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Biogeography and genetic diversity of the atlantid heteropods

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ABSTRACT

The atlantid heteropods are regularly encountered, but rarely studied marine planktonic gastropods. Relying on a small (< 14 mm), delicate aragonite shell and living in the upper ocean means that, in common with pteropods, atlantids are likely to be affected by imminent ocean changes. Variable shell morphology and widespread distributions indicate that the family is more diverse than the 23 currently known species. Uncovering this diversity is fundamental to determining the distribution of atlantids and to understanding their environmental tolerances. Here we present phylogenetic analyses of all described species of the family Atlantidae using 437 new and 52 previously published cytochrome *c* oxidase subunit 1 mitochondrial DNA (mtCO1) sequences. Specimens and published sequences were gathered from 32 Atlantic Ocean stations, 14 Indian Ocean stations and 21 Pacific Ocean stations between 35°N and 43°S. DNA barcoding and Automatic Barcode Gap Discovery (ABGD) proved to be valuable tools for the identification of described atlantid species, and also revealed ten additional distinct clades, suggesting that the diversity within this family has been underestimated. Only two of these clades displayed obvious morphological characteristics, demonstrating that much of the newly discovered diversity is hidden from morphology-based identification techniques. Investigation of six large atlantid collections demonstrated that 61% of previously described (morpho) species have a circumglobal distribution. Of the remaining 39%, two species were restricted to the Atlantic Ocean, five occurred in the Indian and Pacific oceans, one species was only found in the northeast Pacific Ocean, and one occurred only in the Southern Subtropical Convergence Zone. Molecular analysis showed that seven of the species with wide distributions were comprised of two or more clades that occupied distinct oceanographic regions. These distributions may suggest narrower environmental tolerances than the described morphospecies. Results provide an updated biogeography and mtCO1 reference dataset of the Atlantidae that may be used to identify atlantid species and provide a first step in understanding their evolutionary history and accurate distribution, encouraging the inclusion of this family in future plankton research.

1. Introduction

Zooplankton are a vital component of open ocean food webs. However, plankton species living close to the ocean-atmosphere boundary, where CO_2 dissolves into the ocean and direct warming occurs, may be particularly vulnerable to ocean changes (Hays et al., 2005). The most vulnerable holozooplankton to changing ocean chemistry are the calcium carbonate shell-forming groups, both of which are gastropods; pteropods and heteropods (Kroeker et al., 2013). To date, ocean acidification research has focused on the thecosome pteropods, because their shell is formed of aragonite, a polymorph of calcium carbonate that is 50% more soluble in seawater than calcite (Mucci, 1983; Sun et al., 2015). Ocean acidification and ocean warming have been shown to negatively impact thecosome pteropods, with shell

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dissolution already occurring in field populations (Bednaršek et al., 2016; Bednaršek and Ohman, 2015). Thus far, the atlantid heteropods (Gastropoda: Pterotracheoidea: Atlantidae) have not been considered in any global change research, despite having an aragonite shell, being morphologically similar to pteropods, and sharing the same habitat. Atlantid heteropods and thecosome pteropods are not closely related (Lalli and Gilmer, 1989), and belong to lineages that have independently colonized the pelagic environment. However, these groups are likely to face similar direct effects of ocean acidification and ocean warming. Atlantids may be under additional stress because they also rely on thecosome pteropods as a primary source of prey (Lalli and Gilmer, 1989; Newman, 1990).

Atlantids live in the upper 250 m of the ocean and are characterised by small (< 14 mm), transparent, lenticular shaped shells into which the body can fully retract. Atlantids have well-developed eyes, a foot that has adapted into swimming fins and a shell periphery that is fringed with a keel (Lalli and Gilmer, 1989). There are three genera within the Atlantidae; *Atlanta, Protatlanta* and *Oxygyrus,* that together contain 23 described species (Seapy, 2011; Wall-Palmer et al., 2016a,b). Our current understanding of atlantid diversity and biogeography is poor, which is likely the result of their complicated taxonomy, often based on minute shell ornamentation and subtle variations in shell size and shape (Seapy, 2011). However, accurate species identification is fundamental to understanding atlantid ecology and species distributions, and therefore, to detecting what constitutes change in their abundance and distribution.

Based on morphological adaptations, it has been suggested that *Atlanta*, with a shell composed entirely of aragonite, is the earliest diverged genus of the Atlantidae. The morphology-based evolutionary history of the atlantids proposed by Richter (1974, 1973, 1968, 1961) suggests that atlantid evolution has taken two trajectories, both originating from an ancestor of the extant species with the most plesiomorphic characters, *Atlanta brunnea.* These paths are supported by radula, eye and operculum morphology (Richter, 1974), as well as by chromosome studies (Thiriot-Quiévreux and Seapy, 1997). Along one route, atlantid shell morphology has supposedly evolved to become more efficient by incorporating conchiolin in place of heavier aragonite in the shell, and the body has become more elongated. This gradual adaptation to increase buoyancy leads from the genus *Atlanta* to the genus *Protatlanta,* with a shell of aragonite and a keel of conchiolin, and finally to the genus *Oxygyrus,* with a shell largely composed of conchiolin to reduce shell mass (Lalli and Gilmer, 1989; Richter, 1961; Richter and Seapy, 1999). The extinct species *Protatlanta rotundata* supports this theoretical evolutionary trajectory, exhibiting shell characters of both *Protatlanta* and *Oxygyrus* (Janssen, 2007). In the second direction of evolution, in which the majority of atlantid species are included, it was proposed that the aragonite atlantid shells have become flatter, the shell walls have become thinner and the central spire has evolved to be narrower or tilted. These evolutionary trends are likely the result of selection pressure to improve swimming efficiency, since the large, flat shell is essential for directed swimming (to counteract the side-to-side action of the swimming fin) and hence, effective hunting. In the supposedly more derived atlantids, the shell becomes unwound slightly in the final whorls (for example *Atlanta fragilis* and *Atlanta gibbosa*). These trends suggest a path of evolution towards the partially shelled heteropod family Carinariidae and the shell-less family Pterotracheidae. Along both evolutionary pathways, the atlantid shells become more symmetrical, to balance shell weight and enhance swimming efficiency (Richter, 1973). However, no clear heteropod ancestor has been identified in the fossil record and their evolutionary history remains uncertain (Wall-Palmer et al., 2016c). Richter (1973) noted that the swimming fin and flat shell of the atlantids must have developed simultaneously with a planktonic mode of life, because without the flattened shell, directed swimming would not have been possible. However, the oldest potential fossil atlantid described from the Cretaceous of Britain (Tracey, 2010), *Bellerophina minuta,* most closely resembles the shell of juvenile *Oxygyrus* and not the more basal genus *Atlanta,* suggesting that the morphology based hypotheses of Richter (1974, 1973, 1968, 1961) may be incorrect.

Atlantid taxonomy has, until recently, relied almost exclusively upon morphological characters and ornamentation of the shell, although many authors have commented on the difficulty in distinguishing some species owing to the striking similarity of atlantid shells. Richter (1973, 1961) emphasized that the investigation of the shell alone was insufficient to describe or reject new species, and it is evident that within many described species, shell morphology and ornamentation is highly variable. For example, the spire ornamentation of *Atlanta selvagensis* can vary from no ornamentation to multiple well developed spiral lines (De Vera and Seapy, 2006; Janssen and Seapy, 2009). Additional characteristics, including morphology of the eyes (3 types), radula (2 types) and operculum (3 types), are also used in atlantid taxonomy (Seapy, 2011, 1990; Seapy et al., 2003). However, the use of the radula has been a contentious issue, with some regarding it as the most valuable taxonomic character (Bonnevie, 1920; Vayssière, 1904, 1902), while others completely rejected classifications based on the radula (Buchman, 1924; Tesch, 1949). Although not particularly useful for identifying species because, amongst other things, they vary with ontogenetic stage, the radula has supported the suggested evolutionary history within the family (Richter, 1968, 1961).

Despite the detailed taxonomic work of many authors, even the use of multiple morphological features is not adequate to reveal the probable hidden, or 'cryptic' diversity within the atlantid heteropods. Richter (1973) predicted that the number of heteropod species had been grossly underestimated and Richter and Seapy (1999) emphasized that large areas of the oceans are still poorly investigated. To date, only a single molecular phylogeny for the atlantids has been published (Jennings et al., 2010). Even with a limited dataset of 13 specimens from four species, Jennings et al. (2010) detected significant genetic variation between conspecific specimens from different ocean regions (*Atlanta inclinata*). Recently, integrative taxonomy that combines morphological characters with biogeography and molecular analysis has been used successfully to describe the new atlantid species *Atlanta ariejansseni,* and to reinstate the species *Protatlanta sculpta* (Wall-Palmer et al., 2016a,b). In these cases, the species validations using molecular methods also highlighted key morphological characters that can now be used to identify the species. The discovery of new species also adds valuable information about species distributions that can inform our understanding of atlantid ecology.

Tesch (1908) predicted that most atlantid species would be found to have a cosmopolitan distribution in tropical and subtropical regions. Our understanding of atlantid biogeography has advanced little in 40 years, since the work of Van der Spoel (1976), and many species of atlantid are still assumed to have broad geographical distributions (Richter and Seapy, 1999; Wall-Palmer et al., 2016c). However, Richter (1993) anticipated that atlantid species exhibiting global distributions were more likely to be the exception rather than the rule. This view is supported by recent research, which has found several atlantids with more restricted distributions in particular oceanographic regions (Janssen and Seapy, 2009; Jennings et al., 2010; Wall-Palmer et al., 2016a,b). For example, the genus *Protatlanta* was previously considered monotypic containing only the species *Protatlanta souleyeti*, which was described to have a wide distribution in the Atlantic Ocean. However, with the discovery that *P. sculpta* (originally described by Issel, 1911) is a valid species (Wall-Palmer et al., 2016b), it was revealed that *P.*

souleyeti had a distribution restricted to the oligotrophic north and south gyres, whereas *P. sculpta* had a distribution within more eutrophic regions outside of the subtropical gyres. Other examples include *Atlanta californiensis,* which is restricted to the northeast Pacific Ocean (Angulo-Campillo et al., 2011; Moreno-Alcántara et al., 2014; Seapy and Richter, 1993), and *A. ariejansseni,* which is a 'transition zone' species with a circumglobal distribution within a narrow band of latitude, between 37 and 48°S (Wall-Palmer et al., 2016a).

These studies, and others, demonstrate the value of integrated molecular, morphological and biogeographical methods as complementary approaches to identify species reliably, allowing accurate assessment of diversity and distribution (Barco et al., 2016; Bode et al., 2017; Burridge et al., 2015; Cornils et al., 2017; Goetze, 2010; Morard et al., 2009; Nigro et al., 2016). This information is becoming particularly important in the context of global change impacts on the ocean. Without the ability to identify species reliably, we cannot fully understand the environmental tolerances of atlantids, and detect changes in their abundance and distribution. The variable shell morphology within many described atlantid species implies that the family Atlantidae may be much more diverse than traditional morphological taxonomy alone suggests. This study aims to investigate diversity of atlantids through the production of a mitochondrial cytochrome *c* oxidase subunit 1 (mtCO1) phylogeny for all described morphospecies in the family, and to provide a reference mtCO1 dataset illustrated with specimen images to aid and encourage future research on this group. To improve our understanding of the distribution of atlantids, an updated biogeography of morphospecies is presented and compared to that of new clades that are identified through DNA barcoding. These results provide a baseline for future studies that address atlantid environmental tolerances and distributions in relation to ocean changes.

2. Materials and methods

2.1. Specimen collection for molecular analysis

A total of 477 atlantid specimens, and four carinarid specimens were obtained from the Atlantic, Indian and Pacific oceans (Table 1, Fig. 1). These specimens were selected randomly (or all specimens were used) from available material that had been appropriately preserved for molecular analysis at each station. Where possible, specimens from known type localities were included in the analysis. Of these specimens, 196 derive from 25 stations in the Atlantic Ocean and were largely collected during the Atlantic Meridional Transect cruise in 2014 (AMT24, N = 195), with one specimen collected during the AMT cruise in 2012 (AMT22, N = 1). In the Indian Ocean, 166 atlantid specimens and four carinarid specimens were collected from 14 stations during three oceanographic cruises, VANC10MV (N = 21), Snellius II G0 (N = 1) and SN105 (N = 144 + 4). A further 115 specimens were collected from 19 stations in the Pacific Ocean during six cruises; ACE-ASIA (N = 6), KM1109 (N = 3), S226 (N = 7), DRFT (N = 5), KH1110 (N = 91) and NOAA WCOA16 (N = 3).

Specimens were collected using a variety of plankton nets (e.g. Bongo, ring, multinet, midwater trawl) vertically hauled or obliquely towed, with the exception of the Dutch-Indonesian Snellius II G0 cruise, on which a plankton pump was used. Collection methods have been previously described for most of the stations sampled (Burridge et al., in press a; Goetze, 2005, 2003; Halbert et al., 2013; Hirai et al., 2015; Kroon and Nederbragt, 1990). Methods for only two of the cruises, SN105 and NOAA WCOA16, have not been previously published and we detail them here. Cruise SN105 took place on board the OVR *Sagar Nidhi* in the Indian Ocean in December 2015 as the first cruise of the International Indian Ocean Expedition 2 (IIOE-2). Specimens were collected in the upper 100 m using a ring net with an aperture diameter of 1 m, a mesh size 350 µm and a tow time of 20 min. On board, plankton samples were immediately preserved in 96% ethanol and specimens were sorted from the bulk material. Cruise NOAA WCOA16 took place in the northeast Pacific Ocean on board the RV *Ronald H. Brown* in May 2016. Specimens were collected in the upper 100 m using a Bongo net with an aperture diameter of 0.7 m, a mesh size of 333 µm and a tow time of approximately 30–40 min. Upon recovery, atlantid specimens were separated and immediately preserved in 100% ethanol. On both cruises, ethanol was replaced within 24 h of initial preservation and samples were maintained at −20 °C.

Species of the family Atlantidae were identified using morphological characteristics of the shell and eyes, following the taxonomic keys of Richter and Seapy (1999), Seapy (2011, 1990) and Seapy et al. (2003). All morphological species identifications were carried out by D. Wall-Palmer to the level of described species.

2.2. DNA extraction and amplification

All specimens were imaged prior to analysis using a Zeiss SteREO Discovery V20 stacking microscope (images deposited in BOLD). Because specimen shells are destroyed during DNA extraction, the collection of images allows a 'double check' in case of disputes between morphologically identified specimens and molecular results. DNA was extracted from whole specimens, using the NucleoMag 96 Tissue kit (Macherey-Nagel) on a Thermo Scientific KingFisher Flex magnetic particle processor, with a final elution volume of 75 µl. The standard barcoding fragment of the mitochondrial cytochrome *c* oxidase subunit 1 gene (mtCO1) (Hebert et al., 2003) was amplified using primers jgLCO1490 and jgHCO2198 (Geller et al., 2013). Primers were tailed with M13F and M13R for sequencing (Messing, 1983). PCR reactions contained 17.75 µl mQ, 2.5 µl 10x PCR buffer, 0.5 µl 25 mM $MgCl_2$, 0.5 µl 100 mM BSA, 1.0 µl 10 mM of each primer, 0.5 µl 2.5 mM dNTPs and 0.25 µl 5U Qiagen Taq, with 1.0 µl of template DNA, which was diluted 10 or 100 times for some samples. PCR was performed using an initial denaturation step of 180 s at 94 °C, followed by 40 cycles of 15 s at 94 °C, 30 s at 50 °C and 40 s at 72 °C, and finishing with a final extension of 300 s at 72 °C and holding temperature of 12 °C. Sequencing was carried out by Macrogen, Europe and Base Clear. Sequences were edited using Geneious (R8) and checked for stop-codons in AliView (Larsson, 2014). All sequences and specimen images are publicly available through BOLD and GenBank (accession numbers in Table 1). mtCO1 sequences of *A. ariejansseni* (N = 17), *A. selvagensis* (N = 5), *P. souleyeti* (N = 10) and *P. sculpta* (N = 8) were published in Wall-Palmer et al. (2016a,b). In addition, 12 atlantid mtCO1 sequences from GenBank (Jennings et al., 2010), originally identified as *Atlanta* sp., *Atlanta gaudichaudi*, *A. inclinata*, *Atlanta peronii*, *Oxygyrus inflatus* and *Firoloida desmarestia,* one sequence from BOLD (PJP084, Amy Maas, Bermuda Institute of Ocean Sciences, unpublished data) and one sequence from the GOLCA0701 cruise (María Moreno-Alcántara, unpublished data) were included. New sequences of *Carinaria lamarckii* (N = 4) and GenBank sequences of *F. desmarestia* (N = 2) were used as outgroups for the phylogenetic analysis.

