

1 **REVIEW ARTICLE**

2
3 **A review of the ecology, palaeontology and distribution of atlantid heteropods**
4 **(Caenogastropoda: Pterotracheoidea: Atlantidae)**

5
6 Deborah Wall-Palmer¹, Christopher W. Smart¹, Richard Kirby², Malcolm B. Hart¹,
7 Katja T. C. A. Peijnenburg^{3,4} and Arie W. Janssen³

8
9 ¹*School of Geography, Earth and Environmental Sciences, Plymouth University,*
10 *Drake Circus, Plymouth, PL4 8AA, UK.*

11 ²*Marine Biological Association, Citadel Hill, Plymouth, PL1 2PB, UK.*

12 ³*Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, The Netherlands.*

13 ⁴*Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam,*
14 *P. O. Box 94248, 1090 GE Amsterdam, The Netherlands.*

15
16 ATLANTID HETEROPODS

17
18 (Received 6 February 2015; accepted 2 November 2015)

19
20 Correspondence:

21 D. Wall-Palmer; email: deborah.wall-palmer@plymouth.ac.uk

ABSTRACT

35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68

Fewer than 1% of marine gastropod species live a holoplanktic life. Of these, the shelled heteropods of the family Atlantidae are among the most poorly understood. The atlantids potentially make up an important part of the ocean zooplankton, composing up to 69% of shelled holoplanktic gastropods in the Late Pleistocene to Recent fossil record. They are also likely to be at high risk from current and future global changes, including anthropogenic ocean acidification. However, due to their small size (<12 mm), difficulty of sampling and complicated morphology, we still lack key information about atlantid taxonomy and ecology. This makes it difficult to understand how important they are in the ocean foodweb and how they will be affected by environmental change. Although many studies have been carried out on the atlantids, these have generally been broad and unconnected. Here, we draw together this previous research, summarising what is currently known about atlantid taxonomy, palaeontology, ecology and biogeography, and aiming to provide a foundation for future research on this group. The data indicate complex behaviours involving seasonal and vertical migration, and demonstrate extended geographical ranges, with implications for understanding the role of atlantids in the ocean foodweb and their sensitivity to environmental changes. This review highlights the urgent need for further taxonomic research on the atlantids, including molecular analysis, and for improved sampling techniques.

INTRODUCTION

69

70

71 Heteropods have been studied for over 200 years, since the description of
72 *Pterotrachea* by Forskål (in Niebuhr, 1775). The early oceanographic expeditions
73 generated much interest in heteropods and entire chapters of cruise reports were often
74 dedicated to their description (Smith, 1888; Schiemenz, 1911; Tesch, 1910, 1949;
75 Tokioka, 1955a, b). However, in recent years, heteropods have often been overlooked
76 in plankton studies, which is most likely a result of their small size and complicated
77 taxonomy, combined with inadequate sampling techniques. The fragile shells of
78 heteropods are easily broken during collection, resulting in incomplete descriptions
79 and uncertain identifications. The ability of heteropods to evade capture by standard
80 plankton nets, particularly those of small aperture, has also led to an underestimation
81 of their abundance and diversity (McGowan & Fraundorf, 1966; Seapy, 1990a, b).
82 Recent research on the fossil record of heteropods suggests that they can be quite
83 abundant relative to other holoplanktic gastropods and more tolerant of temperate and
84 cold waters than previously thought (Wall-Palmer *et al.*, 2014). Recent plankton
85 sampling during the 2014 Atlantic Meridional Transect in the Atlantic Ocean found
86 that atlantid heteropods made up an average of 16% (up to 44% of individuals per
87 sample) of calcareous holoplanktic gastropods at each station (A.K. Burrige, pers.
88 comm., September 2015). This indicates that heteropods may be a more important
89 component of the ocean foodweb than previously thought. Atlantids are also likely to
90 be prone to the effects of current and future ocean acidification because they live in
91 the most vulnerable habitat, the surface ocean, and produce an aragonite shell, which
92 is particularly susceptible to dissolution. However, no studies into the effects of ocean
93 acidification have been carried out on atlantids. Research on a similar, but unrelated
94 group of holoplanktic gastropods, the thecosome (shelled) pteropods, suggests that
95 ocean acidification negatively affects shell growth and survival of aragonitic-shelled
96 holoplanktic gastropods (Comeau *et al.*, 2012; Bednaršek *et al.*, 2014).

97

98 This review collates information from published research on the taxonomy,
99 palaeontology, ecology and biogeography of the Atlantidae, extending and updating
100 previous reviews by Thiriou-Quévieux (1973), van der Spoel (1976), Lalli & Gilmer
101 (1989) and Richter & Seapy (1999). Our aim is to provide a foundation on which
102 future research on this group of potentially important and threatened holoplanktic

103 gastropods can be developed. The collated data have been used to generate a series of
104 biogeographical species maps and information on the complicated vertical and
105 seasonal migrations of the atlantids. An overview of atlantid palaeontology is also
106 presented, with the first stratigraphic chart for this group. We have not attempted to
107 review the general biology, anatomy and larval development of atlantids, as this has
108 been done by Thiriote-Quévieux (1973), Martoja & Thiriote-Quévieux (1975), Lalli &
109 Gilmer (1989) and Jamieson & Newman (1989).

110

111

TAXONOMY

112

113 The vernacular name ‘hétéropodes’ (meaning different foot) was created by Lamarck
114 (1812), although Children (1824) formally introduced the order Heteropoda, placing it
115 within the Mollusca next to ‘Gasteropoda’. The heteropods were identified as
116 gastropods by Cuvier (1836), having previously been suggested as a link between
117 cephalopods and fish (Lamarck, 1812). The subsequent taxonomic history of the
118 group has been reviewed by Thiriote-Quévieux (1973). Today, the order Heteropoda
119 is invalid and has been reorganized as the superfamily Pterotracheoidea Rafinesque,
120 1814 within the caenogastropod order Littorinimorpha (Gofas, 2015a). However, the
121 term ‘heteropods’ is still widely used as an informal name for the group. The extant
122 Pterotracheoidea are classified in eight genera in three families (Carinariidae,
123 Pterotracheidae and Atlantidae) (Seapy, 2011). An additional family, the
124 Coelodiscidae, is known exclusively from the fossil record.

125

126 Of the three extant families of heteropods, the shell-bearing Atlantidae is considered
127 to be the least specialized for a holoplanktic existence when compared with the other
128 heteropod families, which have either reduced shells (Carinariidae) or lack shells in
129 the adult stage (Pterotracheidae) and have a correspondingly larger body size (Thiriote-
130 Quévieux & Seapy, 1997). However, the Atlantidae are the most species-rich family,
131 containing over 60% of all heteropod species (Seapy, 2011). Atlantids are also
132 consistently found to be the most abundant heteropods in plankton samples (Richter,
133 1968; Seapy *et al.*, 2003; Ohman *et al.*, 2009; Ossenbrügger, 2010). The family
134 contains three genera (*Atlanta*, *Protatlanta* and *Oxygyrus*) and is characterized by
135 dextrally-coiled, aragonitic shells into which the soft body can fully retract, sealed by
136 a chitinous operculum that is attached to the foot (Fig. 1A, C). Apparent adaptations

137 of the atlantids for a holoplanktic life include reduction in shell-wall thickness (3–40
138 μm) or (in the genera *Protatlanta* and *Oxygyrus*) a partially uncalcified (conchiolin)
139 shell, a peripheral shell keel, a tendency for the body and shell to be transparent, well-
140 developed eyes and the modification of the foot into a swimming fin (Lalli & Gilmer,
141 1989) (Fig. 1).

142

143 The genus *Atlanta*, including two species, was introduced by Lesueur (1817).
144 Subsequently, many species, collected during the expedition of *La Bonite*, were
145 beautifully illustrated by Eydoux & Souleyet (1841), but only indicated with
146 vernacular names. However, before Souleyet (1852) was able fully to describe and
147 name these species (13 of which were new), they were formally named by J.E. Gray
148 (1850) from a collection of figures produced by M.E. Gray for the use of students.
149 Tesch (1949) clarified the systematics of the family, revising the number of species to
150 ten, using specimens collected during the Dana Expeditions. Since then, a number of
151 species have been reinstated or newly described, the latest being *A. selvagensis* de
152 Vera & Seapy, 2006. There are currently 21 extant species (Seapy, 2011; Gofas,
153 2015b) and nine extinct species of Atlantidae (Table 1). Extant species of *Atlanta* are
154 organized into seven ‘species groups’ based on morphological features of the shell,
155 eyes, operculum and radula (Seapy, 2011; Fig. 2). Species descriptions and keys have
156 been published by Seapy (1990a, 2011) and Seapy *et al.* (2003).

157

158 The taxonomy of the Atlantidae largely relies on shell morphology, in particular
159 protoconch shape (number of whorls) and ornamentation. However, shell morphology
160 is often not sufficient to identify closely related species reliably, so that the eyes (Fig.
161 1A–C), radula and operculum are necessary for identification (Seapy & Richter,
162 1993). For example, in the Pacific Ocean the shells of *A. inflata* and *A. helicinoidea*
163 are similar and eye type has to be used to differentiate the two species (Seapy, 2011).
164 Three eye and three opercular types were originally described by Richter (1961) and
165 these have been summarized for each species, together with radula type, by Seapy
166 (2011).

167

168 So far there has been only a single molecular study including atlantids. Jennings *et al.*
169 (2010) analysed four atlantid species, *A. gaudichaudi*, *A. inclinata*, *A. peronii* and
170 *Oxygyrus inflatus*, from various locations in the Atlantic Ocean. They found

171 molecular differences between two forms of *A. inclinata*, one with a golden shell keel
172 sampled in the northwestern Atlantic Ocean and one with a colourless keel sampled in
173 the northeastern and southeastern Atlantic Ocean, suggesting that these were distinct
174 species. This indicates that identification based on traditionally used morphological
175 features may not always be reliable.

176

177 Many areas of the world ocean have not been thoroughly sampled for atlantids
178 (Richter & Seapy, 1999). The four most recently-described species, *A. fragilis*, *A.*
179 *frontieri*, *A. californiensis* and *A. selvagensis*, all appear to have restricted
180 distributions (de Vera & Seapy, 2006), so it is likely that there are additional atlantids
181 still to be discovered. Improvements in sampling techniques and the application of
182 combined morphological and molecular analyses are all necessary to improve
183 understanding of atlantid taxonomy, evolution and biogeography.

184

185

PALAEONTOLOGY

186

187 Although atlantid shells are frequently preserved in marine sediments, the age and
188 origin of this group is uncertain. The oldest taxon (Fig. 3) considered to belong to the
189 Atlantidae is *Bellerophina minuta* (Sowerby, 1814), described from the Cretaceous
190 (Albian, Gault Clay Formation) of Britain (for illustration see Tracey, 2010: pl. 24,
191 figs 16, 17; Janssen & Peijnenburg, 2014: fig. 19.6). This species is 75 Myr older than
192 any other known atlantid, but resembles the extant *Oxygyrus inflatus* so strongly that
193 Forbes (1844) erroneously considered the two species to be synonymous. However,
194 the fossil record of *O. inflatus* is not known to extend beyond the Pliocene (Janssen,
195 1998, 2007, 2012b). Therefore, if *B. minuta* is an atlantid, there is a large gap in the
196 fossil record of atlantids for which we have no data, with the next oldest potential
197 species appearing in the Oligocene.

198

199 Cossmann (1889) added the new extinct genus *Eoatlanta* to the Atlantidae, with the
200 species *E. spiruloides* from the Eocene (Lutetian) of the Paris Basin. However,
201 Lozouet (2012) and Schnetler (2013) have recently demonstrated the nonplanktic
202 nature of this species and transferred it to the benthic Vanikoroidea. *Atlanta*
203 *arenularia* Gougerot & Braillon, 1965, previously thought to be the oldest species in
204 the genus *Atlanta*, is also found in the Eocene (Bartonian) of the Paris Basin.

