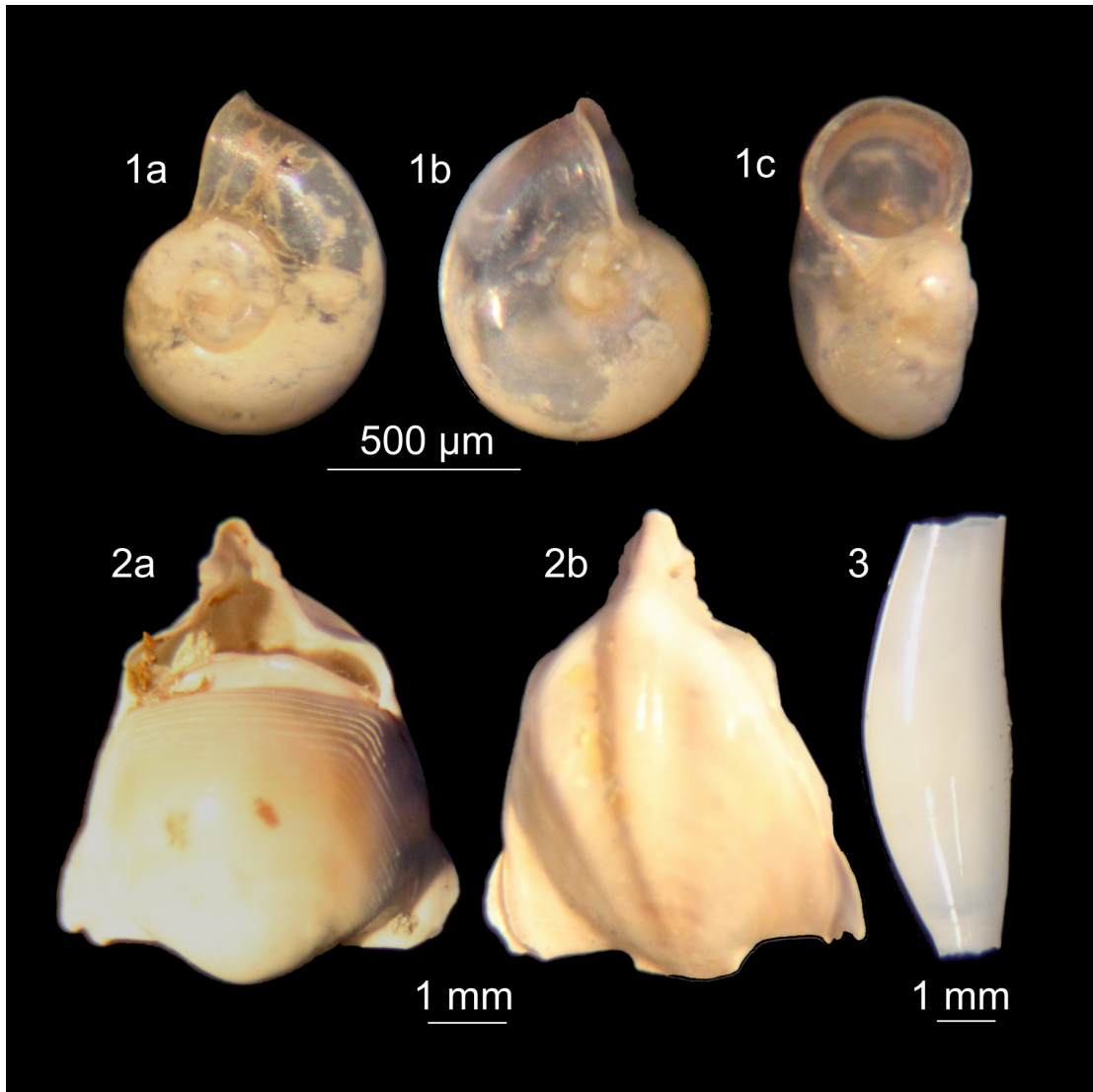
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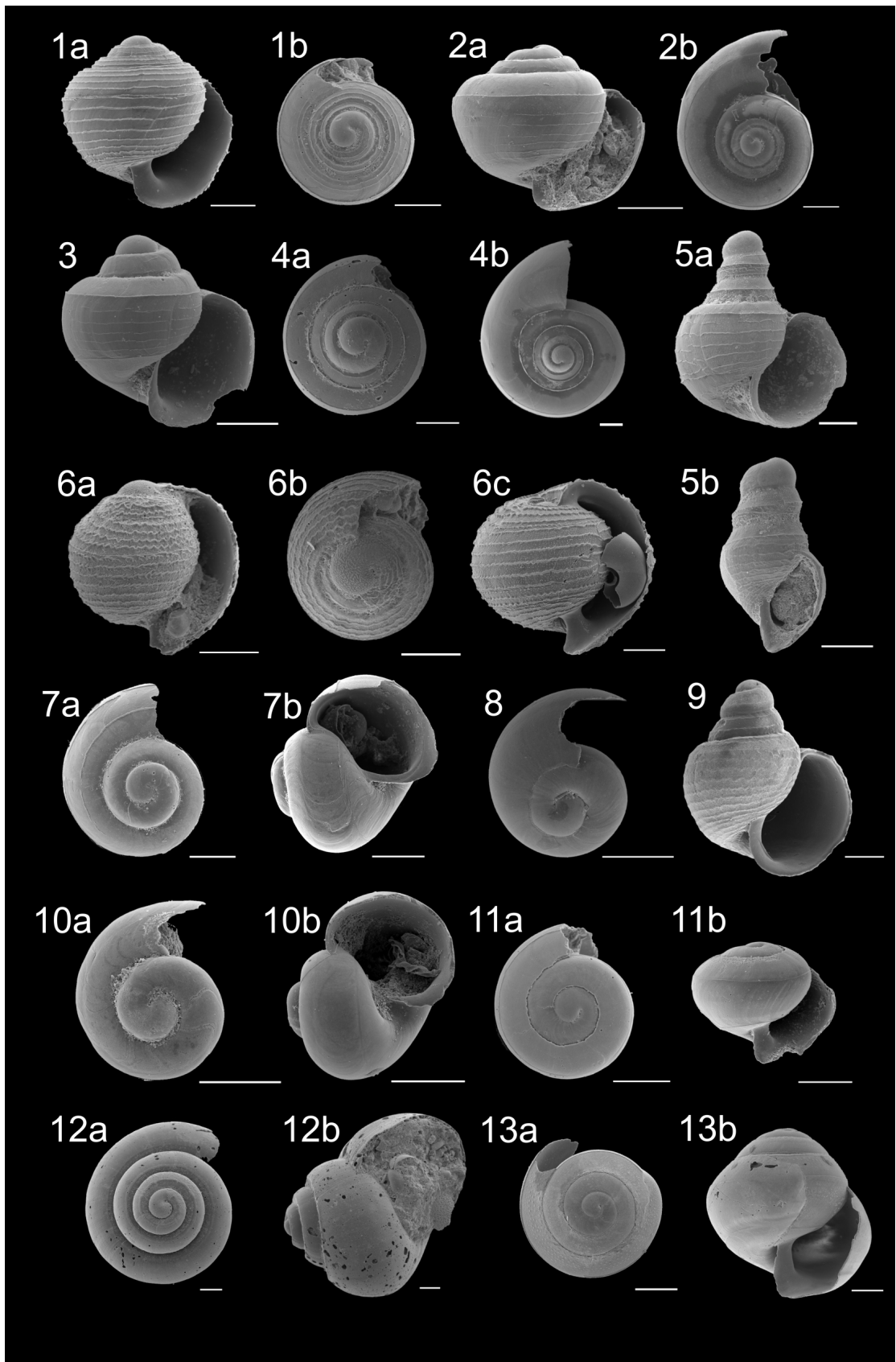**PLATE 3. FAMILY LIMACINIDAE AND CAVOLINIIDAE PHOTOMICROSCOPE IMAGES. 1.** *Limacina* **sp. C** (CAR-MON 2, 50 cm): a) apical view; b) umbilical view; c) apertural view. **2.** *Diacavolinia longirostris* (CAR-MON 2, 5 cm): a) ventral and apertural view; b) dorsal view. **3.** *Cuvierina columnella* (CAR-MON 2, 310 cm) side view.