2.3. Phylogenetic analyses

Multiple sequence alignment was performed using MAFFT 7 (Katoh and Standley, 2013) under default parameters. Maximum likelihood analysis was performed using the Phylostack pipeline (Doorenweerd, 2016). Maximum likelihood analyses were run with RAxML 8.2.9 (Stamatakis, 2014) using the General Time Reversible (GTRCAT) model. The best maximum likelihood tree was inferred using the –D parameter, which expedites the process (Doorenweerd, 2016). A multiparametric bootstrap search was performed, which stopped

Table 1
Specimens included in the phylogenetic analysis for this study.

Species	Number of sequences	Ocean	Cruise or publication	Station	Latitude	Longitude	BOLD process ID or GenBank (GB) accession number
Atlanta ariejansseni	2	Atlantic	AMT24	26	−37.89	−28.74	KX343177 - KX343178 (GB)
	5		AMT24	27	−40.12	−30.91	KX343179 - KX343183 (GB)
	1		AMT24	28	−41.48	−33.86	KX343184 (GB)
	7		AMT24	29	−43.02	−37.14	KX343185 - KX343191 (GB)
	2	Pacific	DRFT	14	−38.32	−161.14	KX343192 - KX343193 (GB)
Atlanta brunnea	1	Atlantic	AMT24	5	34.75	−26.62	AGD001-17
	2	Indian	SN105	4	8.02	67.08	AGD008-17 - AGD009-17
	4		SN105	8	4.38	67.00	AGD010-17 - AGD013-17
	1	Pacific	KH1110	5	−23.00	180.00	AGD002-17
	3		KH1110	15	−23.00	−119.27	AGD003-17 - AGD005-17
	2		KH1110	21	−23.00	−100.00	AGD006-17 - AGD007-17
Atlanta californiensis	1	Pacific	NOAA WCOA16	24	31.62	−116.91	AGD014-17
	1		NOAA WCOA16	30	33.16	−118.42	AGD015-17
	1		NOAA WCOA16	31	32.77	−119.23	AGD016-17
	1		GOLCA0701		28.45	−122.10	
Atlanta echinogyra	4	Indian	SN105	4	8.02	67.08	AGD022-17 - AGD025-17
	2		SN105	8	4.38	67.00	AGD026-17 - AGD027-17
	3		SN105	19	−2.95	66.99	AGD028-17 - AGD030-17
	1	Pacific	KH1110	15	−23.00	−119.27	AGD017-17
	3		KH1110	21	−23.00	−100.00	AGD018-17 - AGD020-17
	1		S226	10	13.083	−159.343	AGD021-17
Atlanta fragilis	2	Atlantic	AMT24	13	7.29	−26.49	AGD032-17 - AGD033-17
	1		AMT24	19	−14.66	−25.07	AGD034-17
	1		AMT24	20	−18.32	−25.09	AGD035-17
	1		AMT24	21	−20.86	−25.08	AGD036-17
	4		AMT24	22	−24.46	−25.04	AGD037-17 - AGD040-17
	4		AMT24	27	−40.12	−30.91	AGD041-17 - AGD044-17
	1	Indian	VANC	9	−31.83	52.61	AGD051-17
	1		VANC	16	−19.75	78.01	AGD052-17
	1		VANC	17	−18.43	80.92	AGD053-17
	1	Pacific	ACAS	8	31.24	173.92	AGD031-17
	1		DRFT	11	−36.05	−149.29	AGD045-17
	1		KH1110	15	−23.00	−119.27	AGD046-17
	3		KH1110	18	−30.00	−107.00	AGD047-17 - AGD049-17
	1		KH1110	21	−23.00	−100.00	AGD050-17
Atlanta frontieri	5	Indian	SN105	1	11.89	66.97	AGD059-17 - AGD063-17
	4		SN105	4	8.02	67.08	AGD064-17 - AGD067-17
	4		SN105	8	4.38	67.00	AGD055-17 - AGD058-17
	1	Pacific	KH1110	2	−23.00	160.00	AGD054-17
Atlanta gaudichaudi	1	Indian	VANC	1	−35.05	23.73	AGD068-17
Atlanta gibbosa	2	Indian	SN105	8	4.38	67.00	AGD070-17 - AGD071-17
	1	Pacific	S226	29	1.477	−160.133	AGD069-17
Atlanta helicinoidea	3	Atlantic	AMT24	6	31.30	−27.73	AGD072-17 - AGD074-17
	1		AMT24	7	27.50	−28.89	AGD075-17
	1		AMT24	8	24.06	−29.91	AGD076-17
	2		AMT24	13	7.29	−26.49	AGD077-17 - AGD078-17
	1		AMT24	14	3.80	−25.78	AGD079-17
	3		AMT24	16	−3.89	−25.03	AGD080-17 - AGD082-17
	1		AMT24	20	−18.32	−25.09	AGD083-17
	3		AMT24	22	−24.46	−25.04	AGD084-17 - AGD086-17
	2		AMT24	25A	−34.18	−27.21	AGD087-17 - AGD088-17
	1		AMT24	27	−40.12	−30.91	AGD089-17
	4	Indian	SN105	8	4.38	67.00	AGD101-17 - AGD104-17
	1		VANC	5	−34.36	37.73	AGD105-17
	1		VANC	17	−18.43	80.92	AGD106-17
	1		VANC	22	−12.86	94.29	AGD107-17
	1		VANC	24	−13.21	104.66	AGD108-17
	4	Pacific	KH1110	2	−23.00	160.00	AGD090-17 - AGD093-17
	2		KH1110	5	−23.00	180.00	AGD094-17 - AGD095-17
	2		KH1110	8	−22.79	−158.101	AGD096-17 - AGD097-17
	2		KH1110	15	−23.00	−119.27	AGD098-17 - AGD099-17
	1		S226	9	13.87	−159.12	AGD100-17

(*continued on next page*)

Table 1 (*continued*)

Species	Number of sequences	Ocean	Cruise or publication	Station	Latitude	Longitude	BOLD process ID or GenBank (GB) accession number
Atlanta inclinata	1	Atlantic	AMT24	12	10.78	−27.21	AGD109-17
	3		AMT24	13	7.29	−26.49	AGD110-17 - AGD112-17
	5		AMT24	14	3.80	−25.78	AGD113-17 - AGD117-17
	2		AMT24	15	0.08	−25.02	AGD118-17 - AGD119-17
	3		AMT24	16	−3.89	−25.03	AGD120-17 - AGD122-17
	2		AMT24	18	−11.04	−25.05	AGD123-17 - AGD124-17
	1		Jennings et al. (2010)		−13.42	−0.65	FJ876840 (GB)
	1		Jennings et al. (2010)		11.68	−20.42	FJ876847 (GB)
	2	Indian	SN105	4	8.02	67.08	AGD126-17 - AGD127-17
	2		SN105	19	−2.95	66.99	AGD128-17 - AGD129-17
	1	Pacific	S226	45	9.47	−154.42	AGD125-17
Atlanta inflata	2	Indian	SN105	1	11.89	66.97	AGD137-17 - AGD138-17
	3		SN105	8	4.38	67.00	AGD139-17 - AGD141-17
	5		SN105	19	−2.95	66.99	AGD142-17 - AGD146-17
	2	Pacific	KH1110	2	−23.00	160.00	AGD130-17 - AGD131-17
	4		KH1110	5	−23.00	180.00	AGD132-17 - AGD135-17
	1		KH1110	8	−22.79	−158.101	AGD136-17
Atlanta lesueurii	2	Atlantic	AMT24	11	14.21	−27.93	AGD147-17 - AGD148-17
	1		AMT24	15	0.08	−25.02	AGD149-17
	4		AMT24	16	−3.89	−25.03	AGD150-17 - AGD153-17
	1	Indian	SN105	8	4.38	67.00	AGD154-17
	2		SN105	19	−2.95	66.99	AGD155-17 - AGD156-17
Atlanta meteori	2	Atlantic	AMT24	8	24.06	−29.91	AGD157-17 - AGD158-17
	2		AMT24	23	−27.76	−25.01	AGD159-17 - AGD160-17
	1		Jennings et al. (2010)		25.06	−60.62	FJ876845 (GB)
	2	Indian	SN105	1	11.89	66.97	AGD162-17 - AGD163-17
	4		SN105	4	8.02	67.08	AGD164-17 - AGD167-17
	2		SN105	8	4.38	67.00	AGD168-17 - AGD169-17
	4		SN105	19	−2.95	66.99	AGD170-17 - AGD173-17
	1	Pacific	KH1110	8	−22.79	−158.101	AGD161-17
Atlanta oligogyra	1	Indian	PGO	119	8.97	69.74	AGD183-17
	6		SN105	1	11.89	66.97	AGD185-17 - AGD190-17
	6		SN105	4	8.02	67.08	AGD191-17 - AGD196-17
	4		SN105	8	4.38	67.00	AGD197-17 - AGD200-17
	2		SN105	19	−2.95	66.99	AGD201-17 - AGD202-17
	3		VANC	1	−35.05	23.73	AGD203-17 - AGD205-17
	2		VANC	2	−35.07	24.50	AGD206-17 - AGD207-17
	3	Pacific	KH1110	2	−23.00	160.00	AGD175-17 - AGD177-17
	4		KH1110	5	−23.00	180.00	AGD178-17 - AGD181-17
	1		KH1110	18	−30.00	−107.00	AGD182-17
	1		S226	10	13.083	−159.343	AGD184-17
	1	Atlantic	AMT24	19	−14.66	−25.07	AGD174-17
Atlanta peronii	1	Atlantic	AMT22	27	17.70	−36.46	AGD209-17
	1		AMT24	6	31.30	−27.73	AGD210-17
	2		AMT24	8	24.06	−29.91	AGD211-17 - AGD212-17
	6		AMT24	9	20.45	−29.27	AGD213-17 - AGD218-17
	3		AMT24	16	−3.89	−25.03	AGD219-17 - AGD221-17
	4		AMT24	18	−11.04	−25.05	AGD222-17 - AGD225-17
	2		AMT24	21	−20.86	−25.08	AGD226-17 - AGD227-17
	2		AMT24	22	−24.46	−25.04	AGD228-17 - AGD229-17
	3		AMT24	23	−27.76	−25.01	AGD230-17 - AGD232-17
	1		AMT24	25	−34.18	−27.22	AGD233-17
	1		AMT24	27	−40.12	−30.91	AGD234-17
	4	Indian	SN105	19	−2.95	66.99	AGD241-17 - AGD244-17
	1		VANC	15	−21.04	75.14	AGD245-17
	1	Pacific	ACAS	2	28.21	−162.14	AGD208-17
	2		DRFT	14	−38.32	−161.14	AGD235-17 - AGD236-17
	1		KH1110	18	−30.00	−107.00	AGD237-17
	3		KH1110	21	−23.00	−100.00	AGD238-17 - AGD240-17
Atlanta plana	3	Indian	SN105	4	8.02	67.08	AGD246-17 - AGD248-17
	1		SN105	8	4.38	67.00	AGD257-17
	3		SN105	19	−2.95	66.99	AGD258-17 - AGD260-17
	1		VANC	1	−35.05	23.73	AGD261-17
	1		VANC	2	−35.07	24.50	AGD262-17
	4	Pacific	KH1110	8	−22.79	−158.101	AGD249-17 - AGD252-17
	1		KM1109	9	21.333	−158.354	AGD253-17
	1		KM1109	10	21.414	−158.343	AGD254-17
	2		S226	10	13.083	−159.343	AGD255-17 - AGD256-17

(*continued on next page*)

Table 1 (*continued*)

Species	Number of sequences	Ocean	Cruise or publication	Station	Latitude	Longitude	BOLD process ID or GenBank (GB) accession number
Atlanta rosea	4	Atlantic	AMT24	6	31.30	−27.73	AGD263-17 - AGD266-17
	1		AMT24	7	27.50	−28.89	AGD267-17
	1		AMT24	8	24.06	−29.91	AGD268-17
	4		AMT24	19	−14.66	−25.07	AGD269-17 - AGD272-17
	1		AMT24	21	−20.86	−25.08	AGD273-17
	1		AMT24	27	−40.12	−30.91	AGD274-17
	2		Jennings et al. (2010)		24.95	−60.53	FJ876837, FJ876839 (GB)
	1	Indian	VANC	15	−21.04	75.14	AGD285-17
	3		VANC	17	−18.43	80.92	AGD286-17 - AGD288-17
	3	Pacific	KH1110	5	−23.00	180.00	AGD275-17 - AGD277-17
	2		KH1110	15	−23.00	−119.27	AGD278-17 - AGD279-17
	2		KH1110	18	−30.00	−107.00	AGD280-17 - AGD281-17
	3		KH1110	21	−23.00	−100.00	AGD282-17 - AGD284-17
Atlanta selvagensis	2	Atlantic	AMT24	5	34.75	−26.62	KX343194 (GB), AGD289-17
	9		AMT24	6	31.30	−27.73	KX343195 - KX343197 (GB), AGD290-17 - AGD295-17
	3		AMT24	7	27.50	−28.89	AGD296-17 - AGD298-17
	3		AMT24	8	24.06	−29.91	AGD299-17 - AGD301-17
	3		AMT24	9	20.45	−29.27	AGD302-17 - AGD304-17
	3		AMT24	10	17.82	−28.70	AGD305-17 - AGD307-17
	3		AMT24	14	3.80	−25.78	KX343198 (GB), AGD308-17 - AGD309-17
	4		AMT24	15	0.08	−25.02	AGD310-17 - AGD313-17
	4		AMT24	16	−3.89	−25.03	AGD314-17 - AGD317-17
	1		Amy Maas, unpublished data		31.65	−64.20	PJP084
Atlanta tokiokai	1	Atlantic	AMT24	7	27.50	−28.89	AGD319-17
	3		AMT24	8	24.06	−29.91	AGD320-17 - AGD322-17
	4		AMT24	9	20.45	−29.27	AGD323-17 - AGD326-17
	2		Jennings et al. (2010)		25.06	−60.62	FJ876843, FJ876844 (GB)
	9	Indian	SN105	1	11.89	66.97	AGD335-17 - AGD343-17
	7		SN105	4	8.02	67.08	AGD344-17 - AGD350-17
	5		SN105	8	4.38	67.00	AGD351-17 - AGD355-17
	4		SN105	19	−2.95	66.99	AGD356-17 - AGD359-17
	1		VANC	24	−13.21	104.66	AGD360-17
	1	Pacific	ACAS	14	32.86	149.52	AGD318-17
	1		KH1110	8	−22.79	−158.101	AGD327-17
	3		KH1110	15	−23.00	−119.27	AGD328-17 - AGD330-17
	2		KH1110	18	−30.00	−107.00	AGD331-17 - AGD332-17
	2		KH1110	21	−23.00	−100.00	AGD333-17 - AGD334-17
Atlanta turriculata	6	Indian	SN105	1	11.89	66.97	AGD367-17 - AGD372-17
	4		SN105	4	8.02	67.08	AGD373-17 - AGD376-17
	4		SN105	8	4.38	67.00	AGD377-17 - AGD380-17
	4		SN105	19	−2.95	66.99	AGD381-17 - AGD384-17
	3	Pacific	KH1110	5	−23.00	180.00	AGD361-17 - AGD363-17
	3		KH1110	8	−22.79	−158.101	AGD364-17 - AGD366-17
Oxygyrus inflatus	2	Atlantic	AMT24	7	27.50	−28.89	AGD389-17 - AGD390-17
	1		AMT24	9	20.45	−29.27	AGD391-17
	3		AMT24	14	3.80	−25.78	AGD392-17 - AGD394-17
	3		AMT24	18	−11.04	−25.05	AGD395-17 - AGD397-17
	2		Jennings et al. (2010)		3.51	−14.01	FJ876848, FJ876849 (GB)
	1		Jennings et al. (2010)		33.57	−69.65	FJ876846 (GB)
	3	Indian	SN105	4	8.02	67.08	AGD406-17 - AGD408-17
	3		SN105	8	4.38	67.00	AGD409-17 - AGD411-17
	3		SN105	19	−2.95	66.99	AGD412-17 - AGD414-17
	1	Pacific	KH1110	2	−23.00	160.00	AGD398-17
	3		KH1110	8	−22.79	−158.101	AGD399-17 - AGD402-17
	2		KH1110	18	−30.00	−107.00	AGD403-17 - AGD404-17
	1		KM1109	9	21.333	−158.354	AGD405-17
Protatlanta sculpta	3	Atlantic	AMT24	9	20.45	−29.27	KU841485 - KU841487 (GB)
	1		AMT24	10	17.82	−28.70	KU841488 (GB)
	4		AMT24	13	7.29	−26.49	AGD415-17 - AGD418-17
	3		AMT24	16	−3.89	−25.03	KU841489 - KU841491 (GB)
	3		AMT24	20	−18.32	−25.09	AGD419-17 - AGD421-17
	1		AMT24	25	−34.18	−27.22	KU841492 (GB)