205 However, the shell morphology of this species suggests that it actually belongs within
206 the Carinariidae.

207

208 The first certain representatives of the genus *Atlanta* (two unidentified species) were
209 recorded from the Late Oligocene (Chattian) and Miocene (Burdigalian-Serravallian)
210 rocks of Malta (Janssen, 2012a). A slightly younger fossil genus, *Mioatlanta*, with
211 one species, *M. soluta*, was described from the Miocene (Langhian) of Vetto d'Enza,
212 northern Italy (Di Geronimo, 1974). However, additional material from the type
213 locality demonstrates the close relationship between *Mioatlanta* and *Atlanta*, thus we
214 are inclined to consider the two as synonymous. A further late Miocene species,
215 known from only a few specimens, *A. cordiformis*, was found in the Dominican
216 Republic (Janssen, 1999) and several unidentified *Atlanta* specimens (juveniles) have
217 also been recorded from the late Miocene (Tortonian) of northern Italy (Janssen,
218 1995).

219

220 A number of *Atlanta* species have been recorded from Pliocene rocks worldwide.
221 Woodring (1928) described two species, *A. diamesa* and *A. (Atlantidea) lissa*.
222 However, the latter species, from the Bowden Beds of Jamaica, has now been
223 interpreted as a synonym of *Protatlanta rotundata* by Janssen (2012a). These deposits
224 were previously considered to be of Miocene age, but a much younger, Early Pliocene
225 (Piacenzian) age has now been demonstrated using calcareous nannoplankton (Aubry,
226 1993), planktic foraminifera (Berggren, 1993) and holoplanktic Mollusca (Janssen,
227 1998). The species *A. plana*, until recently known exclusively from the extant Indo-
228 Pacific fauna, has been recorded from Pliocene rocks in southern France and
229 Estepona, southern Spain (Janssen, 2004, 2012b). A somewhat older occurrence (late
230 Miocene–early Pliocene) of the same species is known from the Fiji Islands (Janssen
231 & Grebneff, 2012). Pliocene (Piacenzian) rocks from Pangasinan (Philippines)
232 contain a remarkable assemblage including thirteen atlantid and three carinariid
233 species (Janssen, 2007), among which three of the atlantids species were newly
234 described (*A. lingayanensis*, *A. richteri* and *A. seapyi*). These are also the most recent
235 atlantid species known to have become extinct. All other atlantid species found from
236 the Pliocene of Pangasinan are extant, as are all atlantids identified from Pleistocene
237 sediments in various localities (Fig. 3).

238

239 The genus *Protatlanta* has a single extant member, *P. souleyeti*, which is known from
240 the Pliocene to the Recent. The oldest species, *P. rotundata* (synonyms *A. lissa* and *P.*
241 *kakekawaensis*) is known from the middle to late Miocene (Mediterranean and
242 Caribbean) and Pliocene (Mediterranean, Caribbean and Japan) (Gabb, 1973;
243 Woodring, 1928; Shibata, 1984, 2008; Zorn, 1997; Janssen, 2004, 2007, 2012a;
244 Janssen & Little, 2010). A second Miocene species, *P. kbiraensis* (Janssen, 2012a), is
245 known only from Malta. However, extinct species of *Protatlanta* differ substantially
246 from the extant type species and are likely, eventually, to be separated at genus level.

247

248 Although we do not know of any global atlantid species extinctions since the
249 Pliocene, the distributions of extant species have changed during the Late Pleistocene.
250 Data for *A. oligogyra*, *A. turriculata*, *A. echinogyra* and *A. plana* suggest that their
251 current distribution is restricted to the Indo-Pacific. However, Wall-Palmer *et al.*
252 (2014, in press) found all four species in Late Pleistocene sediments collected off
253 Montserrat in the Caribbean Sea. These species seem to have ceased living in the
254 Caribbean Sea during the period of climatic warming that followed the Last Glacial
255 Maximum (LGM), potentially suggesting a localized atlantid extinction event. *Atlanta*
256 *plana* was also present in the Mediterranean during the Pliocene (Janssen, 2012c), but
257 is currently thought to be absent from the entire Atlantic Ocean.

258

259 These data emphasise the need for future research on atlantid palaeontology, in
260 particular to investigate the large time gap during the Palaeogene. At present, atlantids
261 are not used in palaeoceanography or as stratigraphic markers. However, our
262 knowledge of the atlantid fossil record, though limited, has already added new insight
263 into their abundance and temperature tolerance (Wall-Palmer *et al.*, 2014), as well as
264 ecological relationships, such as preferred prey (Wall-Palmer *et al.*, in press).
265 Improving our knowledge of the atlantid fossil record is likely to prove useful in
266 understanding the phylogenetic history of atlantids, as well as understanding how they
267 have reacted to past environmental changes.

268

269

270

ECOLOGY

271

272 The importance of atlantids in the ocean foodweb is currently unknown. Atlantids are
273 a family of specialized, mobile carnivores with large eyes that suggest selective
274 predation (Lalli & Gilmer, 1989). Atlantids are also abundant relative to other shelled
275 holoplanktic gastropods, making up an average of 16% (up to 44%) of shelled
276 holoplanktic gastropods collected at each station during AMT24 (A.K. Burridge, pers.
277 comm., September 2015) and up to 28% in net hauls collected off of Baja California
278 (McGowan & Fraundorf, 1966). Atlantids are also consistently found to be the most
279 abundant heteropods (Richter, 1968; Seapy *et al.*, 2003; Ohman *et al.*, 2009;
280 Ossenbrügger, 2010), occurring at densities of up to 17 individuals of a single species
281 (*Atlanta gaudichaudi*) per m³ of water (Newman, 1990a). In plankton-net hauls, larval
282 and juvenile atlantids are generally more abundant than adults (Thiriot-Quévieux,
283 1973; Newman, 1990a). This may, however, be an artefact of net avoidance, a
284 phenomenon demonstrated by McGowan & Fraundorf (1966), who found that
285 estimates of atlantid abundance and diversity were reduced when using nets with
286 smaller apertures. They caught 37–350% more atlantid specimens per 1000 m³ of
287 water with a 140-cm diameter ring net compared with a 20-cm diameter ring net.
288 Seapy (1990b) found that specimens captured using a larger 4-m² aperture ring net
289 were on average 50% larger in size than specimens caught using a 0.7-m² aperture
290 bongo net (although the volume of water filtered was not comparable). Thus, it is
291 likely that adult atlantids, and atlantids in general, are more abundant in our oceans
292 than plankton hauls suggest.

293

294 The Late Pleistocene fossil record of holoplanktic gastropods reveals that atlantids are
295 often abundant in sediments, relative to other shelled holoplanktic gastropods. This is
296 particularly true during warm periods, when atlantids have been found to compose up
297 to 69%, 27% and 33% of holoplanktic gastropod shells in Mediterranean Sea,
298 Caribbean Sea and Indian Ocean (Maldives) sediments, respectively (Wall-Palmer *et*
299 *al.*, 2014). Numerically, atlantids can be as frequent as 3333, 2160 and 2588
300 specimens per gram of sediment in the 150–500 µm fraction in material from these
301 three areas, respectively (data extracted from Wall-Palmer *et al.*, 2014).

302

303 ***Seasonal abundances***

304 Limited published data suggest that atlantids can tolerate a range (approx. 30 to 35
305 PSU) of salinities (Xu & Li, 2005; Xu, 2007; Cruz, 2012). However, they are

306 sensitive to other environmental factors (Cruz, 1996, 1998) and exhibit distinct
307 seasonal changes in abundance (Table 2) under the influence of water temperature
308 and currents (Vane & Colebrook, 1962; Richter 1968; Thiriot-Quévieux, 1968;
309 Cummings & Seapy, 2003; Xu & Li, 2005; Xu, 2007; Seapy, 2008; Angulo-Campillo,
310 2011), monsoonal changes (Mathew *et al.*, 1990), and wet and dry seasons (Frontier,
311 1973a, b). Reproductive seasons do not appear to be strongly linked to seasonal
312 abundances, because larval stages are often found throughout the year (Richter,
313 1968).

314

315 The effects of seasonal currents, both vertical and horizontal, upon atlantid
316 abundances have been identified in several regions. In the Gulf of Naples, all
317 heteropod species show the same seasonal changes in abundance, with a small, not
318 always distinctive maximum in early spring, followed by a minimum in summer and a
319 very distinct maximum in autumn (Richter, 1968). This pattern was inferred to be
320 most likely influenced by hydrographic factors, in particular seasonal vertical
321 convection. Cummings & Seapy (2003) also found a strong link between seasonal
322 currents and the abundance of *A. californiensis* in the San Pedro Basin, California.
323 Highest abundances occurred during the summer, coinciding with the strongest
324 seasonal flow of the California Current and Southern California Eddy. During the
325 winter, when the flow of these currents is weakest, the lowest abundances of *A.*
326 *californiensis* were recorded. In the East China Sea (Xu & Li, 2005; Xu, 2007),
327 higher abundances of atlantids (*A. rosea*, *A. lesueurii* and *A. peronii*) during the
328 summer and autumn were found to be closely related to changes in the water
329 temperature which, in common with other areas, is also related to shifting currents
330 (Taiwan Warm Current).

331

332 In the Indian Ocean, Mathew *et al.* (1990) showed that the monsoon influenced
333 heteropod abundance, with greatest numbers generally collected during November
334 and December. This is during the Indian Ocean winter monsoon, characterized by dry
335 weather and gentle, steady winds. However, the influence of the monsoon appears to
336 be variable geographically. In the eastern Arabian Sea, post-monsoon increases in
337 abundance have been reported, whereas in the Bay of Bengal the increases in
338 abundance occur before the monsoon (Mathew *et al.*, 1990). Consequently, it is likely
339 to be a combination of temperature, shifting water currents and food availability that

340 influences heteropod abundance in these regions, rather than the monsoon *per se*.
341 Frontier (1973a, b) identified a link between changing abundances of *A. gaudichaudi*
342 and wet and dry seasons around the coast of Nosy-Bé, Madagascar. Highest
343 abundances on the shelf coincided with the wet season, with the highest numbers
344 occurring between December and May. It is thought that this link is caused when
345 unusually prolonged dry periods detrimentally affect the juvenile population of the
346 species (Frontier, 1973a, b).

347

348 These studies suggest that the seasonal abundance of atlantid heteropods is complex
349 and closely linked to changes in water currents and food availability, rather than water
350 temperature alone. While this may be a consequence of their weak swimming ability,
351 it is more likely to be driven by movements and availability of prey. Newman (1990a)
352 found that atlantids can remain suspended and stationary while currents flow over
353 them. Therefore, atlantids are able to control how far they travel in currents. A
354 number of studies have found that seasonal variations in atlantid abundance are
355 species specific, with a seasonal succession of species (Evans, 1968; Thiriot-
356 Quévieux, 1968). Lemus-Santana *et al.* (2014) suggest that this seasonal succession is
357 an ecological strategy to avoid competition for prey. Newman (1990b) found that
358 three species of atlantid (*A. gaudichaudi*, *A. lesueurii* and *A. helicinoidea*) showed an
359 opposing pattern of seasonality in two areas of the Great Barrier Reef, Australia, that
360 are 1180 km apart. In the north, the three species were more abundant during the
361 winter sampling, whereas in the south the three were more abundant during the
362 summer sampling. A similar pattern was found off the coast of the British Isles, where
363 higher abundances of atlantids appeared in the northwest later than in the southwest.
364 Vane & Colebrook (1962) attributed this later arrival to currents passing from south to
365 north, suggesting that atlantids travel in species-specific groups. Thiriot-Quévieux
366 (1968) found that off southeastern France larval and adult stages show the same
367 seasonality, supporting this type of horizontal migration.

368

369 ***Vertical distribution and migration***

370 The vertical distribution of atlantids is not well understood. Atlantids have been found
371 to live within the epipelagic zone, the upper 250 m of the water column (Jivaluk,
372 1998; Michel & Michel, 1991; Paulinose *et al.*, 1992; Ossenbrügger, 2010) and often
373 only at much shallower depths (Lalli & Gilmer, 1989; Seapy, 1990b; Ossenbrügger,

374 2010). Lemus-Santana *et al.* (2014) have provided the only detailed species-specific
375 depth ranges for atlantids, but only for the Gulf of Mexico.