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PLATE 4. FAMILY ATLANTIDAE JUVENILE FORMS. All scale bars represent 100 μm. **1.** *Atlanta helicinoidea* a) apertural view (CAR-MON 2, 520 cm); b) apical view (716B, 855 cm). **2.** *Atlanta selvagensis* a) apertural view (716B, 75 cm); b) apical view (B5-1, 290 cm). **3.** *Atlanta plana* apertural view (716B, 855 cm). **4.** *Atlanta frontieri* a) apical view (716B, 775 cm); b) apical view (716B, 475 cm). **5.** *Atlanta turriculata* a) apertural view (716B, 75 cm); b) apertural view (716B, 75 cm). **6.** *Oxygyrus inflatus* a) apertural view (716B, 75 cm); b) apical view (716B, 75 cm); c) apertural view (CAR-MON 2, 90 cm). **7.** *Protatlanta souleyeti* a) apical view (716B, 75 cm); b) apertural view (716B, 75 cm). **8.** *Atlanta rosea?* apical view (B5-1, 150 cm). **9.** *Atlanta brunnea* apertural view (CAR-MON 2, 350 cm). **10.** *Atlanta peronii?* a) apical view (CAR-MON 2, 90 cm); b) apertural view (B5-1, 20 cm). **11.** *Atlanta tokioka?* a) apical view (716B, 855 cm); b) apertural view (716B, 855 cm). **12.** *Atlanta* **sp. D** a) apical view (CAR-MON, 2 80 cm); b) apertural view (CAR-MON 2, 40 cm). **13.** *Atlanta tokioka* a) apical view (CAR-MON 2, 520 cm); b) apertural view (CAR-MON 2, 520 cm).
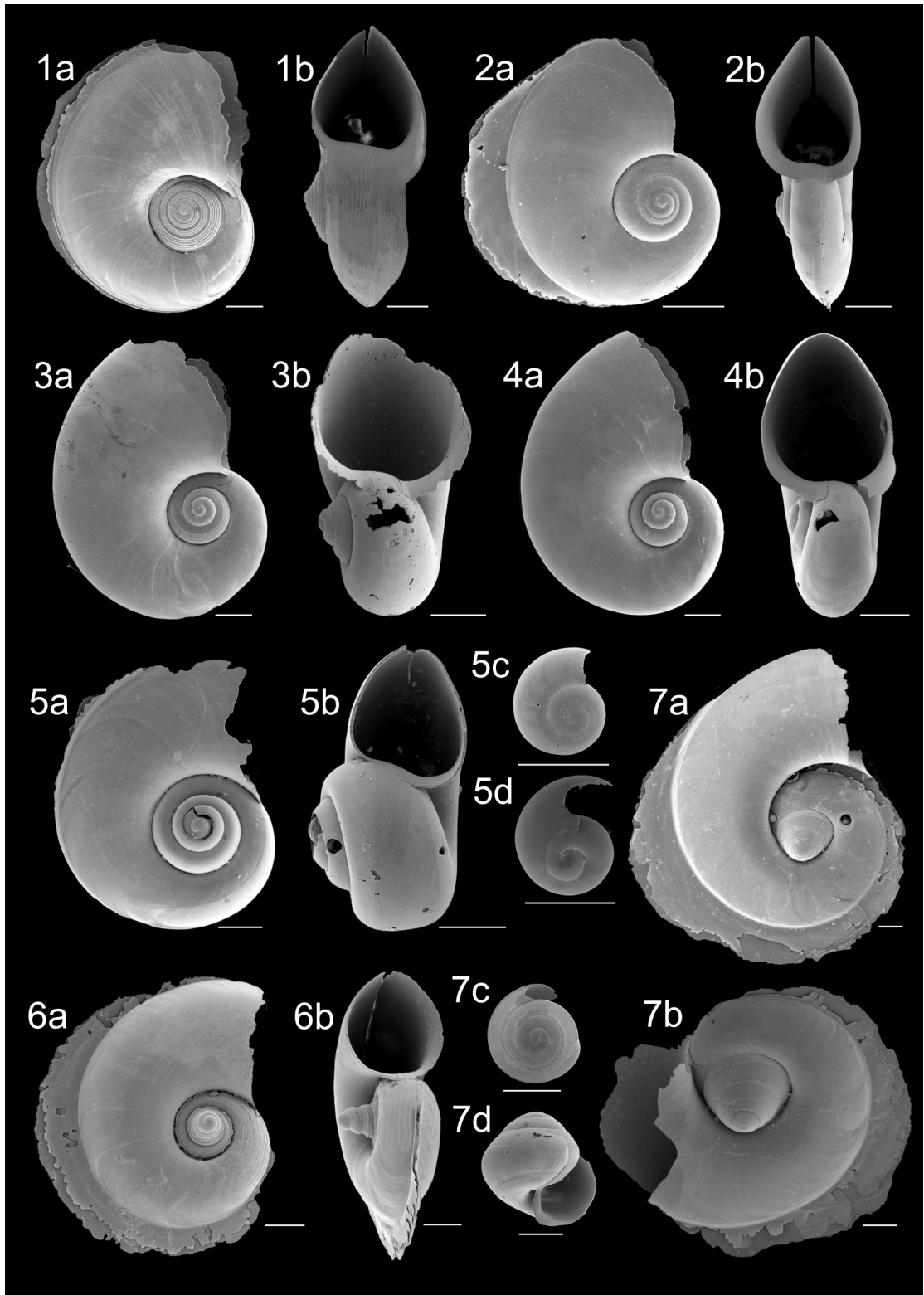