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Table 1 (*continued*)

Species	Number of sequences	Ocean	Cruise or publication	Station	Latitude	Longitude	BOLD process ID or GenBank (GB) accession number
Protatlanta souleyeti	7	Atlantic	AMT24	6	31.30	−27.73	KU841493 - KU841497 (GB), AGD425-17 - AGD426-17
	1		AMT24	18	−11.04	−25.05	KU841500 (GB)
	2		AMT24	19	−14.66	−25.07	KU841501 - KU841502 (GB)
	3		AMT24	20	−18.32	−25.09	AGD427-17 - AGD429-17
	1		AMT24	23	−27.76	−25.01	KU841506 (GB)
	1		AMT24	25A	−34.18	−27.21	KU841507 (GB)
	2		AMT24	27	−40.12	−30.91	AGD430-17 - AGD431-17
	2	Pacific	ACAS	8	31.24	173.92	AGD422-17 - AGD423-17
	1		ACAS	14	32.86	149.52	AGD424-17
	3		KH1110	2	−23.00	160.00	AGD432-17 - AGD434-17
	2		KH1110	8	−22.79	−158.101	AGD435-17 - AGD436-17
	3		KH1110	18	−30.00	−107.00	AGD437-17 - AGD439-17
	3		KH1110	21	−23.00	−100.00	AGD440-17 - AGD442-17
Carinaria lamarckii	1	Indian	SN105	1	11.89	66.97	AGD385-17
	3		SN105	4	8.02	67.08	AGD386-17 - AGD388-17
Firoloida desmarestia	2	Atlantic	Jennings et al. (2010)		14.00	−55.00	FJ876850, FJ876851 (GB)

automatically based on the extended majority rule criterion (if present in > 50% of trees, clades are included, other clades are considered in order of frequency with which they appear until the tree is fully resolved). All branches with poor bootstrap support (< 60%) were collapsed. The resulting tree was visualized in FigTree 1.4.2 (Rambaut, 2014).

Here, we consider a clade to be a well-supported monophyletic group (bootstrap support > 85%). We tested our clade selection using Automatic Barcode Gap Discovery (ABGD) on the complete dataset using Jukes-Cantor genetic distances with default settings (Puillandre et al., 2012). Jukes-Cantor genetic distances were calculated between and within clades identified using our criteria and the ABGD analysis in MEGA 6 (Tamura et al., 2013). Genetic distances are reported in Table S1.

2.4. Biogeography based on museum collections

To demonstrate the wider biogeographical distributions of each of the 23 currently described morphospecies (Plates 1–3), biogeographical data was gathered by examining material held in public collections. These included collections held at the Natural History Museum of Denmark, the Natural History Museum of London, Vrije Universiteit, Amsterdam and the Naturalis Biodiversity Center, Leiden. Additional material from the Plymouth Marine Laboratory (cruise AMT20) and from cruises AMT24 and SN105 was examined. All biogeographical data is reported in Table S2.

3. Results and discussion

The atlantid heteropods have long been divided into groups of closely related species based on morphological characters. Tesch (1908) first separated the genus *Atlanta* into four groups, the *Atlanta inflata, Atlanta turriculata, A. peronii,* and *A. inclinata* groups. The composition of these groups has since largely been revised through the addition of new species, the removal of invalid species and the creation of new species groups. Richter (1993, 1990, 1974) and Richter and Seapy (1999) recognised three new *Atlanta* species groups, the *Atlanta lesueurii, A. gaudichaudi* and *A. gibbosa* groups; thus there are now a total of seven *Atlanta* groups (Table 2). Here, we regard the genus *Protatlanta* and the genus *Oxygyrus* as their own groups, rather than the single group created by Richter and Seapy (1999). The mtCO1 phylogeny presented here supports six of the nine species groupings (Fig. 2,

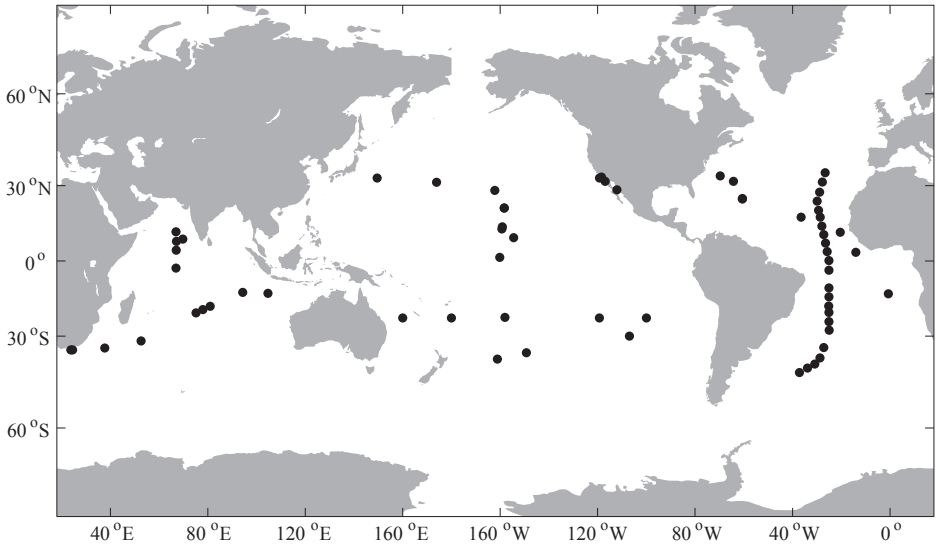

Fig. 1. Specimens for molecular analysis were gathered from a widespread set of stations. See Table 1 for detailed station locations and cruise names.

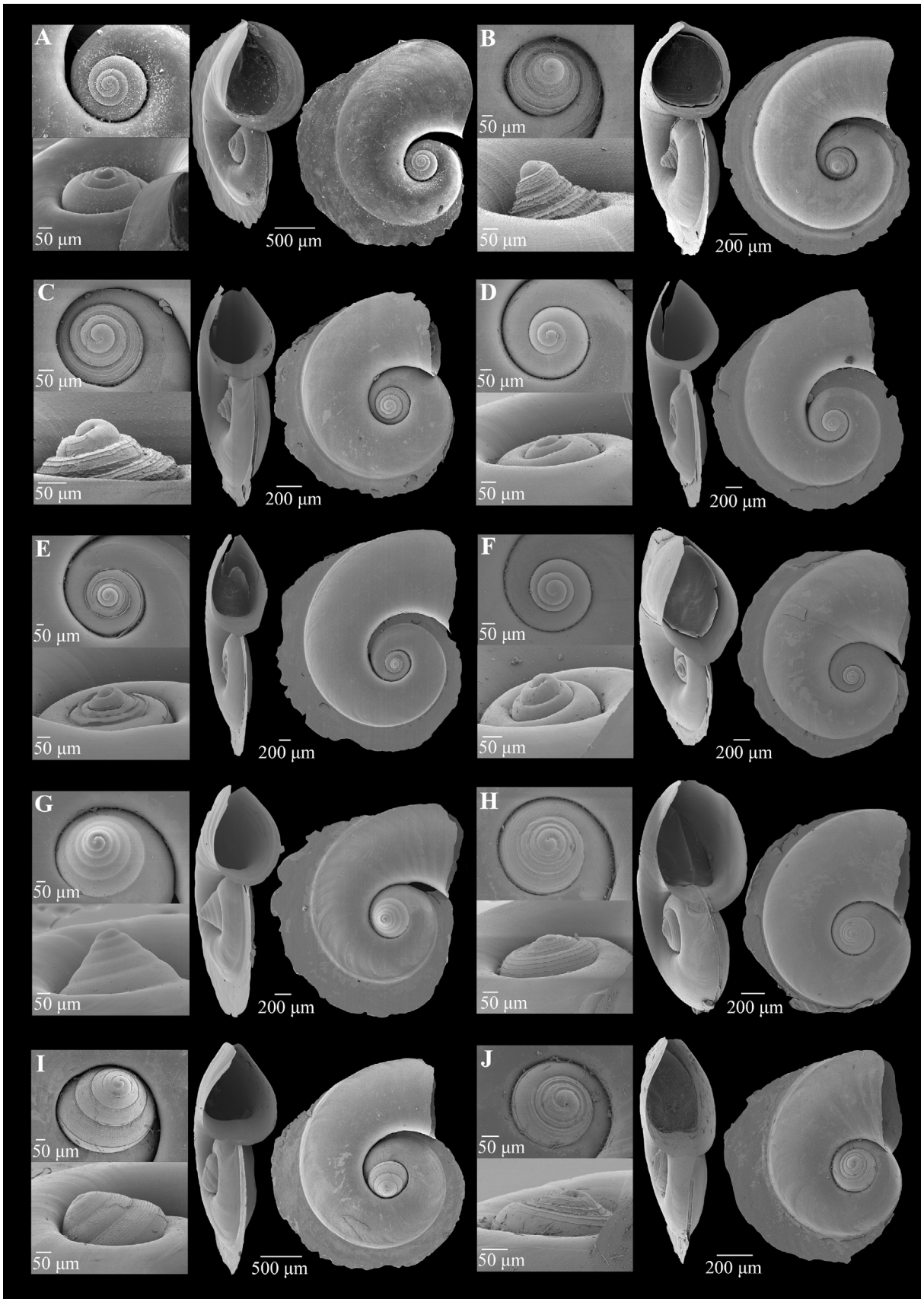

Plate 1. Scanning Electron Microscopy (SEM) images of representative specimens (A) *Atlanta ariejansseni*; (B) *Atlanta brunnea;* (C) *Atlanta echinogyra;* (D) *Atlanta fragilis;* (E) *Atlanta frontieri;* (F) *Atlanta gaudichaudi;* (G) *Atlanta gibbosa;* (H) *Atlanta helicinoidea;* (I) *Atlanta inclinata;* (J) *Atlanta inflata.*

Plate 2. SEM images of representative specimens (A) *Atlanta lesueurii;* (B) *Atlanta meteori*; (C) *Atlanta oligogyra;* (D) *Atlanta plana;* (E) *Atlanta rosea;* (F, G) *Atlanta selvagensis;* (H) *Atlanta tokiokai;* (I) *Atlanta turriculata;* (J) SEM and light microscopy images of *Oxygyrus inflatus.*

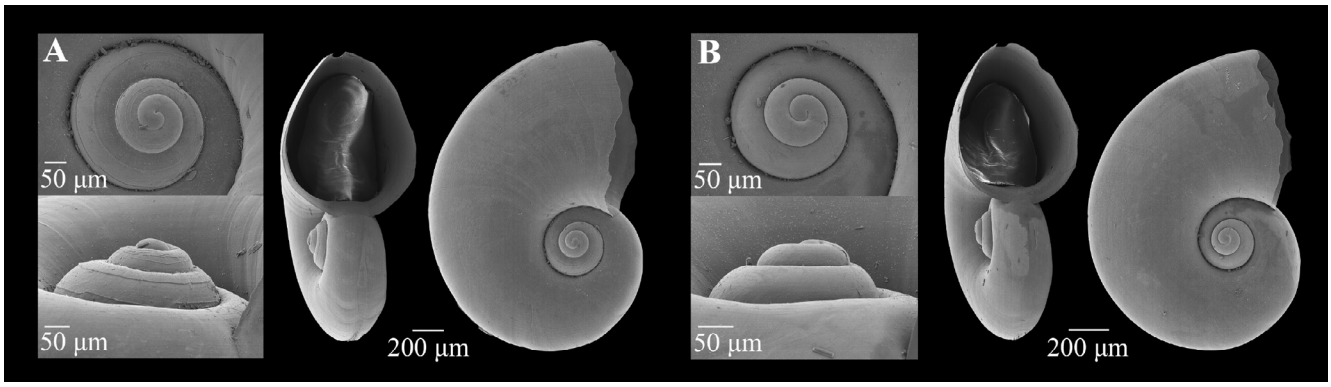

Plate 3. SEM images of representative specimens (A) *Protatlanta sculpta;* (B) *Protatlanta souleyeti.*

Table 2
Distribution of new diversity identified in atlantid species groups. Groups with * indicate those supported by the CO1 phylogeny.

Species group	Number of described species	Number of clades identified here
*Atlanta brunnea**	2	3
*Atlanta inflata**	5	6
Atlanta lesueurii	2	3
Atlanta peronii	4	8
Atlanta gaudichaudi	3	3
*Atlanta inclinata**	2	2
*Atlanta gibbosa**	2	3
*Oxygyrus**	1	3
*Protatlanta**	2	2
Total	23	33

Table 2). Within these nine species groups of the Atlantidae there are currently 23 accepted, described species (Seapy, 2011; Wall-Palmer et al., 2016a,b). However, the results of this study indicate that 23 species is a considerable underestimation of atlantid diversity.

The phylogeny indicates that mtCO1 is saturated at deeper nodes of the family Atlantidae, forming a basal polytomy. Each species group forms one or more separate branches from the base of the atlantids, resolving distinct clades well. The molecular analysis identifies a total of 33 distinct atlantid clades with good bootstrap support (> 85%); 10 clades in addition to the 23 described species (Fig. 2, Table 2). ABGD analysis also identified 33 clades, although these differ slightly from those highlighted by the phylogenetic analysis (ABGD did not identify *A. inclinata* and *Atlanta tokiokai* as separate clades, but did identify a third clade of *Atlanta oligogyra*). Only one genus, *Oxygyrus* was well-resolved (bootstrap 100%), *Protatlanta* was monophyletic, but had support of only 69%. The genus *Atlanta* and other deeper level relationships were not resolved (bootstrap < 60%). The two major lineages suggested by Richter (1961), were not supported by the tree topology, probably because of insufficient information in the relatively fast evolving mtCO1 gene.