376

377 In an attempt to identify at what depth shell calcification takes place, Grossman *et al.*
378 (1986) carried out geochemical analysis of stable oxygen isotopes of both whole
379 atlantid shells (*A. gaudichaudi* and *A. inclinata*) and of specific parts of the shells that
380 represent ontogenetic stages. The study found that *A. gaudichaudi* and *A. inclinata*
381 precipitate their shells in shallow water at depths of less than 75 m, while another
382 *Atlanta* species (not identified to specific level) did so at 75 to 125 m. Different
383 sections of the shell were found to have similar oxygen isotopic compositions,
384 suggesting that these atlantids precipitate their shells at the same depth throughout
385 their lives. However, according to Lalli & Gilmer (1989) atlantids add to their shell
386 thickness throughout their lives, which may explain why there was no difference in
387 isotopic composition between the stages. Further geochemical analysis of shells at
388 different stages of development, using new laser ablation techniques for example, is
389 needed and will help to identify the vertical ranges of atlantids.

390

391 Based on plankton sampling using nets at different depths, it is thought that many
392 (and potentially all) atlantid species show some degree of daily vertical migration
393 within the epipelagic zone. However, many studies have shown conflicting results,
394 suggesting that migration behaviours are often stage- and species-specific, with some
395 species exhibiting nocturnal migration towards the surface and others exhibiting no
396 migration at all (Fig. 4).

397

398 Oberwimmer (1898) was the first to suggest that heteropods, like pteropods, lived at
399 depth during daylight hours and migrated to the surface during darkness. Larval
400 atlantids appear to show the most consistent nocturnal migration patterns (Richter,
401 1973; Seapy & Richter, 1993) and Richter (1973) suggested that the numbers of
402 migrating larvae are likely to be much higher than the numbers of migrating adults.
403 Seapy & Richter (1993) found that larval atlantids migrate in large groups and cover
404 large vertical distances of up to 300 m. Larval atlantids display particular patterns of
405 migration (Fig. 4) with species-specific timing. Generally sunset is followed by high
406 numbers in the surface waters for around 2 h, much lower numbers for a further 2 h,
407 then an increase to a maximum and finally dropping before sunrise (Seapy & Richter,

408 1993). Oberwimmer (1898) also observed two periods of high abundance (18:45–
409 20:45 and 03:45–05:30), separated by a period of low abundance. Seapy & Richter
410 (1993) hypothesized that the feeding behaviour of larval atlantids causes them to
411 migrate in a ‘saw-tooth’ path. Ciliary movements of the velum propel the larvae, thus
412 they must feed as they swim upwards. The larvae alternately feed and rest, which
413 translates to alternating periods of upward swimming and passive sinking.

414

415 Large-sized (shell 6–12 mm) species that reside at greater depths (200–250 m) have
416 also been found to migrate towards the surface during the night (Fig. 3), including *A.*
417 *peronii* (Seapy, 1990b; Michael & Michael, 1991), *Oxygyrus inflatus* (Ossenbrügger,
418 2010) and *A. meteori* (Seapy, 1990b). Lalli & Gilmer (1989) suggested that, similar to
419 the larvae, adults move in a saw-tooth path, swimming upwards for a brief period and
420 then sinking a few centimetres. It is only during the sinking period that the adult
421 atlantids use their scanning eye movements, which detect objects (prey or predators)
422 within the water. Seapy (1990b) and Lalli & Gilmer (1989) proposed that atlantids
423 probably use their large, elaborate eyes to detect prey in low light conditions at night
424 and may feed on bioluminescent prey. Richter (1974) found that species with larger
425 eyes tend to dwell deeper than species with smaller eyes, probably connected with the
426 reduction in light with depth.

427

428 In contrast, *in-situ* observations of *O. inflatus* found it to be inactive at night, hanging
429 motionless from strands of mucus, probably produced by the foot (Lalli & Gilmer,
430 1989). Newman (1990a) also observed individuals of *A. gaudichaudi* suspended in the
431 water by mucous threads attached to the aperture or the foot. This, however, may not
432 be a sign of inactivity, but a technique for detecting prey, because this behaviour is
433 well suited to predators that use downwelling sunlight to locate prey and then pursue
434 it. Newman (1990a) observed in the laboratory that *A. gaudichaudi* often swam
435 upwards, hitting the water surface with the proboscis and ‘attaching’ for a few
436 minutes. The function of this behaviour is not known.

437

438 Environmental factors such as seasonality have also been found to affect vertical
439 migration behaviour. Seapy (2008) found that a number of Hawaiian atlantids
440 (including *Protatlanta souleyeti*, *A. turriculata*, *A. meteori*, *A. peronii* and *A.*
441 *helicinoidea*) only showed nocturnal migration during part of the year. Similarly,

442 Vives (1966) reported an increase in the vertical stratification of *A. helicinoidea* (but
443 not *A. peroni*) during the summer months off northwestern Spain. Lemus-Santana *et*
444 *al.* (2014) found that *A. selvagensis* and *A. gaudichaudi* show increased nocturnal
445 abundances in May and November, respectively.

446

447 Seapy (1990b) found no difference between the numbers of small (shell 1.5–4 mm)
448 atlantid species captured during the day and at night, when using a large 4-m² tow net.
449 From this, it was suggested that small species do not exhibit diel migration and that
450 the apparent migrations of some others may be an artefact of daytime net avoidance
451 (Fig. 4). Similarly, Ossenbrügger (2010) reported species of *Atlanta* to be equally
452 abundant during day and night off the Cape Verde Islands. Seapy (1990b) observed
453 that non-migrating atlantids off Hawaii tended to be the smaller species that reside in
454 shallower waters (<140 m), as supported by *in-situ* observations of shallow-water
455 species (Lalli & Gilmer, 1989).

456

457 From this collated information, it is clear that the vertical migrations of atlantids are
458 complex, being seasonal, specific to stage and species, and also influenced by
459 sampling method. The difficulty in comparing published data is not surprising, taking
460 into account the challenges encountered in collecting representative samples, of
461 observing specimens *in situ* and the unfeasibility of keeping and accurately observing
462 specimens in the laboratory. It is likely that new methods of observing (e.g. *in-situ*
463 ROV and scuba observations) and sampling are needed to understand this
464 complicated behaviour fully.

465

466 ***Trophic relationships***

467 Atlantids are carnivores and are known to prey selectively upon pteropods, other
468 heteropods and copepods (Richter, 1982; Newman, 1990a). This selective predation
469 makes atlantids an important component of the ocean foodweb (Thiriôt-Quévieux,
470 1973). The long proboscis suggests that they are adapted to preying on shelled
471 organisms and they have been observed using their proboscis to reach into elongate
472 pteropod shells (Newman, 1990a). However, the Late Pleistocene to Recent fossil
473 record from the Caribbean Sea suggests that pteropods are not the preferred prey of
474 atlantids. Wall-Palmer *et al.* (in press) found significant negative correlations between
475 the abundance of shelled pteropods and atlantids, suggesting that atlantids were

476 successful at times when pteropods were not (and *vice versa*). This indicates that
477 shelled pteropods are unlikely to be the preferred prey. Noncalcifying zooplankton
478 (such as copepods), which did not leave a fossil record, may be a more likely
479 favoured food source (Wall-Palmer *et al.*, in press). Frontier (1973) reported juveniles
480 of *A. gaudichaudi* at their highest abundance when phytoplankton and phytophagic
481 zooplankton were also at their greatest abundance, which suggests that juvenile
482 atlantids depend upon such prey.

483

484 Atlantids use their specialized scanning eyes (Land, 1982) to detect prey and then
485 snare it using both their sucker fin and hooked protrusible radula (Lalli & Gilmer,
486 1989; Newman, 1990a). They differ from the other heteropod families in their feeding
487 behaviour, scraping and rasping their prey rather than swallowing it whole (Richter,
488 1968).

489

490 While currently there are not any studies quantifying the importance of atlantids in the
491 ocean foodweb, they have been found in the stomach contents of commercially fished
492 species, including dolphin-fish, for which *O. inflatus* is the favoured prey of immature
493 adults (Richter, 1982), spiny lobsters (Wang *et al.*, 2014), bluefin tuna (Dragovich,
494 1970) and Pacific salmon (Nomura & Davis, 2005). In the East China Sea there is a
495 link between high abundances of atlantids and the migration routes of mackerel,
496 suggesting that atlantids are important to fisheries in the area (Xu & Li, 2005). In a
497 study of the stomach contents of longnose lancetfish in the Central Pacific, Moteki *et al.*
498 (1993) reported heteropods (15.45% of prey individuals) to be the third most
499 important prey after crustaceans and fish. Of these, the atlantids (*Atlanta* sp. and *O.*
500 *inflatus*) made up 0.59% of the total prey individuals, which is comparable with the
501 number of pteropods found (0.76%). While atlantids are known to be an important
502 food source for planktivorous reef fish, they may also act as vectors of dinoflagellate
503 toxins and as hosts of parasites detrimental to commercially important species of fish
504 (Newman, 1990b).

505

506

BIOGEOGRAPHY

507

508 With the caveats that there are still large areas of the oceans for which no data are
509 available and that species identification can be subjective, available data (Fig. 5)

510 largely support a warm-water distribution of atlantids as indicated by Thiriot-
511 Quiévreux (1973), de Vera & Seapy (2006) and de Vera *et al.* (2006). No detailed
512 biogeographical data were found for *Atlanta fragilis* (Richter, 1993; Seapy, 2011).
513 Most species live mainly in the circumglobal warm-water region (Figs 5, 6), although
514 around two-thirds show rare occurrences within transitional zones and cold-water
515 regions.

516

517 Although there are few records of atlantids living in cold-water regions (Fig. 5), the
518 Late Pleistocene fossil record demonstrates that they can be common in cold waters
519 (Wall-Palmer *et al.*, 2014). During the LGM in the Mediterranean Sea, when sea
520 surface temperatures were 7–10 °C (Sbaffi *et al.*, 2001; Hayes *et al.*, 2005), atlantids
521 accounted for up to 17% of holoplanktic gastropod individuals (Wall-Palmer *et al.*,
522 2014). Howard *et al.* (2011) identified a small number (13 individuals at two stations)
523 of *Atlanta gaudichaudi* (Fig. 5) from vertical net hauls south of Tasmania, just within
524 the Subantarctic zone of the Southern Ocean (furthest south 44°53'S, 142°59'E).
525 Atlantids have been found in this region during consecutive years (D. Roberts, pers.
526 comm., July 2013), indicating that this is likely to be a longterm population.
527 Pilkington (1970) also found heteropods, identified as *A. helicinoidea*, to be common
528 and even abundant in plankton hauls off Taiaroa Head, New Zealand (45°46'12"S,
529 170°53'24"E). Vane (1961) and Vane & Colebrook (1962) discovered a number of
530 atlantid species living off the west coast of the British Isles during the summer
531 months, up to 57°N, but only identified *A. peronii* to species level.

532

533 *Atlanta californiensis* is thought to prefer colder waters, being largely restricted to the
534 cold California Current, from southern California to British Columbia (Seapy &
535 Richter, 1993; Cummings & Seapy, 2003). However, Moreno-Alcántara *et al.* (2014)
536 recently found that *A. californiensis* also lives in the warmer waters of the Pacific
537 Ocean off southern Mexico, suggesting a tolerance to a wide range of surface water
538 conditions.

539

540 From the collated data (Fig. 5) it is not possible to determine temperature ranges for
541 each species, but some geographical patterns can be seen. Nearly half of the species
542 (*A. brunnea*, *A. gaudichaudi*, *A. helicinoidea*, *A. inclinata*, *A. lesueurii*, *A. meteori*, *A.*
543 *peronii*, *Oxygyrus inflatus* and *Protatlanta souleyeti*) show a cosmopolitan, global

544 distribution, occurring in the Atlantic, Indian and Pacific Oceans. The majority of the
545 species (11 of 21) show a more restricted distribution and nine of these have not been
546 recorded from the Atlantic Ocean, although some rare species, such as *A. rosea* and *A.*
547 *tokiokai*, are likely to have a wider distribution than the data indicate.

548

549 The most restricted distribution is displayed by *A. californiensis*, which has only been
550 reported along the west coast of North America, from Mexico to British Columbia
551 (Fig. 5). However, this species has only recently been described and its occurrence
552 may not have been identified in earlier studies (Seapy & Richter, 1993). A second
553 species with a very restricted distribution, *A. fragilis*, has only been found in the
554 tropical waters of the central Atlantic Ocean (Richter, 1993; Seapy, 2011). A species
555 of thecosome pteropod, *Cuvierina cancapae*, is also known to be confined to the
556 tropical Atlantic Ocean (Burrige *et al.*, 2015), so *A. fragilis* may genuinely be
557 confined to this small geographical area. However, *A. fragilis* has very similar
558 morphological features to *A. peronii* and may have been misidentified elsewhere.