PLATE 5. FAMILY ATLANTIDAE ADULT FORMS. All scale bars represent 200 µm. **1.** *Atlanta helicinoidea* a) apical view (CAR-MON 2, 75 cm); b) apertural view (CAR-MON 2, 75 cm). **2.** *Atlanta selvagensis* a) apical view (CAR-MON 2, 75 cm); b) apertural view (CAR-MON 2, 75 cm). **3.** *Protatlanta souleyeti* a) apical view (CAR-MON 2, cm); b) apertural view (CAR-MON 2, cm). **4.** *Protatlanta souleyeti* a) apical view (CAR-MON 2, 75 cm); b) apertural view (CAR-MON 2, 75 cm). **5.** *Atlanta rosea?* a) apical view (CAR-MON 2, 70 cm); b) apertural view (CAR-MON 2, 75 cm); c) juvenile (B5-1, 150 cm); d) juvenile (B5-1, 150 cm). **6.** *Atlanta turriculata* a) apical view (CAR-MON 2, 80 cm); b) apertural view (CAR-MON 2, 80 cm). **7.** *Atlanta tokioka?* a) large specimen apical view (CAR-MON 2, 80 cm); b) apical view (CAR-MON 2, 80 cm); c) juvenile apical view (CAR-MON 2, 520 cm); d) juvenile apertural view (CAR-MON 2, 520 cm).

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PLATE 6. FAMILY CARINARIIDAE, CLIONIDAE AND CYMBULIIDAE. All scale bars represent 100 µm. **1. *Carinaria lamarckii*** a) larval shell apical view (B5-1, 370 cm); b) umbilical view (B5-1, 370 cm). **2. *Carinaria* sp.** larval shell (B5-1, 310 cm). **3. *Carinaria* sp.** (*galea?*) larval shell (B5-1, 50 cm). **4. *Carinaria pseudorugosa*** a) apical view (B5-1, 20 cm); b) apertural view (B5-1, 20 cm). **5. *Firoloida desmarestia*** a) adult shell apertural view (B5-1, 30 cm); b) apical view (B5-1, 30 cm); c) juvenile shell (B5-1, 10 cm). **6. *Gleba cordata*** a) and b) larval shell (B5-1, 240 cm). **7. Gymnosome veliger** (B5-1, 440 cm). **8. *Paedoclione doliiformis*** larval shell (B5-1, 90 cm).