3.1. *Atlanta brunnea* group

Prior to this study, the *A. brunnea* group contained two accepted species, *A. brunnea* and *A. turriculata* (Plates 1 and 2). Under the classification of Richter (1961), these species were considered the earliest diverged lineages of the atlantids, with a close phylogenetic relationship suggested by the shape of the radula (Richter, 1961). In this study, the mtCO1 phylogeny supports the inference of three clades in the *A. brunnea* group (Fig. 3); *A. brunnea, A. turriculata* and a new clade, with shell characteristics similar to *A. brunnea* and *A. turriculata.* This new clade is more closely related to *A. brunnea* than to *A. turriculata* (bootstrap support of 98%), with a genetic distance of 9% and 13–14% from *A. brunnea* and *A. turriculata,* respectively (Table S1). Additional diversity within this group has been recognised for some time. As early as 1852, Souleyet described the species *Atlanta involuta* alongside *A. brunnea* and *A. turriculata*, with illustrations that show a shell morphology comparable to *A. turriculata. Atlanta involuta* has not been accepted as a valid species since 1906 (Tesch, 1906) and has since been considered as a synonym of *A. turriculata* (Tesch, 1908). Van der Spoel (1976, 1972) also identified an additional clade in this group, referring to it as *A. turriculata* form B. However, it is uncertain whether these previously described forms correspond to the new clade identified in this study, particularly because the phylogeny presented here supports a closer relationship to *A. brunnea.* This new clade will herein be referred to as *A. brunnea* form B. In addition to this third clade, a single specimen of *A. brunnea* form A analysed from the Atlantic Ocean (Fig. 3) may indicate an additional genetic lineage. Genetic distances between this specimen and other *A. brunnea* form A from the Indian and Pacific oceans were 2–4%, compared to distances of 0–1% between specimens within the Indian and Pacific oceans. Richter (1961) also recognised differences between *A. brunnea* specimens from the Atlantic Ocean and specimens from the Indian Ocean. The Indian Ocean specimens had larger shells that were weakly pigmented in comparison to the Atlantic specimens, and differences in the operculum and radula were also found.

The distribution of specimens identified using shell morphology indicates that *A. turriculata* is present in the Pacific and Indian oceans, but is absent from the Atlantic Ocean (Fig. 4). This is in agreement with the specimens sequenced in this study (Fig. 3), as well as published records of *A. turriculata* (Tesch, 1949; Van der Spoel, 1976; Wall-Palmer et al., 2016c). Biogeographical data for the morphospecies *A. brunnea* indicates a broad geographical distribution in the north Atlantic, Indian and Pacific oceans, but a general absence from the equatorial regions (Fig. 4). These observations are in agreement with prior studies (Wall-Palmer et al., 2016c). The type locality for *A. brunnea* is the Indian Ocean (Table 3). Genetic analyses show that *A. brunnea* form A has a broad distribution, however, *A. brunnea* form B was only found in the southeast Pacific Ocean (Fig. 3). The two forms of *A. brunnea* may have non-overlapping distributions, in addition to a large genetic separation, suggesting that *A. brunnea* form B may be a separate species.

3.2. *Atlanta inflata* group

Richter (1973, 1961) considered species within the *A. inflata* group

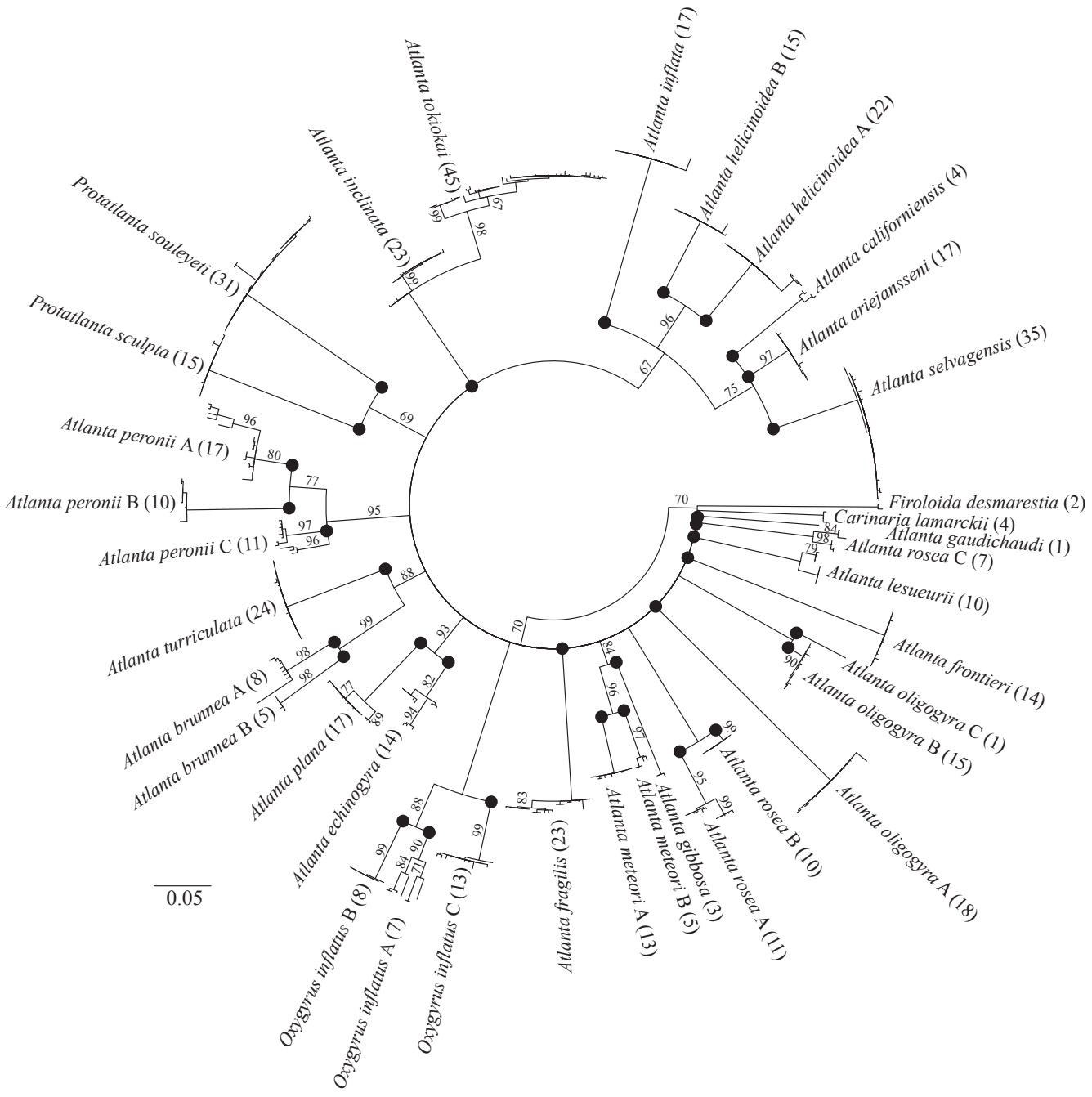

Fig. 2. 60% cut-off Maximum Likelihood best tree based on mitochondrial cytochrome *c* oxidase subunit 1 (mtCO1) sequences of all atlantid morphospecies and representatives of the heteropod families Carinariidae and Pterotracheidae. Bootstrap supports (%) are shown if less than 100%. All branches with bootstrap support < 60% have been collapsed. Branch lengths are proportional to the amount of inferred change, as indicated by the scale bar. Black circles at nodes represent clades supported by ABGD analysis. The number of sequences per clade is shown in brackets. BOLD process IDs and GenBank accession numbers for all sequences are provided in Table 1.

to have the most highly derived *Atlanta* radula along the evolutionary path towards *Protatlanta* and *Oxygyrus*. Prior to this study, the *A. inflata* group contained five species (Plates 1 and 2); *Atlanta helicinoidea, A. inflata* and three of the most recently described atlantid species: *A. selvagensis*, *A. ariejansseni* and *A. californiensis* (De Vera and Seapy, 2006; Richter and Seapy, 1999; Seapy and Richter, 1993; Wall-Palmer et al., 2016a). The molecular results indicate that this group also contains a sixth clade, which is closely related to *A. helicinoidea* (Fig. 5, Table S1). Variation within the species *A. helicinoidea* was recognised by Frontier (1966) and Van der Spoel (1976, 1972), who identified differences in shell morphology, noting a second form, *A. helicinoidea* form B that had a smaller spire with more rapidly increasing whorl diameter, and less expressed shell sculpture. Molecular data presented here shows that the morphospecies *A. helicinoidea* is represented by two clades, each with maximum bootstrap support (Fig. 5). The second clade of *A. helicinoidea* follows Van der Spoel's (1976) description of *A. helicinoidea* form B. This clade with herein be referred to as *A. helicinoidea* form B. Form A and form B have a genetic distance of 0–3% and 0–2% within each clade respectively, and a distance of 11–14% from each other (Table S1).

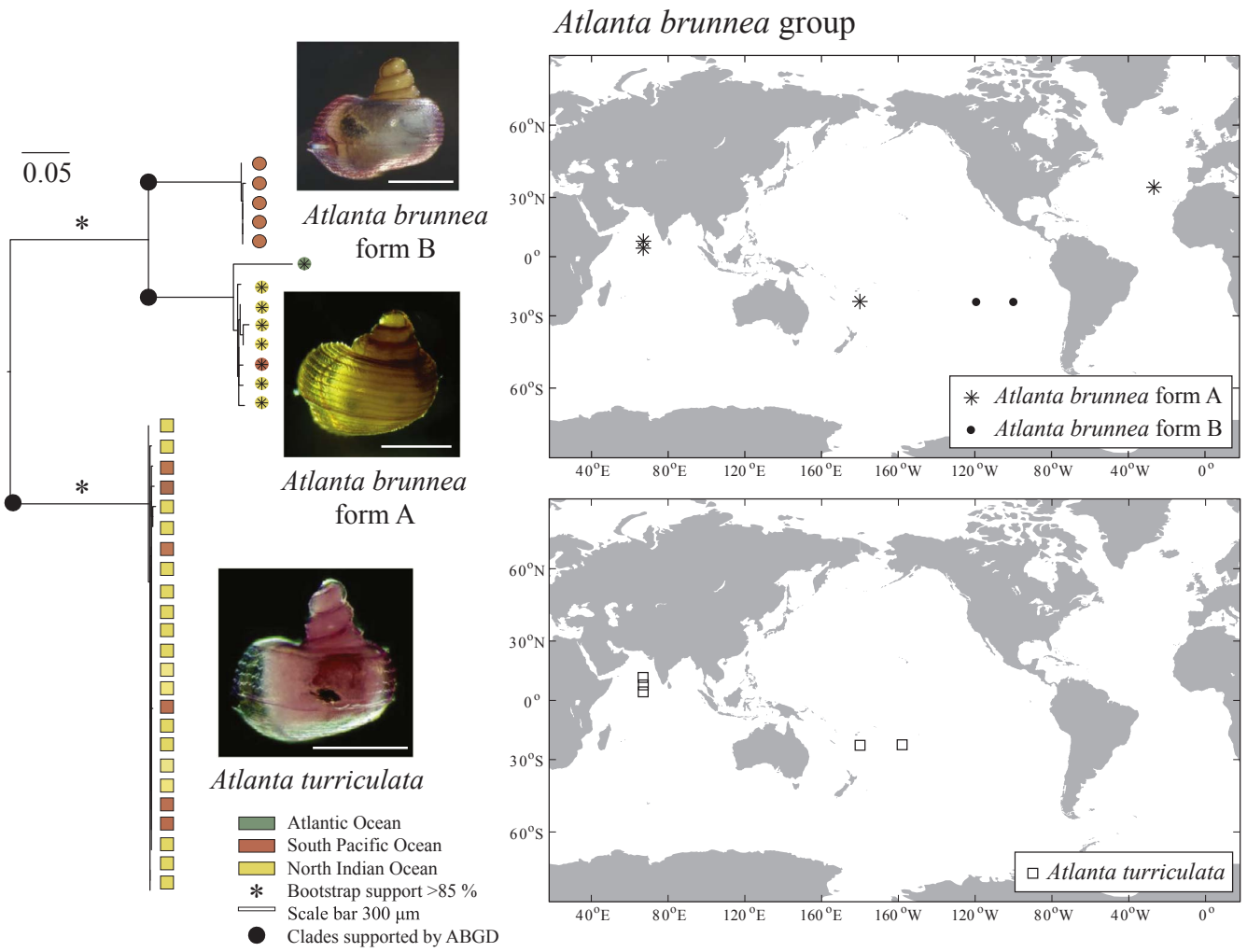

Fig. 3. Maximum likelihood tree showing relationships within the *A. brunnea* species group. Branches with bootstrap support > 85% are denoted with a star. Branch lengths are proportional to the amount of inferred change, as indicated by the scale bar. Black circles at nodes represent clades supported by ABGD analysis. Maps show the biogeographic position of sequenced specimens with different symbols for each clade. Images demonstrate the morphology of representative sequenced specimens. See Plates 1 and 2 for detailed morphological differences of morphospecies.

Observations from collections (Fig. 4) and published biogeographic information suggest that *A. helicinoidea* has a global distribution in temperate and tropical regions (Wall-Palmer et al., 2016c). The type locality for *A. helicinoidea* is the China Sea (Table 3). However, distinction of the two forms (A, B) allows refinement of their biogeography. *Atlanta helicinoidea* form A was found to have a broad distribution in the Atlantic Ocean and it also occurred at very few sites in the southeast Pacific Ocean and the Indian Ocean (Fig. 5). In the material analysed, *A. helicinoidea* form B shows a distinct distribution relative to form A, being present in the east Indian and west Pacific oceans, but absent from the Atlantic Ocean. The type locality for *A. helicinoidea* form B described by Van der Spoel (1976) off Nosy Bé, Madagascar, is concordant with this inferred distribution (Table 3). The two clades overlap at a single site in the north Indian Ocean.

In agreement with published records, the remaining four species of the *A. inflata* group have distinct distributions (Figs. 4 and 5). *Atlanta californiensis* is restricted to the northeast Pacific (Seapy and Richter, 1993) and *A. ariejansseni* is restricted to a narrow circumpolar band around the Southern Subtropical Convergence Zone (Wall-Palmer et al., 2016a). Following the description of *A. selvagensis,* Janssen and Seapy (2009) proposed that all of the records of *A. inflata* within the Atlantic and Indian oceans were actually *A. selvagensis* due to geographical separation of these species. Molecular data shows, however, that *A. selvagensis* is restricted to the Atlantic Ocean, while *A. inflata* is absent from the Atlantic Ocean, but found in the Indian and Pacific oceans (Figs. 4 and 5).

3.3. *Atlanta lesueurii group*

The *A. lesueurii* group is characterised by a shell that has a reduced number of adult and larval shell whorls (Plate 2), an evolutionary adaptation thought to reduce shell weight (Richter and Seapy, 1999). Species within this group have only 2½ whorls in the juvenile shell, potentially indicating a close relationship to the genus *Protatlanta,* whose members have 2½ to 3¼ whorls (Wall-Palmer et al., 2016b). Prior to this study, the *A. lesueurii* group was thought to contain just two species, *A. lesueurii* and *A. oligogyra.* These two species have strikingly similar shell morphology and several authors have considered the two species to be synonymous since the description of *A. oligogyra* in 1906 (Tesch, 1949; Van der Spoel, 1976). However, Richter (1986, 1974) resurrected the species name and described clear differences from *A. lesueurii,* including the distinct eye type (Richter and Seapy, 1999).