559

560 The occurrence of the most recently described species, *A. selvagensis*, was believed to
561 be restricted to the eastern Atlantic Ocean. However, in a recent review of *A. inflata*
562 and *A. selvagensis*, two species with similar shell morphology, Janssen & Seapy
563 (2009) showed that *A. inflata* is restricted to the Pacific Ocean, while all specimens
564 previously identified as *A. inflata* in the Atlantic and Indian Oceans are *A.*
565 *selvagensis*, thus broadening the range of the latter. In addition to the tropical and
566 subtropical distribution described by Seapy (2011) for these two species, they are also
567 found within cooler transitional waters (Figs 5, 6).

568

569 The remaining species, *A. turriculata*, *A. frontieri*, *A. echinogyra*, *A. gibbosa* and *A.*
570 *plana* have been reported only in the Indian and Pacific Oceans (Fig. 4). *Atlanta*
571 *oligogyra* was previously thought to have a global distribution, but the data show that
572 it is also restricted to Indo-Pacific waters.

573

574 ***Shelf vs open ocean***

575 There are a number of conflicting findings on the preference of atlantids for onshore
576 (neritic) and offshore (oceanic) waters. While some studies have found no preference
577 (Frontier, 1973a, b; Mathew *et al.*, 1990), most have shown a difference between the

578 abundances of atlantids in neritic and oceanic waters. Frontier (1966, 1973a, b) found
579 that although adult *A. gaudichaudi* showed no preference of water depth, the more
580 abundant juveniles preferred neritic waters and that, as a result, species richness and
581 abundances generally decreased from the shelf to the open ocean. This trend was also
582 reported by Van der Spoel (1996), who suggested that heteropods avoid the central
583 areas of oceans. However, a number of studies have revealed the opposite trend, with
584 increased abundance in oceanic waters. Seapy (2008) showed heteropods to be
585 consistently more abundant at offshore stations (up to 15 nmi from the coast) than
586 more coastal stations (less than 1 nmi) in southwest Oahu, Hawaii. Similarly,
587 Ossenbrügger (2010) found heteropod abundances to be higher in the open ocean than
588 on the flanks of a seamount in the Cape Verde Islands. Grice & Hart (1962) reported
589 atlantids to be almost absent from coastal waters in the eastern Atlantic, with only a
590 single species (*P. souleyeti*) in the neritic zone and 11 heteropod species in the
591 oceanic Gulf Stream and Sargasso Sea. To the west of the British Isles *A. peronii*
592 generally inhabits offshore waters over 180 m (Vane, 1961). These varying trends
593 may be due to onshore and offshore currents, which strongly influence the position
594 and abundance of atlantids. There could also be stage- and species-specific
595 preferences for water depth. For instance, Newman (1990a) found veligers of *A.*
596 *gaudichaudi* to be more abundant closer to the shore, whereas adults of the same
597 species showed a preference for the deeper, open ocean.

598

599 In summary, the overall geographical area sampled for atlantids is still relatively
600 small and much research is still required on atlantid biogeography. Data are currently
601 not available for large areas of the southern Atlantic Ocean, southern Indian Ocean
602 and much of the Pacific Ocean. There are also very few records for subpolar and polar
603 waters (which may be because atlantids do not live in these areas). Most species have
604 geographically restricted distributions, so it is important that all areas of the ocean are
605 sampled. Improved sampling techniques and species identification will also reveal
606 more accurate distributions.

607

608

NEXT STEPS

609

610 We suggest that the most pressing needs in atlantid research are in the basic, but
611 fundamental areas of taxonomy, sampling techniques, vertical distributions and

612 biogeography. Understanding these key areas will facilitate subsequent research on
613 the response of atlantids to environmental changes, the importance of atlantids in the
614 ocean foodweb and their significance to commercially fished species.

615

616 The improvement and updating of atlantid taxonomy is the most important priority.
617 The development of combined molecular and morphological identification (e.g.
618 Burrige *et al.*, 2015) will improve the quantity and quality of data on atlantids. In
619 addition to the detailed scanning electron microscopy images of atlantids that are
620 already available (e.g. Seapy, 2011; Janssen, 2012c), new methods should be
621 considered, such as microCT imaging, which allows interactive examination of virtual
622 specimens. Advances in DNA barcoding and application of molecular methods for
623 identifying species boundaries are also extremely important for improving atlantid
624 taxonomy, to determine whether morphological variations indicate different species
625 or variation within a species.

626

627 The second priority for future research is the improvement of sampling techniques.
628 The use of larger-aperture nets reduces net-avoiding behaviour (McGowan &
629 Fraundorf, 1966; Seapy, 1990a). Capture of atlantids will also be improved by
630 adopting techniques used to catch small, fast-swimming fish (such as using slightly
631 larger-mesh nets, up to 500 μm), sampling with horizontal net tows rather than
632 vertical net hauls and by using faster towing speeds.

633

634 Determining the geographic ranges, depth distributions and migration behaviour of
635 atlantids should also be considered as an important part of improving sampling
636 techniques, so that nets can more accurately target the optimum depth and time of
637 day. Discovering the vertical distribution of atlantids will involve a combination of
638 stratified net collections, shell geochemistry and field observations. Knowledge of the
639 biogeography, vertical distributions and migration behaviour of atlantids is also
640 crucial to understanding their environmental requirements. This information will be
641 fundamental to predicting how atlantids will be affected by global environmental
642 changes. For example, it has been suggested that shelled pteropods that exhibit diel
643 migration may be more resistant to the effects of ocean acidification (Maas *et al.*,
644 2012) and this could also be true of atlantids. New information of ecology and
645 biogeography will also improve our interpretation of the rich fossil record of atlantids,

646 providing insights into their evolutionary history and past responses to global
647 changes.

648

649

650

ACKNOWLEDGEMENTS

651

652 We thank the National Marine Biological Library, Plymouth for assistance with
653 historical publications, Donna Roberts for discussion about atlantids in the Southern
654 Ocean and Alice K. Burridge for discussion about the proportion of atlantids in
655 zooplankton samples collected during AMT24. We acknowledge the scientists and
656 crew that took part in the 2012 and 2014 Atlantic Meridional Transect cruises
657 (AMT22 and AMT24) onboard the R/V *James Cook*. We are extremely grateful to
658 Jeremy Young, Fred Wells, an anonymous reviewer and David Reid for constructive
659 comments on our manuscript. DW-P, CS and RK were funded by the Leverhulme
660 Trust (RPG-2013-363, 2014-2017), DW-P also received funding from the Naturalis
661 Biodiversity Center Martin-fellowship (2015).

662

663

REFERENCES

664

665 ANGULO-CAMPILLO, O., ACEVES-MEDINA, G. & AVEDAÑO-IBARRA, R.
666 2011. Holoplanktonic mollusks (Mollusca: Gastropoda) from the Gulf of California,
667 México. *Check List*, **7**: 337–342.

668

669 ARAVINDAKSHAN, P.N. & STEPHEN, R. 1996. Composition of heteropods in the
670 Andaman Sea. *Proceedings of the Second Workshop on Scientific Results of FORV*
671 *Sagar Sampada*, 193–196.

672

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

676

677 AYÓN, P., CRIALES-HERNANDEZ, M.I., SCHWAMBORN, R. & HIRCHE, H.-J.
678 2008. Zooplankton research off Peru: a review. *Progress in Oceanography*, **79**: 238–
679 255.

680

681 BEDNARŠEK, N., FEELY, R.A., REUM, J.C.P., PETERSON, B., MENKEL, J.,
682 ALIN, S.R., & HALES, B. 2014. *Limacina helicina* shell dissolution as an indicator
683 of declining habitat suitability owing to ocean acidification in the California Current
684 Ecosystem. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**:
685 20140123.

686

687 BENSON, W.H. 1835. Account of *Oxygyrus*; a new genus of pelagian shells allied to
688 the genus *Atlanta* of Lesueur, with a note on some other pelagian shells lately taken
689 on board the ship Malcolm. *Journal of the Asiatic Society of Bengal*, **4**: 173–176.

690

691 BERGGREN, W.A. 1993. Neogene planktonic foraminiferal biostratigraphy of
692 eastern Jamaica. In: *Biostratigraphy of Jamaica* (R.M. Wright & E. Robinson, eds),
693 pp. 179–217. *Geological Society of America Memoir*, **182**.

694

695 BONNEVIE, K.R. 1920. Heteropoda. *Reports of Scientific Research, Michael Sars*
696 *North Atlantic Deep-Sea Expedition 1910, Zoology*, **3**: 3–16.

697

698 BURRIDGE, A.K., GOETZE, E., RAES, N., HUISMAN, J. & PEIJNENBURG,
699 K.T.C.A. 2015. Global biogeography and evolution of *Cuvierina* pteropods. *BMC*
700 *Evolutionary Biology*, **15**: 39.

701

702 CASTELLANOS, I. & SUAREZ-MORALES, E. 2001. Heteropod molluscs
703 (Carinariidae and Pterotracheidae) of the Gulf of Mexico and the western Caribbean
704 Sea. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México,*
705 *Serie Zoología*, **72**: 221–232.

706

707 ÇEVIK, C., KIDEYS, A., TOKLU, B., ERGÜDEN, D. & SARIHAN. 2006. New
708 pelagic Gastropoda species encountered on the Turkish coast of the Levant Sea.
709 *Turkish Journal of Veterinary and Animal Sciences*, **30**: 151–157.

710

711 [CHILDREN, J.G.] 1824. Lamarck's genera of shells. *Quarterly Journal of Science,*
712 *Literature, and Arts*, **15**: 216–258.

713

714 COMEAU, S., ALLIOUANE, S., & GATTUSO, J. P. 2012. Effects of ocean
715 acidification on overwintering juvenile Arctic pteropods *Limacina helicina*. *Marine*
716 *Ecology Progress Series*, **456**: 279–284.

717

718 COSSMANN, M. 1889. Catalogue illustré des coquilles fossiles de l'Éocène des
719 environs de Paris 4. *Annales de la Société Royale Malacologique de Belgique*, **24**: 3–
720 385.

721

722 CRUZ, M. 1996. Pteropodos tecosomados y heteropodos (Gasterópodos) como
723 bioindicadores del evento 'El Niño' 1992, en la estación fija 'La Libertad', Ecuador.
724 *Acta Oceanográfica del Pacífico*, **8**: 51–66.

725

726 CRUZ, M. 1998. Gasterópodos planctónicos (pterópodos y heterópodos) como
727 bioindicadores de los eventos 'El Niño' 1992 y 1997–1998 en la estación fija 'La
728 Libertad', Ecuador. *Acta Oceanográfica del Pacífico*, **9**: 129–144.

729

730 CRUZ, M. 2012. Preferencia y rangos de tolerancia a la temperatura y salinidad de los
731 pterópodos y heterópodos frente a la Costa Ecuatoriana. *Acta Oceanográfica del*
732 *Pacífico*, **17**: 93–125.

733

734 CUMMINGS, F.A. & SEAPY, R.R. 2003. Seasonal abundances of euthecosomatous
735 pteropods and heteropods from waters overlying San Pedro Basin, California. *Veliger*,
736 **46**: 305–313.

737

738 CUVIER, G.L.C.F.D. 1836. *Le règne animal distribué d'après son organisation*, vol.
739 2. Hauman, Brussels.

740

741 DI GERONIMO, I. 1974. Molluschi pelagici in livelli di marne mioceniche presso
742 Vetto (R. Emilia). *Conchiglie*, **10**: 181–192.

743

744 DRAGOVICH, A. 1970. The food of bluefin tuna (*Thunnus thynnus*) in the western
745 North Atlantic Ocean. *Transactions of the American Fisheries Society*, **99**: 726–731.

746

747 EVANS, F. 1968. Le zooplancton de Malte. *Pelagos*, **9**: 5–20.

748

749 EYDOUX, J.F.T. & SOULEYET, L.F.A. 1841 (?). Voyage autour du monde executé
750 pendant les années 1836 et 1837 sur la corvette ‘La Bonite’ Histoire Naturelle,
751 Zoologie. Atlas. Paris.(for publication date see Janssen & Seapy, 2009 : 156).

752

753 FORBES, E. 1844. Report on the Mollusca and Radiata of the Aegean Sea, and on
754 their distribution, considered as bearing on geology. *Reports of the British Association*
755 *for the Advancement of Science*, **1843**: 130–193.

756

757

758 FRONTIER, S. 1966. Notes morphologiques sur les *Atlanta* récoltées dans le
759 plancton de Nosy-Bé (Madagascar). *Cahiers ORSTOM Oceanographie*, **4**: 131–139.

760

761 FRONTIER, S. 1973a. Zooplancton de la région de Nosy-Bé VII Ptéropodes,
762 Hétéropodes—deuxième partie: espèces néritiques-externes et océaniques tolérantes.
763 *Cahiers ORSTOM Oceanographie*, **11**: 291–302.

764

765 FRONTIER, S. 1973b. Zooplancton de la région de Nosy-Bé VI Ptéropodes,
766 Hétéropodes—première partie: espèces holonéritiques et néritiques-internes. *Cahiers*
767 *ORSTOM Oceanographie*, **11**: 273–289.

768

769 FURNESTIN, M.-L. 1961. Pteropodes et heteropods du plankton Marocain. *Revue*
770 *des Travaux de l'Institut des Peches Maritimes*, **25**: 293–326.

771

772 GABB, W.M. 1873. On the topography and geology of Santo Domingo. *Transactions*
773 *of the American Philosophical Society*, **15**: 49–259.

774

775 GOFAS, S. 2015a. Pterotracheoidea Rafinesque, 1814. In: *MolluscaBase (2015)*.
776 Accessed through: World Register of Marine Species at
777 <http://www.marinespecies.org/aphia.php?p=taxdetails&id=387338> on 2015-10-27

778

779 GOFAS, S. 2015b. Atlantidae Rang, 1829. In: *MolluscaBase (2015)*. Accessed
780 through: World Register of Marine Species at
781 <http://www.marinespecies.org/aphia.php?p=taxdetails&id=22990> on 2015-10-09

782
783 GONZÁLEZ, N.E. 1998. Mollusks of the expedition of R/V *Edwin Link* on the shores
784 of Mexican Caribbean. *Revista de Biología Tropical*, **46**: 625–631.
785
786 GOUGEROT, L. & BRAILLON, J. 1965. Découverte d'une nouvelle espèce
787 d'*Atlanta* (hétéropode) dans le Bartonien de Barisseuse (Oise). *Bulletin de la Société*
788 *Géologique de France*, **7**: 302–303.
789
790 GRAY, J.E., 1850. Explanation of plates. In: *Figures of molluscos animals*, Vol. 4
791 (M.E. Gray, ed.), pp. 1–124. London.
792
793 GRICE, G.D. & HART, A.D. 1962. The abundance, seasonal occurrence and
794 distribution of the epizooplankton between New York and Bermuda. *Ecological*
795 *Monographs*, **32**: 287–309.
796
797 GROSSMAN, E.L., BETZER, P.R., DUDLEY, W.C. & DUNBAR, R.B. 1986.
798 Stable isotopic variation in pteropods and atlantids from north Pacific sediment traps.
799 *Marine Micropaleontology*, **10**: 9–22.
800
801 HAYES, A., KUCERA, M., KALLEL, N., SBAFFI, L. & ROHLING, E. J. 2005.
802 Glacial Mediterranean Sea surface temperatures based on planktonic foraminiferal
803 assemblages. *Quaternary Science Reviews*, **24**: 999–1016.
804
805 HERNÁNDEZ, M.P., FERRANDIS, E. & LOZANO SOLDEVILLA, F. 1993.
806 Pteropoda Thecosomata y Heteropoda (Mollusca, Gastropoda) en aguas del
807 archipiélago canario. *Boletín del Instituto Español de Oceanografía*, **9**: 263–283.
808
809 HOWARD, W.R., ROBERTS, D., MOY, A.D., LINDSAY, M.C.M., HOPCROFT,
810 R.R., TRULL, T.W. & BRAY, S.G. 2011. Distribution, abundance and seasonal flux
811 of pteropods in the Sub-Antarctic Zone. *Deep-Sea Research II*, **58**: 2293–2300.
812
813 JAMIESON, B.G.M. & NEWMAN, L.J. 1989. The phylogenetic position of the
814 heteropod *Atlanta gaudichaudi* Souleyet (Mollusca, Gastropoda), a spermatological
815 investigation. *Zoologica Scripta*, **18**: 269–278.

816

817 JANSSEN, A.W. 1995. Sytematic revision of holoplanktonic Mollusca in the
818 collections of the Dipartimento di Scienze della Terra at Torino, Italy. *Museo*
819 *Regionale di Sienze Naturali Torino, Monografie*, **17**: 1–233.

820

821 JANSSEN, A.W. 1998. Holoplanktonic Mollusca (Gastropoda: Heteropoda and
822 Thecosomata) from the Pliocene Bowden Beds, Jamaica. *Contributions to Tertiary and*
823 *Quaternary Geology*, **35**: 95–111.

824

825 JANSSEN, A.W. 1999. Neogene paleontology in the northern Dominican Republic,
826 20. Holoplanktonic mollusks (Gastropoda: Heteropoda and Thecosomata). *Bulletins*
827 *of American Paleontology*, **358**: 5–40.

828

829 JANSSEN, A.W. 2004. Holoplanktonic molluscan assemblages (Gastropoda,
830 Heteropoda, Thecosomata) from the Pliocene of Estepona (Spain, Málaga). *Palaeontos*
831 **5**: 103–131.

832

833 JANSSEN, A.W. 2007. Holoplanktonic Mollusca (Gastropoda: Pterotracheoidea,
834 Janthinoidea, Thecosomata and Gymnosomata) from the Pliocene of Pangasinan
835 (Luzon, Phillipines). *Scripta Geologica*, **135**: 29–177.

836

837 JANSSEN, A.W. 2012a. Systematics and biostratigraphy of holoplanktonic mollusca
838 from the Oligo-Miocene of the Maltese Archipelago. *Museo Regionale di Scienze*
839 *Naturali Torino, Bullettino*, **28**: 191–601.

840

841 JANSSEN, A.W. 2012b. Early Pliocene heteropods and pteropods (Mollusca,
842 Gastropoda) from Le Puget-sur-Argens (Var), France. *Cainozoic Research*, **9**: 145–
843 187.

844

845 JANSSEN, A.W., 2012c. Late Quaternary to Recent holoplanktonic Mollusca
846 (Gastropoda) from bottom samples of the eastern Mediterranean Sea: systematics,
847 morphology. *Bollettino Malacologico*, **48** suppl.: 1–105.

848

849 JANSSEN, A.W. & GREBNEFF, A. 2012. Notes on the systematics, morphology and
850 biostratigraphy of fossil holoplanktonic Mollusca, 22. Further pelagic gastropods
851 from Viti Levu, Fiji Archipelago. *Basteria*, **76**: 15–30.
852

853 JANSSEN, A.W. & LITTLE, C.T.S. 2010. Holoplanktonic gastropoda (Mollusca)
854 from the Miocene of Cyprus: systematics and biostratigraphy. *Palaeontology*, **53**:
855 1111–1145.
856

857 JANSSEN, A.W. & PEIJNENBURG, K.T.C.A. 2014. Holoplanktonic Mollusca:
858 Development in the Mediterranean Basin during the last 30 million years and their
859 future. In: *The Mediterranean Sea* (S. Goffredo & Z. Dubinsky, eds), pp. 341–362.
860 Springer, The Netherlands.
861

862 JANSSEN, A.W. & SEAPY, R.R. 2009. On the identity and distribution of *Atlanta*
863 *inflata* Gray, 1850 (Gastropoda, Pterotracheoidea, Atlantidae) in the world's oceans.
864 *Basteria*, **73**: 139–157.
865

866 JENNINGS, R.M., BUCKLIN, A., OSSENBRÜGGER, H. & HOPCROFT, R.R.
867 2010. Species diversity of planktonic gastropods (Pteropoda and Heteropoda) from
868 six ocean regions based on DNA barcode analysis. *Deep-Sea Research*, **57**: 2199–
869 2210.
870

871 JIVALUK, J. 1998. Distribution, abundance and composition of zooplankton in the
872 South China Sea, Area II: Sabah, Sarawak and Brunei Darussalam waters.
873 *Proceedings of the Second Technical Seminar on Marine Fishery Resources Survey in*
874 *the South China Sea, Kuala Lumpur, Malaysia*, 288–309.
875

876 LALLI, C.M. & GILMER, R.W. 1989. *Pelagic snails: the biology of holoplanktonic*
877 *mollusks*. Stanford University Press, California.
878

879 LAMARCK, J.B.P.A. 1812. *Extrait du cours de zoologie du Muséum d'Histoire*
880 *Naturelle sur les animaux sans vertèbres (Mollusques, Hétéropodes)*. d'Hantel et
881 Gabon, Paris.
882

883 LAND, M.F. 1982. Scanning eye movements in a heteropod mollusc. *Journal of*
884 *Experimental Biology*, **96**: 427–430.
885

886 LEMUS-SANTANA, E., SANVICENTE-AÑORVE, L., HERMOSO-SALAZAR, M.
887 & FLORES-COTO, C. 2014. The holoplanktonic Mollusca from the southern Gulf of
888 Mexico. Part 1: Heteropods. *Cahiers de Biologie Marine*, **55**: 229–239.
889

890 LESUEUR, C.A. 1817. Mémoire sur deux nouveaux genres de mollusques, Atlante et
891 Atlas. *Journal de Physique, de Chimie, et d'Histoire Naturelle*, **85**: 390–393.
892

893 LOZANO SOLDEVILLA, F. & HERNÁNDEZ HERNÁNDEZ, P. 1991. Preliminary
894 list of zooplankton of the Canary Islands. II Siphoniphora, Pteropoda, Heteropoda,
895 Ostracoda, Amphipoda and Decapoda. *Boletín do Museu Municipal do Funchal*, **43**:
896 149–158.
897

898 LOZOUET, P. 2012. Position systématique de quelques gastéropodes de l'Éocène à
899 dernier tour disjoint (Mollusca, Gastropoda, Caenogastropoda): *Delphinula conica*,
900 *Omalaxis*, *Eoatlanta*. *Cossmanniana*, **14**: 57–66.
901

902 MAAS, A.E., WISHNER, K.F. & SEIBEL, B.A. 2012. The metabolic response of
903 pteropods to acidification reflects natural CO₂-exposure in oxygen minimum zones.
904 *Biogeosciences*, **9**: 747–757.
905

906 MARTOJA, M & THIRIOT- QUIÉVREUX, C. 1975. Données histologiques sur
907 l'appareil digestif et la digestion des Atlantidae (Prosobranchia: Heteropoda).
908 *Malacologia*, **15**: 1–27.
909

910 MATHEW, K.J., NAOMI, T.S., ANTONY, G. & SOLOMON, K. 1990. Distribution
911 and abundance of pteropod and heteropod molluscs in the EEZ and adjoining waters
912 of India. *Proceedings of the First Workshop on Scientific Results of FORV Sagar*
913 *Sampada*, 155–163.
914

915 McGOWAN, J.A. & FRAUNDORF, V.J. 1966. The relationship between size of net
916 used and estimates of zooplankton diversity. *Limnology and Oceanography*, **11**: 456–
917 469.

918

919 MICHEL, H.B. & MICHEL, J.F. 1991. Heteropod and thecosome (Mollusca:
920 Gastropoda) macroplankton in the Florida Straits. *Bulletin of Marine Science*, **49**:
921 562–574.

922

923 MORENO-ALCÁNTARA, M., ACEVES-MEDINA, G., ANGULO-CAMPILLO, O.
924 & MURAD-SERRANO, J.P. 2014. Holoplanktonic molluscs (Gastropoda :
925 Pterotracheoidea, Thecosomata and Gymnosomata) from the southern Mexican
926 Pacific. *Journal of Molluscan Studies*, **80**: 131–138.