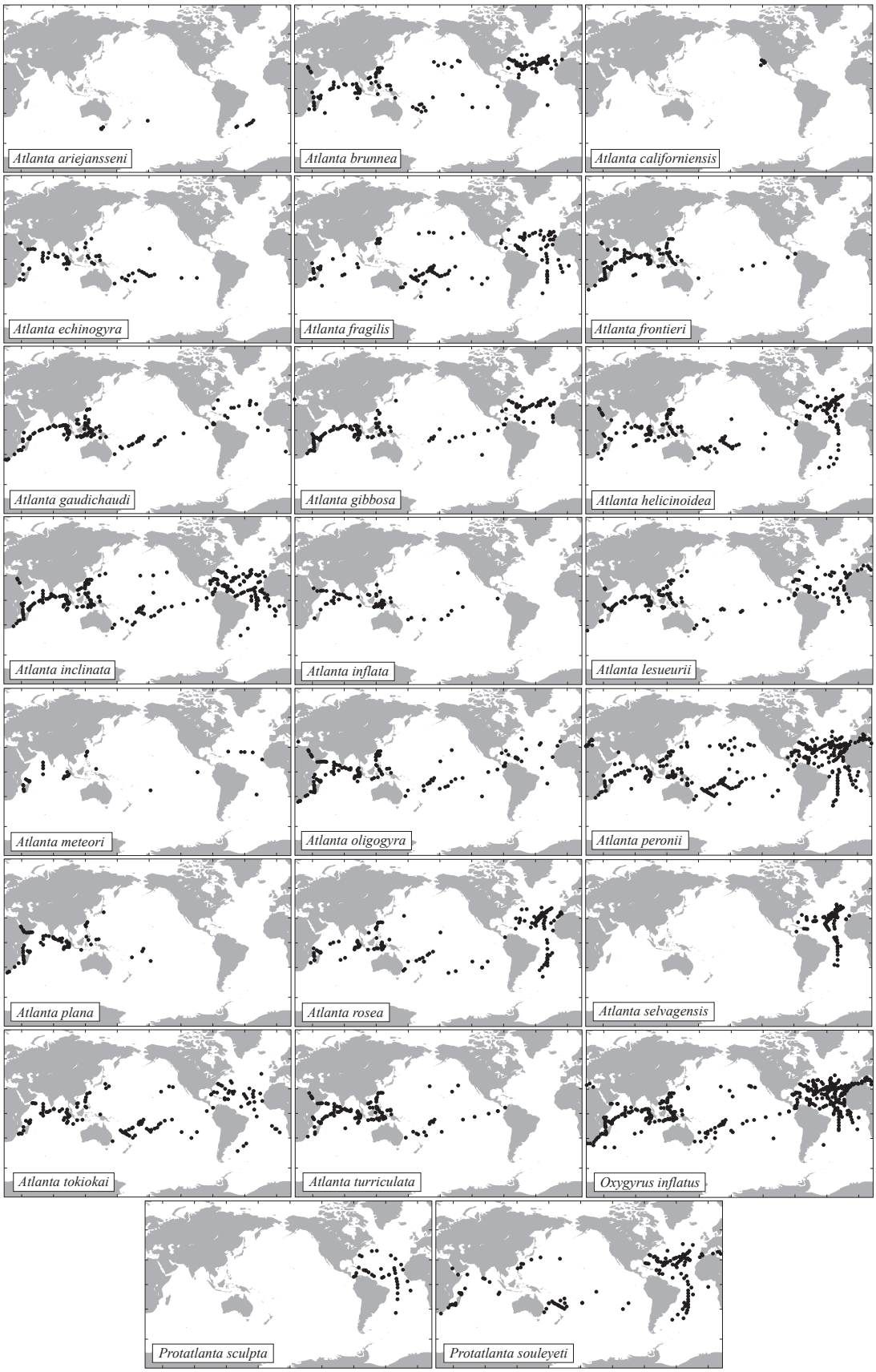

Fig. 4. Biogeography of atlantid morphospecies from plankton collections held at the Natural History Museum, Denmark; the Natural History Museum, London; Vrije Universiteit, Amsterdam, Plymouth Marine Laboratory, Plymouth; Naturalis Biodiversity Center, Leiden.

Table 3
Type localities for atlantid morphospecies. Information from Van der Spoel (1976), Van der Spoel and Troost (1972) and Richter (1993, 1972).

Species	Type locality
Atlanta ariejansseni	41.48°S, 33.86°W
Atlanta brunnea	Indian Ocean
Atlanta californiensis	33.06°N, 118.41°W
Atlanta echinogyra	Indian Ocean
Atlanta fragilis	1.33°S, 22.35°W
Atlanta frontieri	14.57°N, 73.42°E
Atlanta gaudichaudi	Pacific Ocean
Atlanta gibbosa	Unknown
Atlanta helicinoidea	China Sea
Atlanta inclinata	Atlantic Ocean
Atlanta inflata	China Sea
Atlanta lesueurii	Atlantic Ocean
Atlanta meteori	Indian Ocean
Atlanta oligogyra	5.49°S, 127.54°E
Atlanta peronii	Atlantic Ocean
Atlanta plana	Indian Ocean
Atlanta rosea	Unknown
Atlanta selvagensis	30.09°N, 15.87°W
Atlanta tokiokai	12.03°N, 68.37°W
Atlanta turriculata	Unknown
Oxygyrus inflatus	South Atlantic Ocean
Protatlanta sculpta	17.50°N, 24.02°W
Protatlanta souleyeti	18.40°N, 63.47°W

The described structure of the *A. lesueurii* group is not supported by our molecular analysis, with high genetic divergence between the two described morphospecies, *A. lesueurii* and *A. oligogyra* (Figs. 2 and 6), and a third clade that was morphologically identified as *A. oligogyra*. Both *A. oligogyra* clades have maximum bootstrap support (herein *A. oligogyra* form A and *A. oligogyra* form B), giving a total of three well-supported clades in this species group (Fig. 6). ABGD analysis also identified that a single specimen from the Atlantic Ocean may represent a further distinct clade (herein *A. oligogyra* form C). *Atlanta oligogyra* form A and form B have a genetic distance of 14–16% from each other, and a distance of 7–15% from *A. oligogyra* form C (Table S1). Despite these relatively large genetic distances, there were no obvious differences in shell morphology. Previously only known from the Pacific and Indian oceans (Wall-Palmer et al., 2016c), and with a type locality of the waters off South Lucipara Island, Indonesia (Table 3), the distribution derived here from collections material demonstrates that the morphospecies *A. oligogyra* is present throughout the Atlantic Ocean (Fig. 4). However, some minor variations in biogeography were detected between *A. oligogyra* forms A and B. Specimens of form A and form B were found to inhabit the same stations in the Indian and southwest Pacific oceans, but only *A. oligogyra* form A was found in the central and east Pacific, and only *A. oligogyra* form C was found in the Atlantic Ocean (Fig. 6).

Atlanta lesueurii has a genetic distance of 21–23%, 18–20% and 18% from *A. oligogyra* form A, form B and form C respectively (Table S1). This species has been recorded from the Atlantic, Pacific and Indian oceans (Van der Spoel, 1976; Wall-Palmer et al., 2016c), which is supported by new records here. However, *A. lesueurii* specimens for molecular analysis were not found at any Pacific Ocean stations for this study.

3.4. *Atlanta peronii* group

Members of the *A. peronii* group have long been regarded as the most common atlantid species. However, historically there has been much systematic confusion over the species that comprise this group (Richter, 1993; Tesch, 1949). Molecular results presented here indicate that this is the most diverse and complex of the atlantid groups, containing at least twice as many clades (N = 8) as there are described species (N = 4, Fig. 7, Table 2).

Atlanta peronii is the type species for *Atlanta* and is thought to have the largest shell of the Atlantidae, although several other species are now known to grow to a similar size (Richter, 1993; Seapy, 2011). Molecular results show that this 'species' has high diversity, and is comprised of three clades that differ in genetic distance by 7–15% (Table S1). No obvious differences in shell morphology were observed among the clades. *Atlanta peronii* form A and form C harbour high levels of diversity, with intraclade genetic distances of 0–7% and 0–9%, respectively. These two forms have geographical distinct subclades (Fig. 7). For example, *A. peronii* form C has two distinct populations, one in the Pacific Ocean and one in the Atlantic Ocean. *Atlanta peronii* form B has intraclade genetic distances of 0–2% (Table S1). *Atlanta peronii* has long been described to have a global distribution in tropical and subtropical waters (Van der Spoel, 1976; Wall-Palmer et al., 2016c). Despite the relatively low geographical resolution of our molecular data, we suggest that genetically distinct clades (also identified by ABGD analysis) generally inhabit different ocean regions (Fig. 7). *Atlanta peronii* form A and form B have widespread distributions in subtropical waters, although they were only found to overlap in the north Atlantic Ocean. Form C was only found in the equatorial Atlantic and the southeast Pacific Ocean, which may signify a more restricted distribution.

Atlanta rosea is another species that was originally described by Souleyet in 1852, but has been treated with caution by several authors since, due to similarities in the shell morphology to *A. peronii* (Tesch, 1949; Van der Spoel, 1976). *Atlanta rosea* is considered to be a valid species by current workers in this field, identified by the smooth, almost globular appearance of the spire, which is caused by extremely shallow whorl sutures (Plate 2). The mtCO1 phylogeny confirms that *A. rosea* is a separate species, however this described species was also found to harbour cryptic diversity with at least three distinct clades (up to five, Fig. 7) that differ in genetic distance by 3–16% (Table S1). Intraclade genetic distances are variable, with values of 0–4%, 0% and 0–8% for *A. rosea* form A, form B and form C respectively. The morphospecies *A. rosea* tends to be relatively rare amongst the atlantids, but distributed globally in temperate and tropical regions (Fig. 4). We found *A. rosea* form A to be in the Pacific and Indian oceans only, *A. rosea* form B was found only in the Atlantic Ocean and *A. rosea* form C was found in the Pacific and Atlantic oceans. However, when distributions are examined at the subclade level, distinct geographical distributions were found (Fig. 7), suggesting that the subclades each have particular environmental tolerances.

Atlanta fragilis was described by Richter (1993) from the mid Atlantic Ocean, but only a single record of this species has been published since (Burridge et al., in press a). The mtCO1 phylogeny confirms that this is a valid species, with specimens forming a single clade with a genetic distance of 12–21% from other species in the *A. peronii* group. Observations from collections indicate that *A. fragilis* is a widespread species in the Atlantic, Pacific and Indian oceans (Figs. 4 and 7).

Atlanta frontieri was also described by Richter (1993), and was found in the mtCO1 analysis to form a single clade with a genetic distance of 14–22% from other species in the *A. peronii* group (Table S1). There are very few published records of *A. frontieri* (Angulo-Campillo et al., 2011; Moreno-Alcántara et al., 2014; Seapy et al., 2003), however, these agree with our findings of an Indian and Pacific Ocean distribution and a total absence from the Atlantic Ocean (Figs. 4 and 7). The type locality for *A. frontieri* is in the eastern Arabian Sea, off the coast of India (Table 3). Investigation of the original Dana Expedition material reveals that many specimens of *A. frontieri* were collected across the Indian and Pacific oceans (Wall-Palmer, pers. obs.). It is

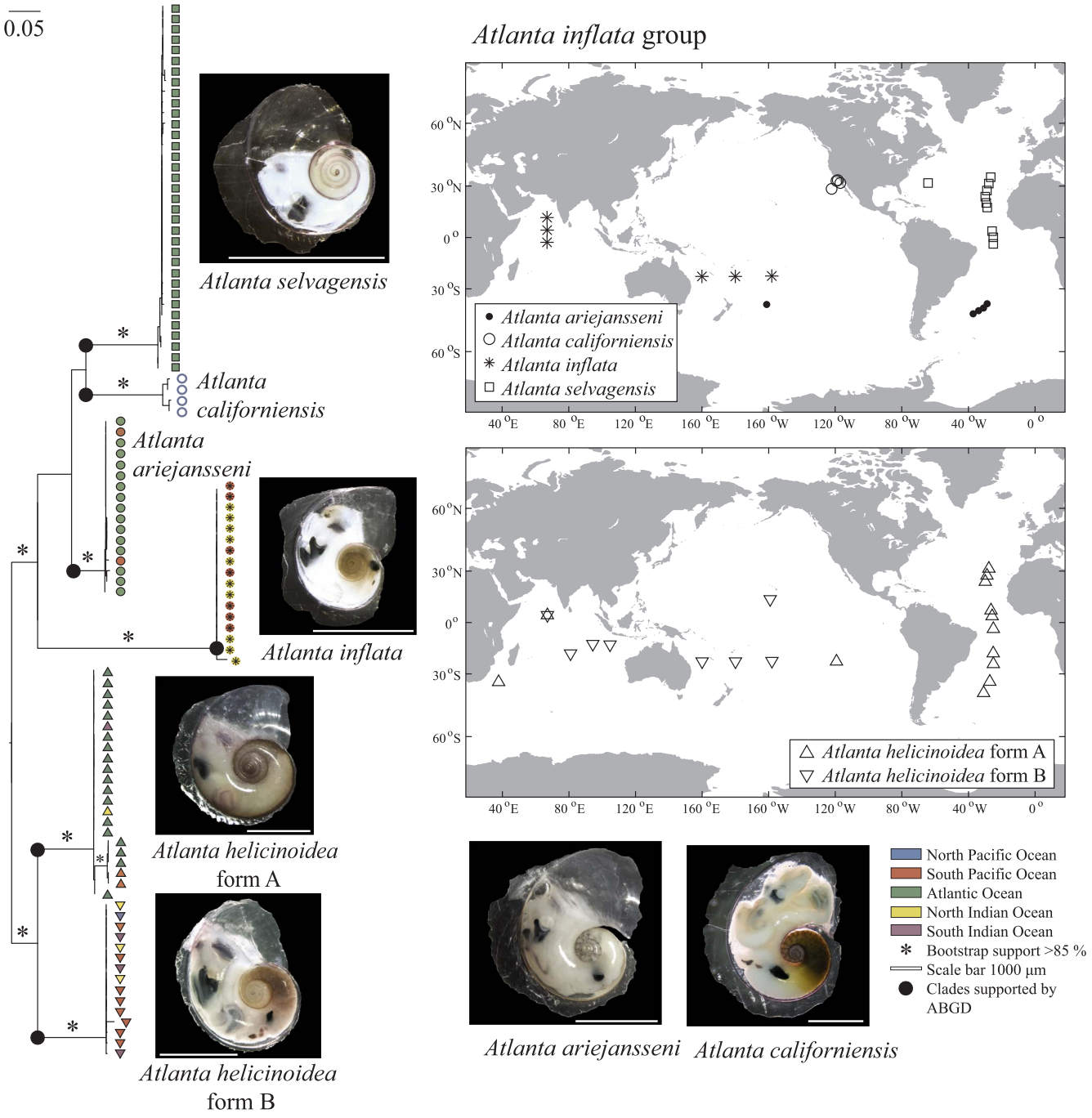

Fig. 5. Maximum likelihood tree showing relationships within the *A. inflata* species group. Branches with bootstrap support > 85% are denoted with a star. Branch lengths are proportional to the amount of inferred change, as indicated by the scale bar. Black circles at nodes represent clades supported by ABGD analysis. Maps show the biogeographic position of sequenced specimens with different symbols for each clade. Images demonstrate the morphology of representative sequenced specimens. See Plates 1 and 2 for detailed morphological differences of morphospecies.

assumed that *A. frontieri* specimens were probably included with *A. peronii* in the work of Tesch (1949) because the species was not described until 1993 (Richter, 1993).