927

928 MOTEKI, M., FUJITA, K. & KOHNO, H. 1993. Stomach contents of longnose
929 lancetfish, *Alepisaurus ferox*, in Hawaiian and central equatorial Pacific waters.
930 *Journal of Tokyo University of Fisheries*, **80**: 121–137.

931

932 NEWMAN, L.J. 1990a. The taxonomy, distribution and biology of *Atlanta*
933 *gaudichaudi* Souleyet, 1952 (Gastropoda, Heteropoda) from the Great Barrier Reef,
934 Australia. *American Malacological Bulletin*, **8**: 85–94.

935

936 NEWMAN, L.J. 1990b. *Holoplanktonic molluscs (Gastropoda; Thecosomata,*
937 *Gymnosomata and Heteropoda) from the waters of Australia and Papua New Guinea:*
938 *their taxonomy, distribution and biology*. PhD thesis, University of Queensland.

939

940 NIEBUHR, C. 1775. *Descriptiones animalium avium, amphibiorum, piscium,*
941 *insectorum, vermium; quae in itinere orientali observavit Petrus Forskål.* Möller,
942 Havniae.

943

944 NOMURA, T. & DAVIS, N.D. 2005. Lipid and moisture content of salmon prey
945 organisms and stomach contents of chum, pink and sockeye salmon in the Bering Sea.
946 *NPAFC Technical Report*, **6**: 59–61.

947

948 OBERWIMMER, A. 1898. Zoologische Ergebnisse 10; Mollusken 2. Heteropoden
949 und Pteropoden, *Simusigera*, gesammelt von S.M. Schiff 'Pola' 1890–1894.
950 *Denkschriften der kaiserlichen Akademie der Wissenschaften, Wien; mathematisch-*
951 *naturwissenschaftliche Classe*, **65**: 573–594.

952

953 OHMAN, M.D., LAVANIEGOS, B.E. & TOWNSEND, A.W. 2009. Multi-decadal
954 variations in calcareous holozooplankton in the California Current system:
955 Thecosome pteropods, heteropods and foraminifera. *Geophysical Research Letters*,
956 **36**: L18608, doi:10.1029/2009GL039901.

957

958 OLIVER, M.J. & IRWIN, A.J. 2008. Objective global ocean biogeographic
959 provinces. *Geophysical Research Letters*, **35** : L15601, doi :10.1029/2008GL034238.

960

961 ORBIGNY, A. D'. 1834-1847. *Voyage dans l'Amérique méridionale*. P. Bertrand,
962 Paris. (for publication date see Sherborn & Griffin, 1934).

963

964 OSSENBRÜGGER, H. 2010. *Distribution patterns of pelagic gastropods at the Cape*
965 *Verde Islands*. Semester thesis, Helmholtz Centre for Ocean Research, Kiel.

966

967 PAULINOSE, V.T., GOPALAKRISHNAN, T.C., NAIR, K.K.C. &
968 ARAVINDAKSHAN, P.N. 1992. Stratification of zooplankton in the northwestern
969 Indian Ocean. In: *Oceanography of the Indian Ocean* (B.N. Desai, ed.), pp. 113–120.
970 Oxford and IBH, New Delhi.

971

972 PILKINGTON, M.C. 1970. Young stages and metamorphosis in an atlantid heteropod
973 occurring off south-eastern New Zealand. *Proceedings of the Malacological Society*
974 *of London*, **39**: 117–124.

975

976 RALPH, P.M. 1957. A guide to the New Zealand heteropod molluscs. *Tuatara*, **6**:
977 116–120.

978

979 RICHTER, G. 1961. Die radula der Atlantiden (Heteropoda, Prosobranchia) und ihre
980 bedeutung für die systematik und evolution der familie. *Zeitschrift für Morphologie*
981 *und Ökologie der Tiere*, **50**: 163–238.

982

983 RICHTER, G. 1968. Heteropoden und Heteropodenlarven im Oberflächen plankton
 984 des Golfs von Neapel. *Pubblicazioni della Stazione Zoologica di Napoli*, **36**: 346–
 985 400.

986

987 RICHTER, G. 1972. Zur Kenntnis der Gattung *Atlanta* (Heteropoda: Atlantidae).
 988 *Archiv für Molluskenkunde*, **102**: 85–91.

989

990 RICHTER, G. 1973. Field and laboratory observations on the diurnal vertical
 991 migration of marine gastropod larvae. *Netherlands Journal of Sea Research*, **7**: 126–
 992 134.

993

994 RICHTER, G. 1974. The heteropods of the Meteor Expedition to the Indian Ocean
 995 1964/65. *'Meteor' Forstungsergebnisse*, **17**: 55–78.

996

997 RICHTER, G. 1982. Mageninhaltuntersuchungen an *Oxygyrus keraudreni* (Lesueur)
 998 (Atlantidae, Heteropoda). Beispiel einer Nahrungskette im tropischen Pelagial.
 999 *Senckenbergiana maritima*, **14**: 47–77.

1000

1001 RICHTER, G. 1993. Zur Kenntnis der Gattung *Atlanta*, 5. Die *Atlanta peroni*-Gruppe
 1002 und *Atlanta gaudichaudi* (Prosobranchia: Heteropoda). *Archiv für Molluskenkunde*,
 1003 **122**: 189–205.

1004

1005 RICHTER, G. & SEAPY, R.S. 1999. Heteropoda. In: *South Atlantic zooplankton* (D.
 1006 Boltovskoy, ed.), pp. 621–647. Backhuys, Leiden.

1007

1008 SÁNCHEZ-HIDALGO Y ANDA, M. 1989. Gasterópodos holoplanctónicos de la
 1009 costa occidental de Baja California Sur, en mayo y junio de 1984. *Investigaciones*
 1010 *Marinas CICIMAR*, **4**: 1–14.

1011

1012 SBAFFI, L., WEZEL, F. C., KALLEL, N., PATERNA, M., CACHO, I., ZIVERI, P.
 1013 & SHACKLETON, N. 2001. Response of the pelagic environment to palaeoclimatic
 1014 changes in the central Mediterranean Sea during the Late Quaternary. *Marine*
 1015 *Geology*, **178**: 39–62.

1016
1017 SCHIEMENZ, P. 1911. *Die Heteropoden der Plankton-Expedition der Humbolt-*
1018 *Stiftung*. Verlag von Lipsius and Tischer, Kiel.
1019
1020 SCHNETLER, K.I. 2013. *Eoatlanta ravni* nov. sp. (Mollusca: Gastropoda,
1021 ?Hipponicidae) from the Danian (early Paleocene) of Faxe, Denmark. *Cainozoic*
1022 *Research*, **10**: 3–7.
1023
1024 SEAPY, R.R. 2008. Offshore-inshore and vertical distribution patterns of heteropod
1025 mollusks off leeward Oahu, Hawaii. *Marine Biology*, **154**: 985–995.
1026
1027 SEAPY, R.R. 1990a. The pelagic family Atlantidae (Gastropoda: Heteropoda) from
1028 Hawaiian waters: a faunistic survey. *Malacologia*, **32**: 107–130.
1029
1030 SEAPY, R.R. 1990b. Patterns of vertical distribution in epipelagic heteropod
1031 molluscs off Hawaii. *Marine Ecology Progress Series*, **60**: 235–246.
1032
1033 SEAPY, R.R. 2011. Atlantidae. In: *Tree of life web project*. Available at
1034 <http://tolweb.org/Atlantidae> accessed 7 April 2015.
1035
1036 SEAPY, R.R., LALLI, C.M. & WELLS, F. 2003. Heteropoda from Western
1037 Australian waters. In: *The marine flora and fauna of Dampier, Western Australia*
1038 (F.E. Wells, D.I. Walker & D.S. Jones, eds), pp. 513–546. Western Australian
1039 Museum, Perth.
1040
1041 SEAPY, R.R. & RICHTER, G. 1993. *Atlanta californiensis*, a new species of atlantid
1042 heteropod (Mollusca: Gastropoda) from the California Current. *Veliger*, **36**: 389–398.
1043
1044 SHERBORN, C.D. & GRIFFIN, F.J. 1934. On the dates of publication of the natural
1045 history portions of Alcide d’Orbigny’s ‘Voyage Amérique Meridionale’. *Annals and*
1046 *Magazine of Natural History*, **13**: 130–134.
1047

- 1048 SHIBATA, H. 1984. Pteropods and heteropods from the Upper Cenozoic of
1049 Kakewaga, Shizuoka Prefecture, Japan. *Bulletin of the Mizunami Fossil Museum*, **11**:
1050 73–91.
1051
- 1052 SHIBATA, H. 2008. Pliocene heteropods (Mollusca: Gastropoda) from Miyag-shima,
1053 Okinawa, Japan. *Scientific Reports of the Toyohashi Museum of Natural History*, **19**:
1054 1–9.
1055
- 1056 SMITH, E.A. 1888. Report on the Heteropoda collected by HMS Challenger during
1057 the years 1873–76. *Challenger Reports, Zoology*, **72**(23): 1–47.
1058
- 1059 SOULEYET, F.L.A. 1852. Hétéropodes. In: *Voyage autour du monde exécuté*
1060 *pendant les années 1836 et 1837 sur la corvette 'La Bonite'*, Vol. 2 Zoologie (F.
1061 Eydoux & F.L.A. Souleyet, eds), pp. 289–392. Bertrand, Paris.
1062
- 1063 SOWERBY, J. 1814. *The mineral conchology of Great Britain*, vol. 1, part 10.
1064 Sowerby, London. Pp. 109–124, pls 51–56.
1065
- 1066 SPOEL, S. VAN DER. 1976. *Pseudothecosomata, Gymnosomata and Heteropoda*
1067 *(Gastropoda)*. Bohn, Scheltema & Holkema, Utrecht.
1068
- 1069 SPOEL, S. VAN DER. 1996. Heteropoda. In: *Introducción al estudio del zooplancton*
1070 *marino* (R. Gasca & E. Suárez-Morales, eds), pp. 407–457. ECOSUR/CONACYT,
1071 Mexico.
1072
- 1073 TAKI, I. & OKUTANI, T. 1962. Reports on the biology of the ‘Umitaka-Maru’
1074 expedition, part 2. *Journal of the Faculty of Fisheries and Animal Husbandry*,
1075 *Hiroshima University*, **4**: 81–97.
1076
- 1077 TESCH, J.J. 1906. Die Heteropoden der Siboga-expedition. *Siboga Reports*, **51**: 1–
1078 112.
1079
- 1080 TESCH, J.J. 1910. Pteropoda and Heteropoda. The Percy Sladen Trust Expedition to
1081 the Indian Ocean, 1905. *Transactions of the Linnean Society of London*, **14**: 165–192.