3.5. *Atlanta gaudichaudi* group

No new clades were found within the *A. gaudichaudi* group. The mtCO1 phylogeny and ABGD analysis resolved three species as described by Seapy (2011); *A. gaudichaudi, Atlanta echinogyra* and *Atlanta plana* (Fig. 8). Although *A. gaudichaudi* has often been described as being abundant and widespread (Tesch, 1949), only a single specimen was found in the available material for molecular analysis. Two additional mtCO1 sequences of *A. gaudichaudi* from Jennings et al. (2010) were added to the analysis, however these grouped with the clades of *A. rosea,* suggesting that the specimens were originally misidentified. The interspecific genetic distance within the *A. gaudichaudi*

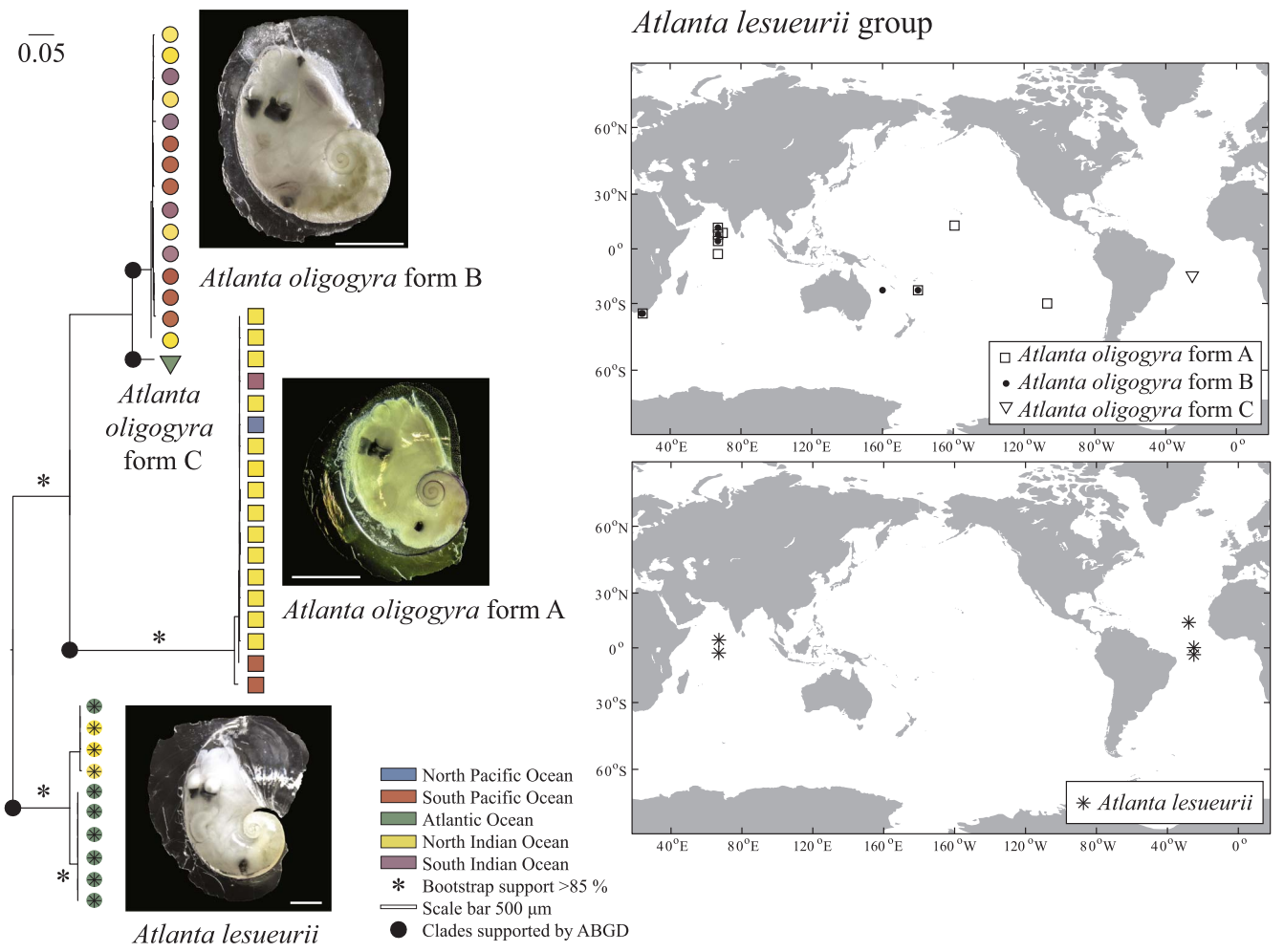

Fig. 6. Maximum likelihood tree showing relationships within the *A. lesueurii* species group. Branches with bootstrap support > 85% are denoted with a star. Branch lengths are proportional to the amount of inferred change, as indicated by the scale bar. Black circles at nodes represent clades supported by ABGD analysis. Maps show the biogeographic position of sequenced specimens with different symbols for each clade. Images demonstrate the morphology of representative sequenced specimens. See Plates 1 and 2 for detailed morphological differences of morphospecies.

group was 8–12% and intraspecific genetic distances were 0–5% and 0–4% for *A. echinogyra* and *A. plana* respectively (Table S1).

Although there are relatively few records of *A. gaudichaudi* in the Atlantic Ocean (Lemus-Santana et al., 2014), our observations from collections data show that this species is present in the Atlantic, Pacific and Indian oceans (Fig. 4). Only a single specimen of *A. gaudichaudi* was included in the molecular analysis and this was from the southern tip of Africa (Fig. 8). *Atlanta plana* and *A. echinogyra* showed similar geographical distributions in the Pacific and Indian oceans that agree with the collections data (Fig. 4) and previously described distributions for these species (Van der Spoel, 1976; Wall-Palmer et al., 2016c).

3.6. *Atlanta inclinata* group

The *A. inclinata* group, along with the *A. gibbosa* group, are characterised by shells with an inclined, triangular shaped spire (Plates 1 and 2). Richter (1990) demonstrated how this spire shape and tilt acts to create a shell that is symmetrical in form and weight. These superficially similar groups were split by Richter and Seapy (1999), who recognised that the two groups represent a convergent evolution and were more closely related to other atlantid groups than to each other. These relationships are apparent in the shape of the radula and the internal structure of the spire (Richter and Seapy, 1999).

The *A. inclinata* group is comprised of two species, *A. inclinata* and *A. tokiokai,* with very similar shell morphology. These described species are distinguished only by patterns of punctae (small projections) on the shell surface and the overall size of the shell (6–7 mm in *A. inclinata,* 3 mm in *A. tokiokai,* Seapy, 2011). The mtCO1 phylogeny supports differentiation of the two species with bootstrap supports of 98% and 99% for *A. tokiokai* and *A. inclinata,* respectively (Figs. 2 and 9). However, ABGD analysis does not support the two as separate clades, grouping *A. inclinata* and *A. tokiokai* into a single 'hypothetical species'. The genetic distance between *A. inclinata* and *A. tokiokai* is only 4–9%. The clades of *A. inclinata* and *A. tokiokai* also contain three and two subclades, respectively, yielding relatively high intraspecific genetic distances of 0–6% for *A. tokiokai* (0–3% for *A. inclinata*, Table S1).

Distribution data gathered from collections suggest that both species have widespread distributions (Fig. 4), however, the similarity in shell morphology between the two species is likely to have caused some misidentification, both in the analysis of museum collections for this study and in prior work. For example, Jennings et al. (2010) described two potential forms of *A. inclinata*. However, within the phylogeny presented here, these mtCO1 sequences for the cryptic form with a 'golden keel base' were found to group with *A. tokiokai,* whereas the

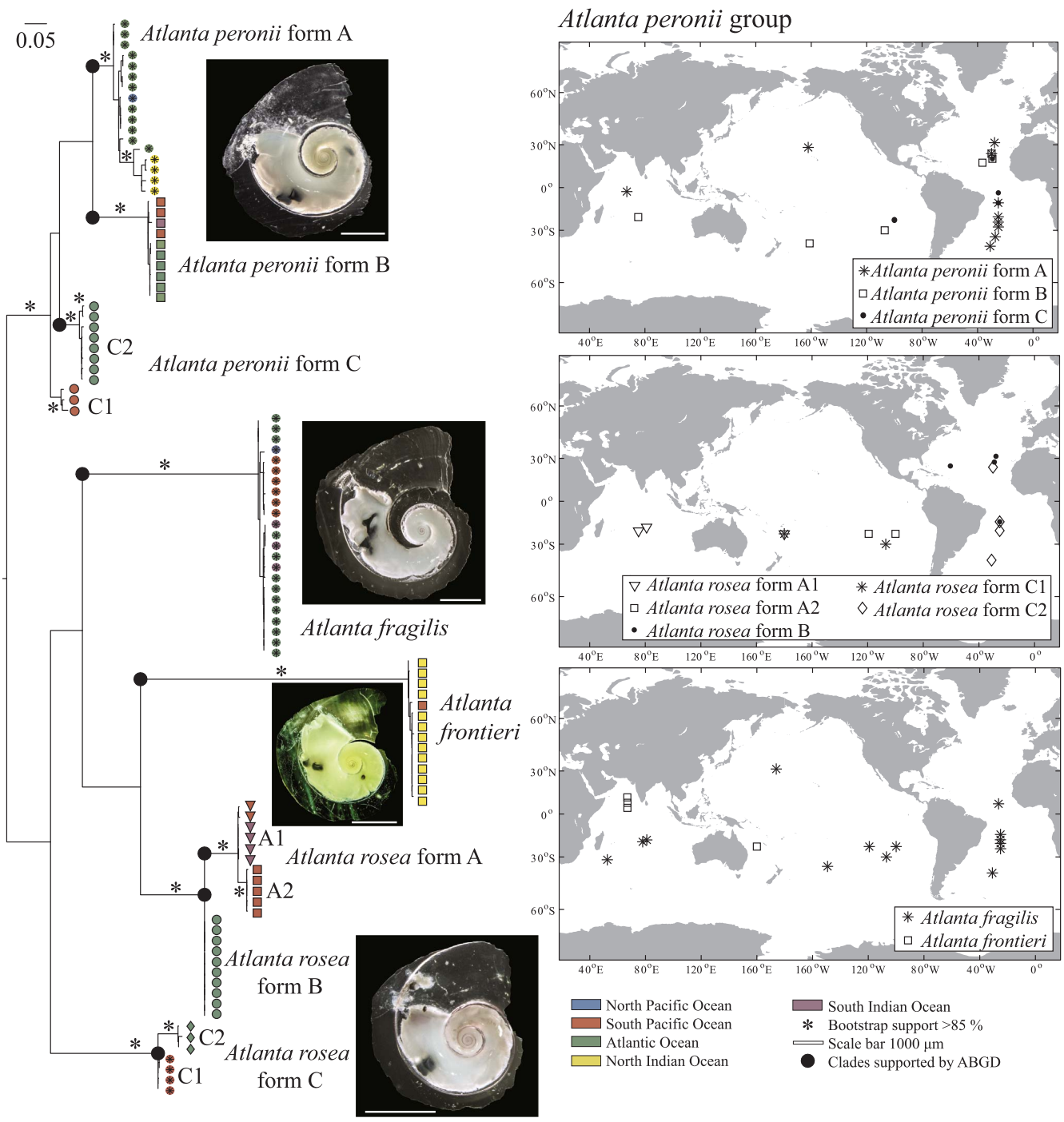

Fig. 7. Maximum likelihood tree showing relationships within the *A. peronii* species group. Branches with bootstrap support > 85% are denoted with a star. Branch lengths are proportional to the amount of inferred change, as indicated by the scale bar. Black circles at nodes represent clades supported by ABGD analysis. Maps show the biogeographic position of sequenced specimens with different symbols for each clade. Images demonstrate the morphology of representative sequenced specimens. See Plates 1 and 2 for detailed morphological differences of morphospecies.

form described with a 'transparent keel base' was found to group with *A. inclinata*. Molecular data presented here indicate that the two species have largely non-overlapping distributions. The type locality of *A. tokiokai,* close to Curaçao, is in agreement with these distributions (Table 3). Unfortunately, the only type locality data known for *A. inclinata* is that it is from the Atlantic Ocean (Van der Spoel, 1976; Van der Spoel and Troost, 1972). The subclades of each species show phylogeographic structure, with distinct clades present in the Atlantic, Pacific and Indian oceans for both species (Fig. 9). However, improved spatial coverage of molecular data is necessary to confirm these phylogeographic patterns.

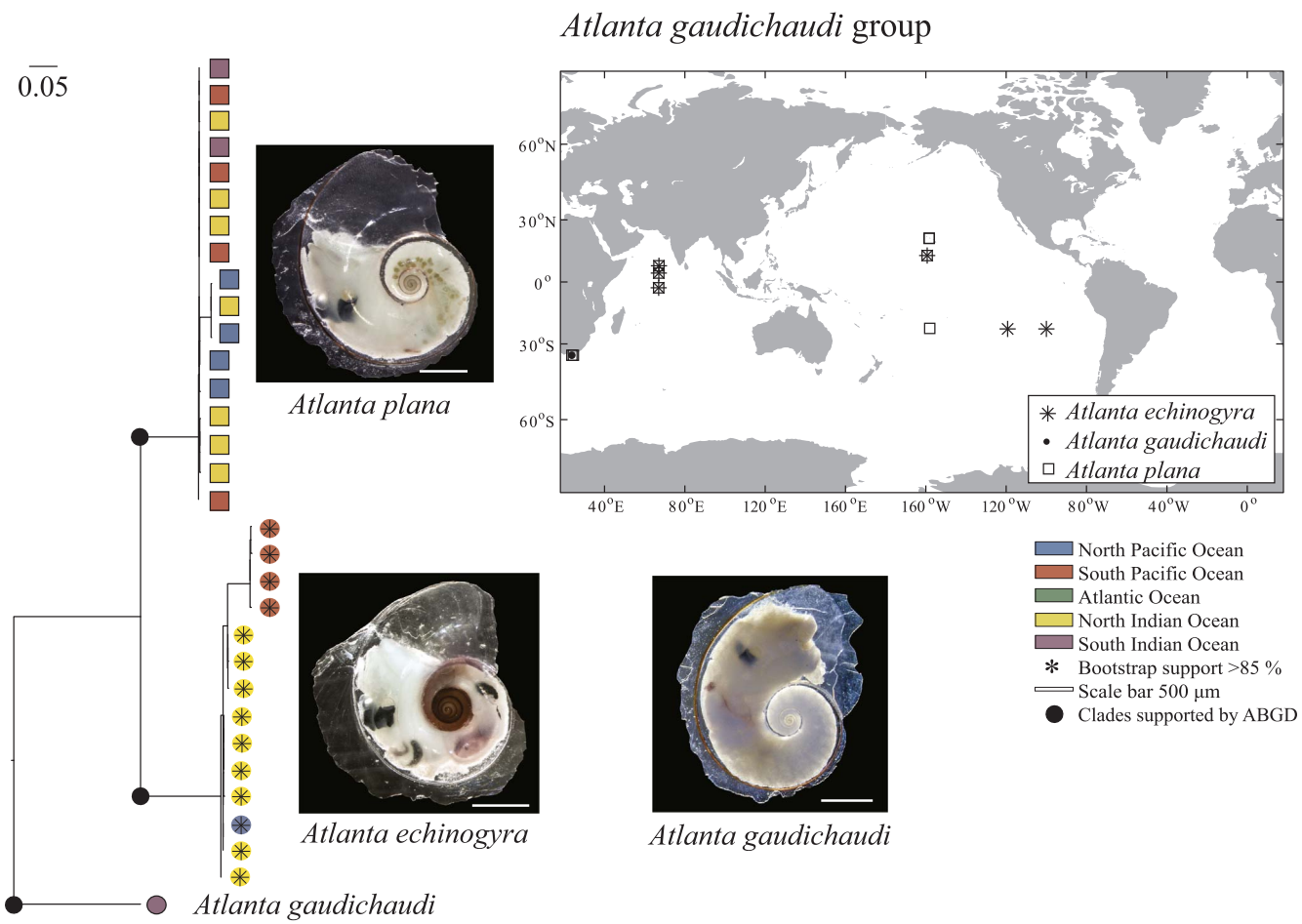

Fig. 8. Maximum likelihood tree showing relationships within the *A. gaudichaudi* species group. Branches with bootstrap support > 85% are denoted with a star. Branch lengths are proportional to the amount of inferred change, as indicated by the scale bar. Black circles at nodes represent clades supported by ABGD analysis. Maps show the biogeographic position of sequenced specimens with different symbols for each clade. Images demonstrate the morphology of representative sequenced specimens. See Plates 1 and 2 for detailed morphological differences of morphospecies.