- 1082
- 1083 TESCH, 1949. Heteropoda. *Dana Report*, **34**: 1–53.
- 1084
- 1085 THIRIOT-QUIÉVREUX, C. 1968. Variations saisonnières des mollusques dans le
1086 plancton de la région de Banyuls-sur-Mer (zone sud de Golfe du Lion) Novembre
1087 1965 – Décembre 1967. *Vie et Milieu*, **19**: 35–83.
- 1088
- 1089 THIRIOT-QUIÉVREUX, C. 1970. Cycles annuels des populations planctoniques de
1090 mollusques en 1968 dans la region de Banyuls-sur-Mer. Comparaison avec les années
1091 précédentes 1965–1967. *Vie et Milieu*, **21** : 311–336.
- 1092
- 1093 THIRIOT-QUIÉVREUX, C. 1973. Heteropoda. *Oceanography and Marine Biology,*
1094 *an Annual Review*, **11**: 237–261.
- 1095
- 1096 THIRIOT-QUIÉVREUX, C. & SEAPY, R.R. 1997. Chromosome studies of three
1097 families of pelagic heteropod molluscs (Atlantidae, Carinariidae, and Pterotracheidae)
1098 from Hawaiian waters. *Canadian Journal of Zoology*, **75**: 237–244.
- 1099
- 1100 TOKIOKA, T. 1955a. Shells of Atlantidae (Heteropoda) collected by the Sôyô-Marû
1101 in the Southern waters of Japan. *Publications of the Seto Marine Biological*
1102 *Laboratory*, **4**: 237–250.
- 1103
- 1104 TOKIOKA, T. 1955b. On some plankton animals collected by the Syunkotu-Marû in
1105 May–June 1954. *Publications of the Seto Marine Biological Laboratory*, **4**: 227–236.
- 1106
- 1107 TRACEY, S. 2010. Gastropods. In: *Fossils of the Gault Clay* (J.R. Young, A.S. Gale,
1108 R. Knight & A.B. Smith, eds), pl. 24, figs 16, 17. Palaeontological Association,
1109 London.
- 1110
- 1111 VANE, F.R. 1961. Contribution towards a plankton atlas of the north-eastern Atlantic
1112 and the North Sea. Part III: Gastropoda. *Bulletins of Marine Ecology*, **5**: 98–101.
- 1113
- 1114 VANE, F.R. & COLEBROOK, J.M. 1962. Continuous plankton records: contribution
1115 towards a plankton atlas of the north-eastern Atlantic and the North Sea. Part VI: the

1116 seasonal and annual distributions of the Gastropoda. *Bulletins of Marine Ecology*, **5**:
1117 247–253.
1118
1119 VAYSSIÈRE, A. 1904. Mollusques hétéropodes provenant des campagnes des yachts
1120 l’Hirondelle et de la Princesse-Alice. *Resultats des Campagnes Scientifiques*
1121 *Accomplies sur son Yacht par Albert I Monaco*, **26**: 3–65.
1122
1123 VERA, A. DE & SEAPY, R.R. 2006. *Atlanta selvagensis*, a new species of heteropod
1124 mollusc from the northeastern Atlantic Ocean (Gastropoda: Carinarioidea). *Vieraea*,
1125 **34**: 45–54.
1126
1127 VERA, A. DE, SEAPY, R.R. & HERNÁNDEZ, F. 2006. Heteropod molluscs from
1128 waters around the Selvagens Islands (Gastropoda: Carinarioidea). *Vieraea*, **34**: 33–
1129 43.
1130
1131 VIVES, F. 1966. Zooplankton nerítico de las aguas de Castellón. *Investigacion*
1132 *Pesquera*, **30**: 49–166.
1133
1134 WALL-PALMER, D., SMART, C.W. & HART, M.B. 2013. In-life pteropod
1135 dissolution as an indicator of past ocean carbonate saturation. *Quaternary Science*
1136 *Reviews*, **81**: 29–34.
1137
1138 WALL-PALMER, D., SMART, C.W., HART, M.B., LENG, M.L., BORGHINI, M.,
1139 MANINI, E., ALIANI, S. & CONVERSI, A. 2014. Late Pleistocene pteropods,
1140 heteropods and planktonic foraminifera from the Caribbean Sea, Mediterranean Sea
1141 and Indian Ocean. *Micropaleontology*, **60**: 557–578.
1142
1143 WALL-PALMER, D., SMART, C.W. & HART, M.B. (in press) The fossil record of
1144 holoplanktic gastropods at IODP Sites U1395 and U1394. *Proceedings of the*
1145 *Integrated Ocean Drilling Program*, **340**:
1146
1147 WANG, M., MACKENZIE, A.D. & JEFFS, A.G. 2014. Lipid and fatty acid
1148 composition of likely zooplankton prey of spiny lobster (*Jasus edwardsii*)
1149 phyllosomas. *Aquaculture Nutrition*, doi: 10.1111/anu.12164.

1150

1151 WOODRING, W.P. 1928. Miocene mollusks from Bowden Jamaica 2. Gastropods
1152 and discussion of results. Contributions to the geology and palaeontology of the West
1153 Indies. *Carnegie Institute of Washington Publication*, **385**: 1–564.

1154

1155 XU, Z.-L. 2007. Areal and seasonal distribution of heteropods in the East China Sea.
1156 *Plankton Benthos Research*, **2**: 147–154.

1157

1158 XU, Z.-L. & LI, C. 2005. Horizontal distribution and dominant species of heteropods
1159 in the East China Sea. *Journal of Plankton Research*, **27** : 373–382.

1160

1161 ZORN, I. 1997. Holoplanktonic gastropods from the Early Messinian of the
1162 Heraklion Basin (Crete, Greece). *Contributions to Tertiary and Quaternary Geology*,
1163 **34**: 31–45.

1164

1165

1166

1167

1168

1169

1170

1171

1172

1173

1174

1175

1176

1177

1178 **TABLES**

1179

1180 **Table 1.** List of all extant and extinct species of Atlantidae

- 1181 *Atlanta brunnea* Gray, 1850
1182 *Atlanta californiensis* Seapy & Richter, 1993
1183 *Atlanta cordiformis* Gabb, 1873*
1184 *Atlanta diamesa* Woodring, 1828*
1185 *Atlanta echinogyra* Richter, 1972
1186 *Atlanta fragilis* Richter, 1993
1187 *Atlanta frontieri* Richter, 1993
1188 *Atlanta gaudichaudi* Gray, 1850
1189 *Atlanta gibbosa* Souleyet, 1852
1190 *Atlanta helicinoidea* Gray, 1850
1191 *Atlanta inclinata* Gray, 1850
1192 *Atlanta inflata* Gray, 1850
1193 *Atlanta lesueurii* Gray, 1850
1194 *Atlanta lingayanensis* Janssen, 2007*
1195 *Atlanta meteori* Richter, 1972
1196 *Atlanta oligogyra* Tesch, 1906
1197 *Atlanta peronii* Lesueur, 1817
1198 *Atlanta plana* Richter, 1972
1199 *Atlanta richteri* Janssen, 2007*
1200 *Atlanta rosea* Gray, 1850
1201 *Atlanta seapyi* Janssen, 2007*
1202 *Atlanta selvagensis* de Vera & Seapy, 2006
1203 *Atlanta soluta* (Di Geronimo, 1974)*
1204 *Atlanta tokiokai* Van der Spoel & Troost, 1972
1205 *Atlanta turriculata* d'Orbigny, 1836
1206 *Bellerophina minuta* (Sowerby, 1814)*
1207 *Oxygyrus inflatus* Benson, 1835
1208 *Protatlanta kbiraensis* Janssen, 2012*
1209 *Protatlanta rotundata* (Gabb, 1973)*
1210 *Protatlanta souleyeti* (Smith, 1888)

1211 Asterisk indicates extinct taxa.

1212

1213

1214

1215 **Table 2.** Factors affecting seasonal abundances, compiled from published literature.

1216

Location	Seasons during which atlantids are most abundant	Attributed reason	References
Gulf of Naples	Early spring and autumn	Seasonal vertical convection	Richter, 1968
San Pedro Basin, California	Summer	California current and Southern California eddy	Cummings & Seapy, 2003
East China Sea	Summer and Autumn	Water temperature related to shifting Taiwan warm current.	Xu & Li, 2005 Xu, 2007
West of UK	August to October	Water currents	Vane & Colebrook, 1962
Bay of Bengal	November and December, premonsoonal	Monsoonal changes	Mathew <i>et al.</i> , 1990
Arabian Sea	November and December, postmonsoonal	Monsoonal changes	Mathew <i>et al.</i> , 1990
Nosy-Bé, Madagascar	December to May	Wet season	Frontier, 1973a, 1973b
Great Barrier Reef, Australia	Summer months	None given	Newman, 1990a
Gulf of Mexico	<i>A. selvagensis</i> May <i>A. gaudichaudi</i> November	None given	Lemus-Santana <i>et al.</i> , 2014
Banyuls-Sur-Mer	March to December, but some species all year	None given	Thiriot-Quévieux, 1970
Castellón	June to August	None given	Vives, 1966
Oahu, Hawaii	April	None given	Seapy, 2008

1217

1218

1219

1220

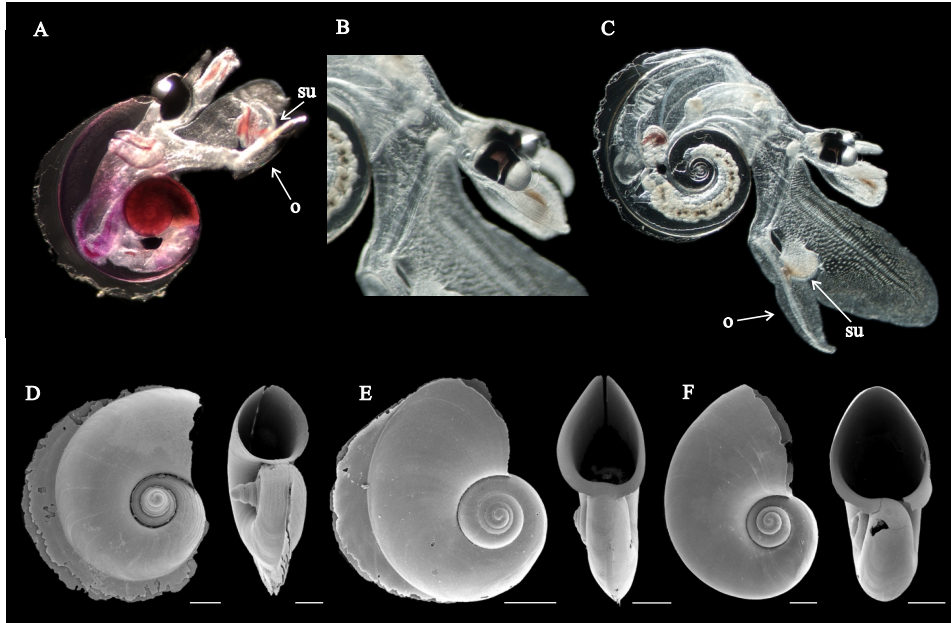
1221

1222

1223

1224 FIGURE CAPTIONS

1225



1226

1227 **Figure 1.** Living heteropods (photographs taken by K.T.C.A. Peijnenburg and E.

1228 Goetze during the Atlantic Meridional Transect cruise, AMT22). **A.** *Atlanta*

1229 *helicinoidea* with eye type c (Seapy & Richter, 1993). **B, C.** *A. peronii* with eye type

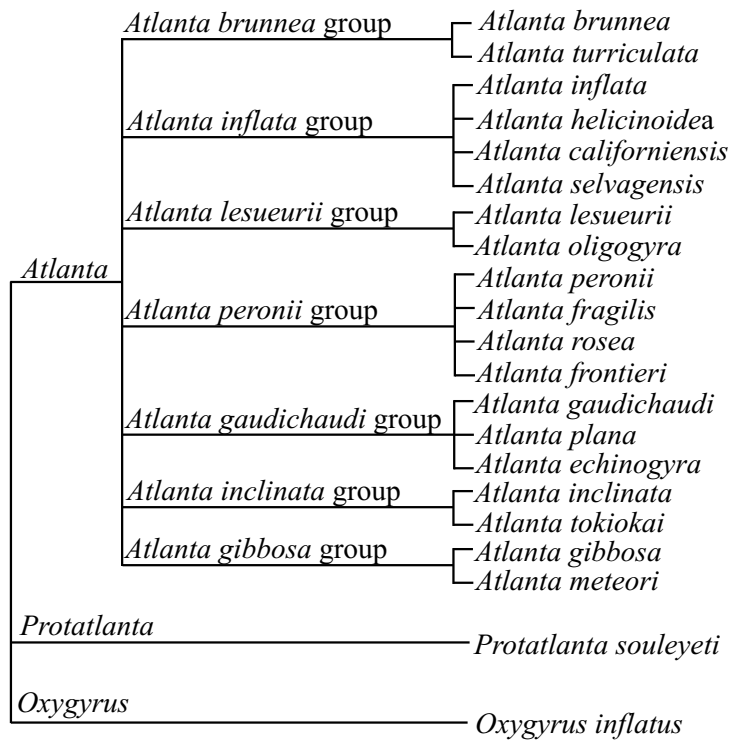
1230 b. **D–F.** Scanning electron microscopy images. **D.** *A. turriculata*. **E.** *A. selvagensis*. **F.**

1231 *Protatlanta souleyeti*. Scale bars = 200 μ m. Abbreviations: o, operculum; su, sucker

1232 used in predation.