3.7. *Atlanta gibbosa group*

The *A. gibbosa* group has shell morphology displaying a conical, tilted spire to balance the shell, a thinning of the shell walls to reduce weight and a broad shell face and tall keel to stabilise swimming. The final whorls are also partially uncoiled, similar to those observed in the heteropod family Carinariidae. Unlike the *A. inclinata* group, in which the inner walls of the spire in the adult form are decalcified, probably to reduce weight, members of the *A. gibbosa* group retain the calcified internal walls of the spire (Richter and Seapy, 1999). This may be a result of their extremely large, deep umbilicus.

The *A. gibbosa* group was thought to contain two species, *A. gibbosa* and *Atlanta meteori.* However, molecular analysis shows that there are three clades within this group, *A. gibbosa, A. meteori* and a third clade (bootstrap support of 97%, Fig. 10). The genetic distance between these three clades is 8–15% and the intraclade genetic distance is 0–1%. The third clade (herein referred to as *A. meteori* form B) does not have the large eye lenses of *A. gibbosa* and shows a closer relationship to *A. meteori,* being separated by a genetic distance of 8–10%.

Members of the *A. gibbosa* group are currently described to occur exclusively in the Indian and Pacific oceans (Wall-Palmer et al., 2016c), although there is a single record of *A. meteori* from the Selvagens Islands in the Atlantic Ocean (De Vera and Seapy, 2006). New biogeographic data presented here shows that *A. gibbosa* actually has a broad distribution in the Atlantic, Pacific and Indian oceans, although specimens of *A. gibbosa* for molecular analysis were only found in the Indian and Pacific oceans. Collection data for *A. meteori* also indicate a broad distribution, however, molecular analysis suggests a geographical separation between form A and form B. *Atlanta meteori* form A was found in the Pacific and Indian oceans, whereas *A. meteori* form B was found in the Atlantic Ocean (Fig. 10).

3.8. *Protatlanta souleyeti group*

Based on morphological analysis, Tesch (1949, 1908) suggested that *Protatlanta* had more derived shell characters and was more similar to *Oxygyrus* compared to *Atlanta. Protatlanta* has a relatively less heavy conchiolin keel, and shows more derived features in radula formation in comparison to *Atlanta* (Richter, 1961). For many years, *Protatlanta* was regarded as a monotypic genus, with the single species *P. souleyeti.* However, the species *P. sculpta,* has now been reinstated (Wall-Palmer et al., 2016b).

In agreement with the findings of Wall-Palmer et al. (2016b), additional mtCO1 sequences confirm that *Protatlanta* contains two species, *P. sculpta* and *P. souleyeti* (Fig. 11, Plate 3), separated by genetic distances of 14–17% (Table S1). While *P. sculpta* was restricted to the

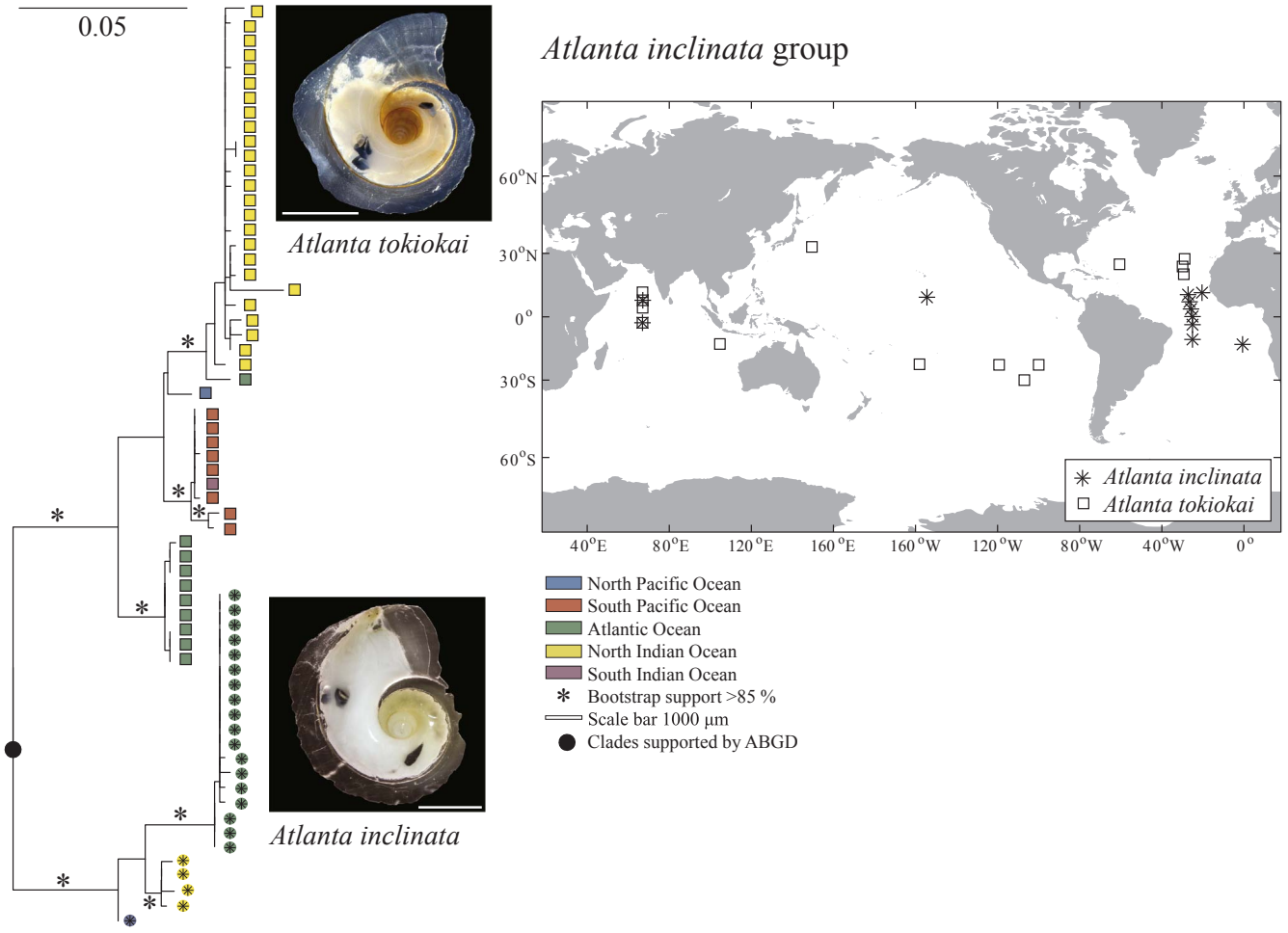

Fig. 9. Maximum likelihood tree showing relationships within the *A. inclinata* species group. Branches with bootstrap support > 85% are denoted with a star. Branch lengths are proportional to the amount of inferred change, as indicated by the scale bar. Black circles at nodes represent clades supported by ABGD analysis. Maps show the biogeographic position of sequenced specimens with different symbols for each clade. Images demonstrate the morphology of representative sequenced specimens. See Plates 1 and 2 for detailed morphological differences of morphospecies.

Atlantic Ocean, *P. souleyeti* was found to have a global distribution in temperate and tropical regions in agreement with collection data, published records and type localities (Smith, 1888; Tesch, 1949; Van der Spoel, 1976; Wall-Palmer et al., 2016b).

3.9. *Oxygyrus inflatus* group

The genus *Oxygyrus* was proposed to be the most derived group based on morphological analyses along one evolutionary path within the family Atlantidae (Richter, 1961). This is reflected in the shell composition, which, in the adult form is largely composed of conchiolin, an important adaptation to reduce shell weight and sinking velocity (Plate 2). Richter (1961) proposed that the development of the radula in the family Atlantidae is concluded in *Oxygyrus*. Given the form and size of the radula, a continuation of development along the same trajectory would be impossible without the development of unsuitable morphology.

Oxygyrus is currently thought to be monotypic, however, the mtCO1 phylogeny demonstrates that the genus is more diverse than previously believed, and is unlikely to be monotypic (Fig. 12). Phylogenetic and ABGD analyses identified three clades of *Oxygyrus* with genetic distances of 7–13% from each other (Table S1). *Oxygyrus inflatus* form B and form C have intraclade genetic distances of 0–1%. *Oxygyrus inflatus* form A is diverse relative to the rest of the *Oxygyrus* group with phylogeographic structure (subclades A1 and A2) and an intraclade genetic distance of 0–7%. A second, but now not valid species, *Oxygyrus rangii* was described by Gray (1850) and may represent one of these newly recognised *Oxygyrus* clades. Tesch (1908, 1906) remarked on the conspicuous differences between *O. inflatus* and *O. rangii* shell morphology that were originally described by Souleyet (1852). Tesch was not entirely convinced that *O. rangii* was not merely the young stages of *O. inflatus,* however, definite differences in the shape of the radula median plate were observed. In a later study of a global collection of material from the Dana Expedition, Tesch (1949) discounted all other species of *Oxygyrus,* leaving only *O. inflatus*. The lack of adult specimens obtained for molecular analysis in this study prevents the morphological characterisation of the new clades identified here, and their comparison to previously described, but presently non-valid species of *Oxygyrus*. Variation in the radula should certainly be investigated in future molecular work to aid in morphologically differentiating between these new clades. Specimens examined in this study did not show any clear differences in shell morphology, other than some colour variation of the soft tissues. However, soft tissue colour is likely to be influenced by diet and is often not a species-specific trait.

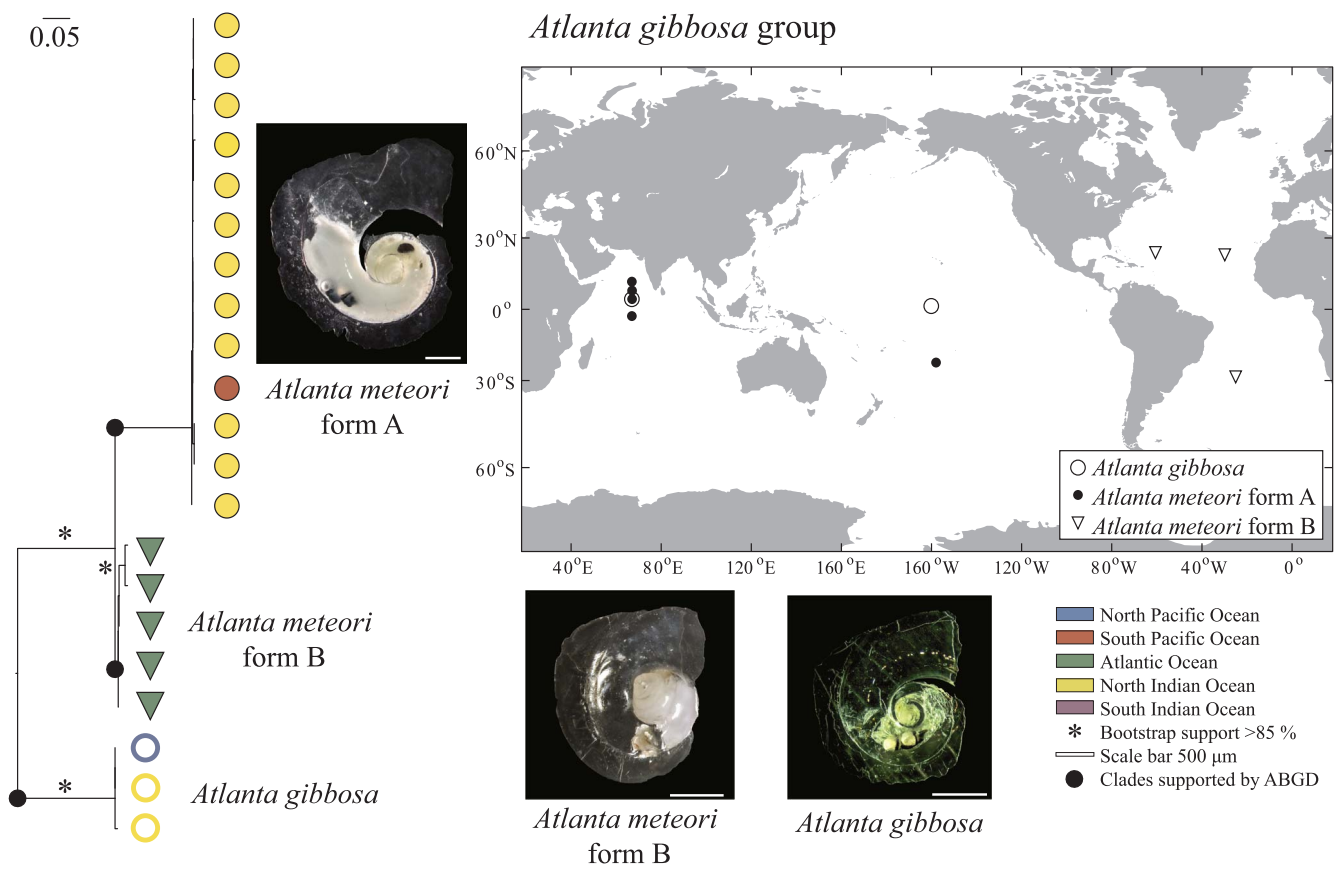

Fig. 10. Maximum likelihood tree showing relationships within the *A. gibbosa* species group. Branches with bootstrap support > 85% are denoted with a star. Branch lengths are proportional to the amount of inferred change, as indicated by the scale bar. Black circles at nodes represent clades supported by ABGD analysis. Maps show the biogeographic position of sequenced specimens with different symbols for each clade. Images demonstrate the morphology of representative sequenced specimens. See Plates 1 and 2 for detailed morphological differences of morphospecies.

Oxygyrus inflatus is known to occupy all tropical and subtropical ocean regions, and the type locality for this species is the south Atlantic Ocean (Tesch, 1949; Van der Spoel, 1976; Wall-Palmer et al., 2016c). The clades identified here appear to occupy distinct ocean regions with little biogeographical overlap. *Oxygyrus inflatus* form A is comprised of two subclades, one was found in the north Atlantic subtropical gyre and one was found in the south Pacific. *Oxygyrus inflatus* form B has an equatorial Atlantic Ocean distribution, while form C has a Pacific and Indian Ocean distribution (Fig. 12).