1233

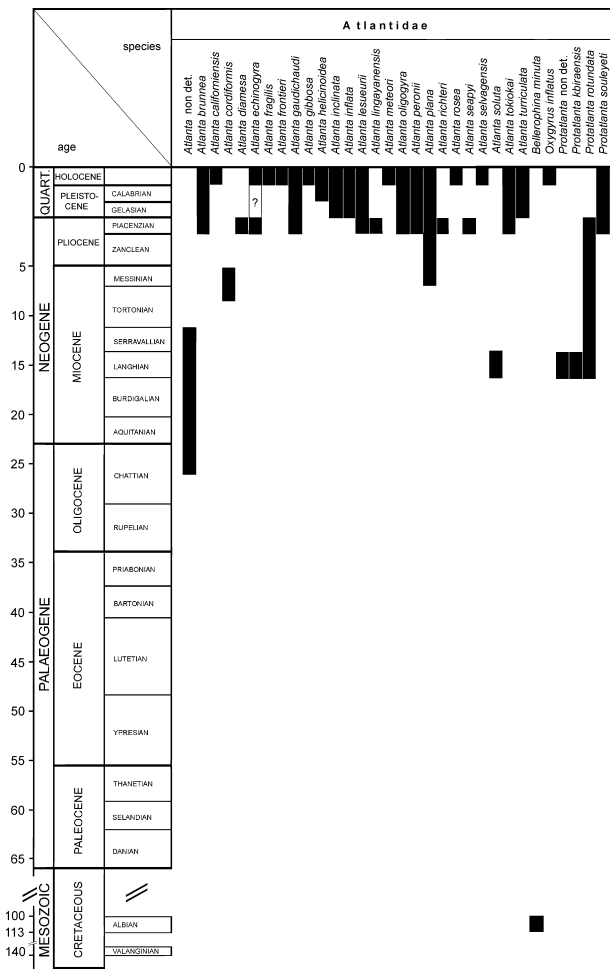
1234



1235

1236 **Figure 2.** Hypothesized organisation of the extant species of the family Atlantidae,
 1237 based on shell morphology (after Seapy, 2011).

1238

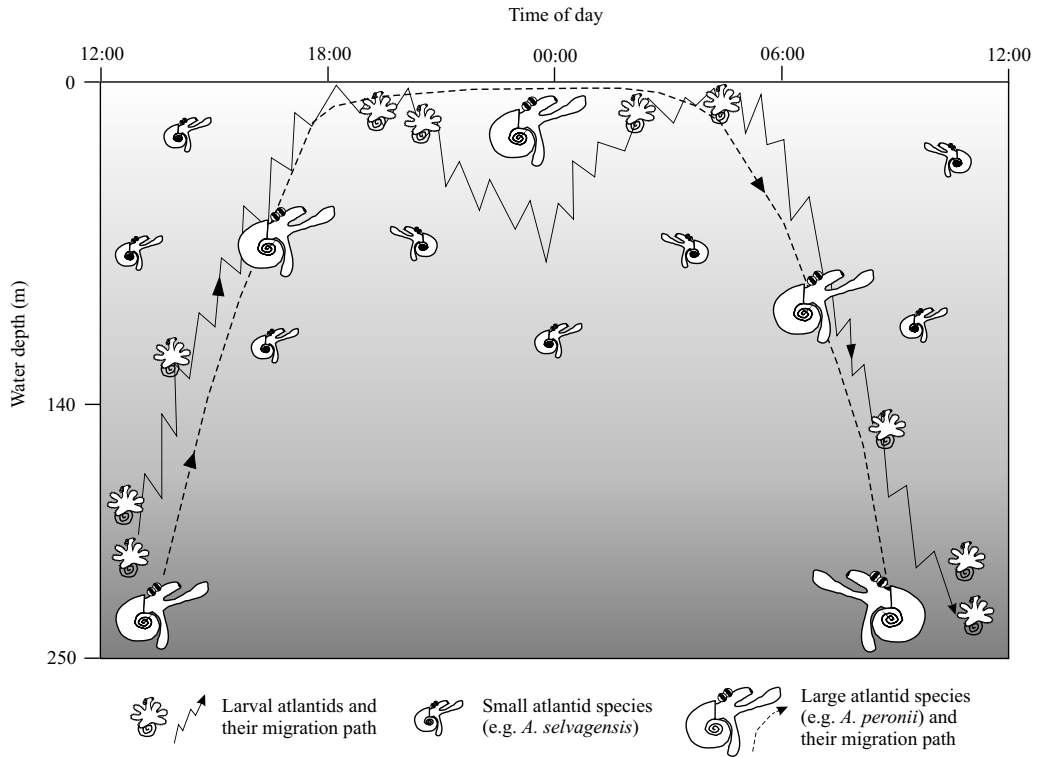


1239

1240 **Figure 3.** The known biostratigraphy of all extinct and extant atlantid species

1241 compiled from published literature.

1242

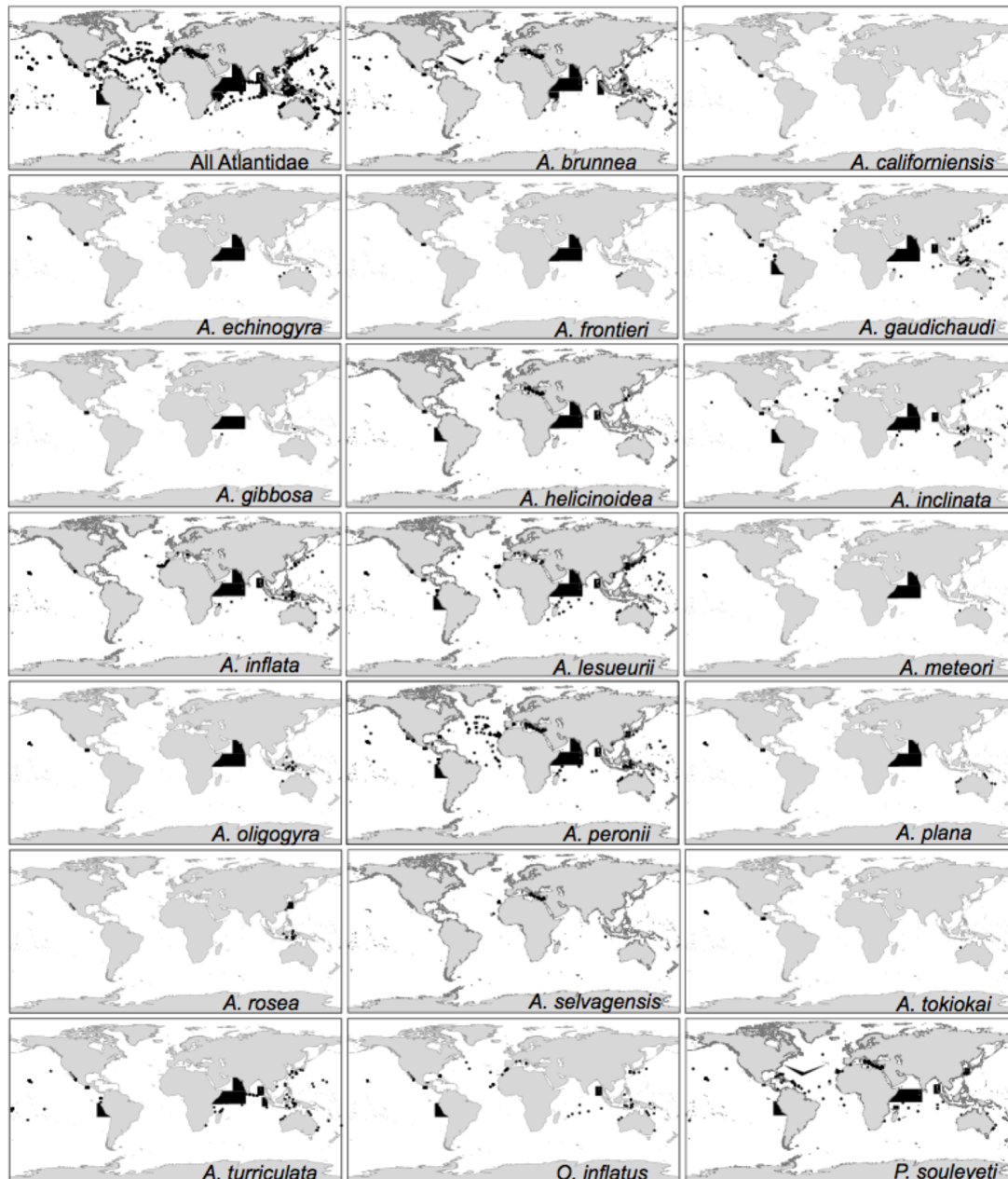


1243

1244

1245 **Figure 4.** Summary of atlantid migrations over 24-h cycle, compiled from published
 1246 literature (Oberwimmer, 1898; Lalli & Gilmer, 1989; Seapy, 1990b; Michael &
 1247 Michael, 1991; Seapy & Richter, 1993; Ossenbrügger, 2010). Larval atlantids exhibit
 1248 a ‘saw-tooth’ nocturnal migration with two periods at the surface. Adults of large
 1249 atlantid species also show a nocturnal migration from deeper waters to the surface.
 1250 Adults of smaller atlantid species live in shallower waters and do not migrate.

1251

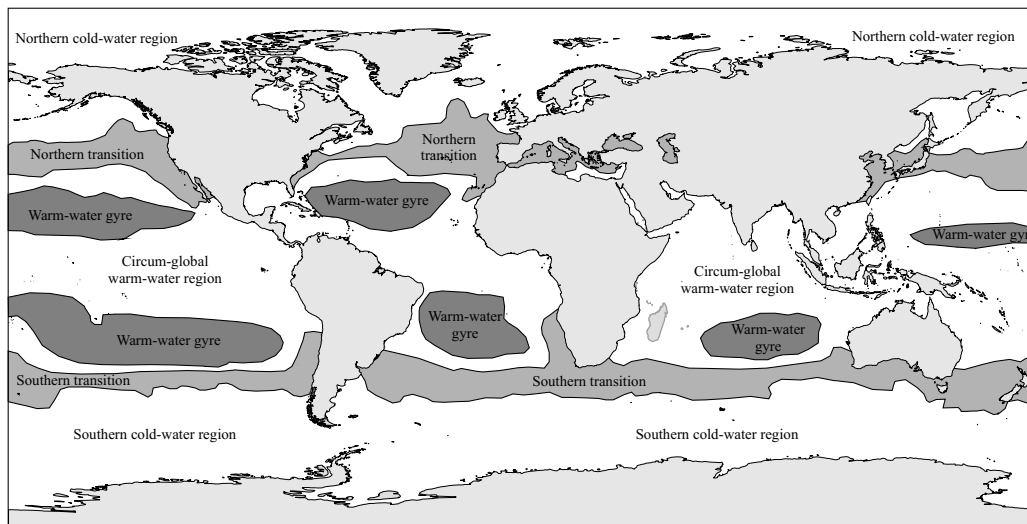


1252

1253

1254 **Figure 5.** Distributions of 20 atlantid species compiled from published literature
 1255 (Smith, 1888; Vayssière, 1904; Schiemenz, 1911; Tesch, 1906, 1910, 1949;
 1256 Bonnevie, 1920; Tokioka, 1955a, b; Ralph, 1957; Furnestin, 1961; Taki & Okutani,
 1257 1962; McGowan & Fraundorf, 1966; Evans, 1968; Richter, 1968, 1974; Pilkington,
 1258 1970; Thiriôt-Quévieux, 1970; Frontier, 1973a, b; Grossman, 1986; Sanchez-Hidalgo
 1259 y Anda, 1989; Newman, 1990a, b; Seapy, 1990a, b; Lozano Soldevilla & Hernández
 1260 Hernández, 1991; Michel & Michel, 1991; Hernández *et al.*, 1993; Seapy & Richter,
 1261 1993; Aravindakshan & Stephen, 1996; Cruz, 1998; González, 1998; Castellanos &

1262 Suarez-Morales, 2001; Cummings & Seapy, 2003; Çevik *et al.*, 2006; Seapy *et al.*,
1263 2003; de Vera *et al.*, 2006; Xu, 2007; de Vera & Seapy, 2006; Ayon *et al.*, 2008;
1264 Seapy, 2008; Ossenbrügger, 2010; Angulo-Campillo *et al.*, 2011; Howard *et al.*,
1265 2011; Lemus-Santana *et al.*, 2014; Moreno-Alcántara *et al.*, 2014).
1266
1267



1268
1269 **Figure 6.** Zooplankton biogeographical provinces, modified from Oliver & Irwin
1270 (2008).
1271