3.10. Cryptic diversity

Molecular analysis shows that seven of the 23 described morphospecies are formed of two or more clades. Van der Spoel (1972) noted that, even within the described species, there were often pairs of morphologically similar species (e.g. *A. selvagensis* and *A. inflata*). Two of the new clades identified in this study, *A. helicinoidea* form B and *A. brunnea* form B, show clear differences in shell morphology and probably represent new species. For the remaining new clades, high resolution morphological information, such as SEM imaging and geometric morphometrics may reveal distinct morphological characters, however, no obvious morphological differences were found between closely related clades in this study (*A. oligogyra*, *A. peronii, A. rosea, A. meteori* and *O. inflatus*). Similar cryptic diversity has been identified across a range of planktonic organisms, where previously assumed wide distributions of a morphospecies have been found to consist of a number of evolutionary distinct populations, many of which have more restricted distributions (Aurahs et al., 2009; Bode et al., 2017; Burridge et al., 2015; Cornils et al., 2017; Goetze et al., in press; Halbert et al., 2013; Hirai et al., 2015; Jennings et al., 2010; Morard et al., 2009). This evolutionary divergence is often caused by physical separation across land masses or by ocean currents, sometimes following large scale environmental changes, such as those caused by glacial cycles or geological events (Bowen et al., 2016; Goetze et al., in press; Sromek et al., 2015). Similar patterns are revealed by the cryptic clades found in this study, which often have distributions that do not overlap with their closely related clades (*A. meteori, O. inflatus* and some *A. peronii* and *A. rosea*). In some cases, however, there is overlap in the distribution of cryptic clades. In these cases, information from independently inherited regions of the genome should be acquired to test whether sympatric clades represent reproductively isolated species or not. For example, both forms of *A. oligogyra* were found to occupy the same stations in the Indian and southwest Pacific oceans. These two clades may represent distinct species that could be vertically separated due to environmental gradients, or competition for resources. Such depth segregation of closely related, or cryptic clades has been found in other planktonic organisms, including foraminifera, copepods and chaetognaths (Fragpoulu et al., 2001; Kehayias et al., 1994; Mackas et al., 1993; Weiner et al., 2012). Further molecular analysis of specimens sampled from numerous narrow vertical ranges would be necessary to investigate the vertical distribution of these two forms of *A. oligogyra.*

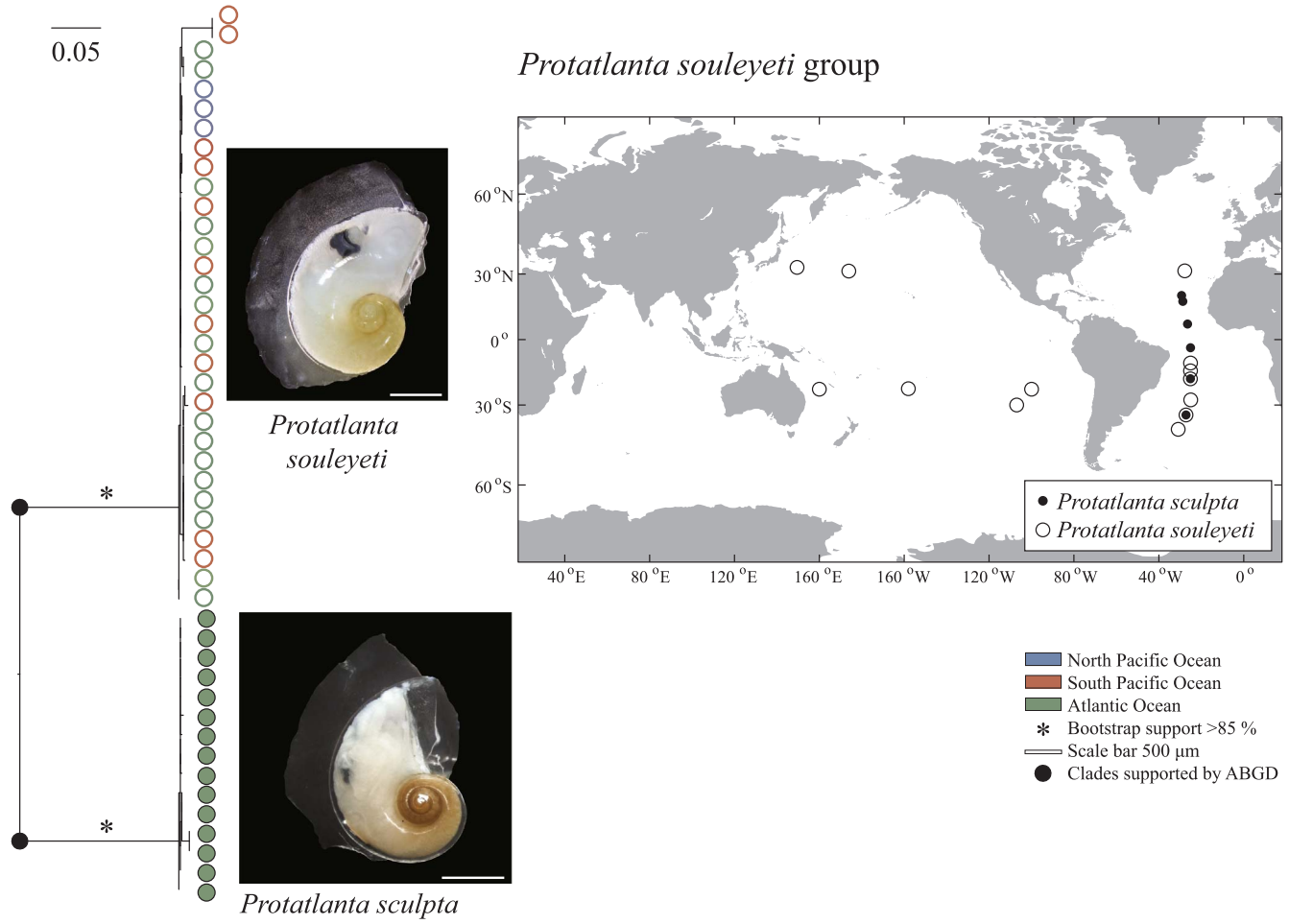

Fig. 11. Maximum likelihood tree showing relationships within the *P. souleyeti* species group. Branches with bootstrap support > 85% are denoted with a star. Branch lengths are proportional to the amount of inferred change, as indicated by the scale bar. Black circles at nodes represent clades supported by ABGD analysis. Maps show the biogeographic position of sequenced specimens with different symbols for each clade. Images demonstrate the morphology of representative sequenced specimens. See Plate 3 for detailed morphological differences of morphospecies.

3.11. Patterns in biogeography

Results reported here indicate that although some atlantid species have broad, often global geographical distributions in temperate and tropical regions (Richter and Seapy, 1999; Tesch, 1949; Van der Spoel, 1976), many others have more restricted distributions. The mtCO1 phylogeny demonstrates that most atlantid species groups contain overlooked diversity, and when this diversity is taken into account, more specific biogeographical patterns are revealed. Richter (1993) also noted, with the description of *A. fragilis* and *A. frontieri,* that improved understanding of the atlantids, and other plankton groups, demonstrated more ecological specialization to particular ocean habitats than was generally supposed, with water masses forming true boundaries to gene flow and promoting evolution of new species. Genetic studies of several other planktonic taxa, including pteropods (Burridge et al., 2015) also support this inference (Bowen et al., 2016; Peijnenburg and Goetze, 2013).

The biogeography of newly recognised atlantid clades presented here is based on limited geographical sites, and is in no way complete. However, even with these initial collections, several patterns within the atlantid distributions can be seen. A number of clades show similar patterns of distribution within particular ocean regions (Table 4). In the Atlantic Ocean, 26% of the Atlantic clades and subclades occur in the north and south oligotrophic gyres (*A. peronii* form A, *A. rosea* form B and C, *A. meteori* form B and *P. souleyeti*). Conversely, some clades were found only in the equatorial waters (*A. lesueurii, A. peronii* form C, *A. inclinata* and *O. inflatus* form B) or only the north or the south gyre (*A. brunnea* form A, *A. ariejansseni, A. oligogyra* form B, *A. peronii* form B, *A. tokiokai* and *O. inflatus* form A). These distributions correspond to ocean provinces described on the basis of biogeochemical characteristics and ecosystem dynamics (Longhurst, 1998), and are reflected in other plankton groups, such as pteropods, copepods and amphipods (Burridge et al., in press a, in press b; Hirai et al., 2015; Woodd-Walker et al., 2002). Several atlantid clades also show an unusual distribution in the Pacific Ocean, with 15% of all Pacific clades and subclades found exclusively in the southeast region (*A. brunnea* form B, *A. helicinoidea* form A, *A. peronii* form C, *A. rosea* form A2). Conversely, 37% of Pacific clades were found to be present in the subtropical gyre in the southwest Pacific, but not in the southeast (*A. brunnea* form A, *A. turriculata*, *A. helicinoidea* form B, *A. inflata, A. oligogyra* form B, *A. frontieri, A. rosea* form A1, *A. plana, A. meteori* form A and *O. inflatus* form C). The clear separation of clades coincides with extremely oligotrophic waters on the eastern margin of the subtropical gyre, with species that are restricted to the southeast Pacific occurring under more oligotrophic conditions. This region can also be identified in the distribution of other planktonic organisms, including several species of copepod;

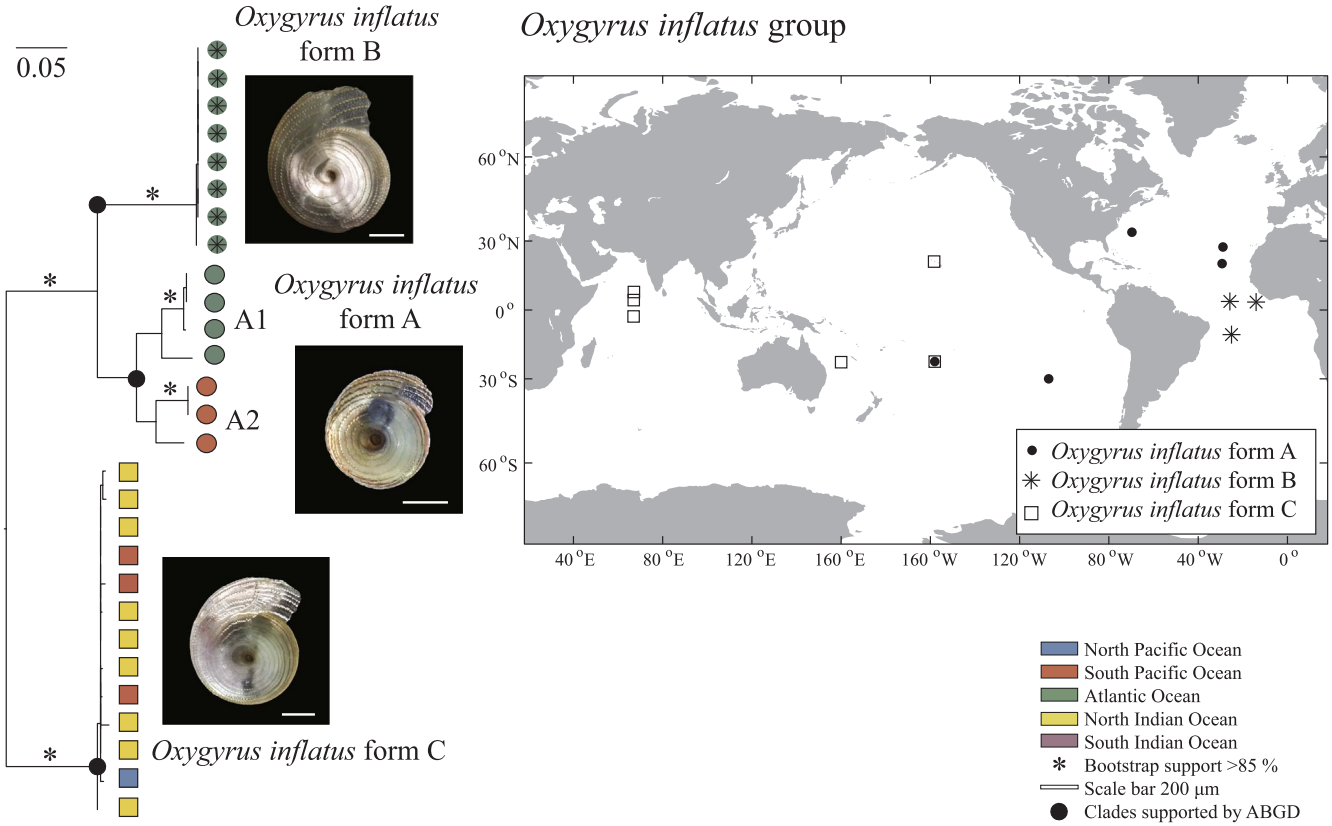

Fig. 12. Maximum likelihood tree showing relationships within the *O. inflatus* species group. Branches with bootstrap support > 85% are denoted with a star. Branch lengths are proportional to the amount of inferred change, as indicated by the scale bar. Black circles at nodes represent clades supported by ABGD analysis. Maps show the biogeographic position of sequenced specimens with different symbols for each clade. Images demonstrate the morphology of representative sequenced specimens. See Plate 2 for detailed morphological differences of morphospecies.

Pleuromamma abdominalis, Nannocalanus minor, Nannocalanus elegans (Hirai et al., 2015; Razouls et al., 2017) and pteropod species of the genera *Cuvierina* (Burridge et al., 2015).

4. Conclusions

In this study, molecular analysis (mtCO1) has been useful in identifying currently accepted atlantid species and revealing previously undetected diversity. mtCO1 sequences of 437 new atlantid specimens, combined with 52 published sequences, demonstrated that genetic diversity within the family Atlantidae is likely over 30% higher than previously thought. At least 10 atlantid clades may represent new, or previously discounted species, in addition to the 23 accepted species. However, to identify species boundaries with confidence, concordant observations in morphology, behaviour and/or distribution must be obtained, in addition to these molecular inferences. Such an approach is also important for identification of these new clades in the absence of molecular analysis, for example, in the fossil record. In some cases, distinct clades have been recognised previously (*A. helicinoidea* form B, *A. brunnea* form B) based on morphological characteristics, and formal descriptions of these new species should be completed. In other cases, a lack of obvious morphological differences between closely related clades (e.g. *A. peronii*) requires more advanced techniques, such as microCT scanning and 3D geometric morphometric analysis, to assess whether concordant variation in morphological traits can be found.

Many of the new clades detected by molecular analysis were found to have distinct geographic distributions that are largely congruent with the Longhurst biogeographical provinces and are comparable to other zooplankton groups. Increased spatial coverage is now needed geographically and vertically in the water column to fully understand the habitat boundaries of each genetic clade. This significant task can only be achieved if the plankton research community reports more consistently on the presence and absence of atlantid species. This in turn depends upon increased awareness of the atlantids, including facilitation of their identification. Such observations will allow determination of environmental tolerances for each species, which will be the key to understanding what constitutes a range shift in response to future ocean changes, as well as providing a more accurate understanding of pelagic diversity and improve interpretation of the atlantid fossil record.

The mtCO1 phylogeny demonstrates that further investigation of the evolutionary history of atlantids is needed. Deeper evolutionary relationships could not be resolved in this study and, although six of the nine original species groups were supported by mtCO1, the evolutionary trajectories proposed by Richter (1961) were not resolved. Further research using more conservative nuclear markers is needed to investigate this, and may give us insight into the timing and potential drivers of atlantid speciation. Variation in spire morphology and shell size, composition and thickness makes the atlantids an extremely interesting group within which to study the evolution of buoyancy and other pelagic adaptations. The considerable variation in atlantid shell morphology may be a response to occupying different habitats (different depths, turbulence), or it may represent different solutions to a specific challenge associated with living in the same habitat.

There are currently few active researchers with sufficient expertise to identify atlantid species based on morphological characteristics. This study provides a reference of mtCO1 sequences that will ensure the

Table 4
Summary of atlantid biogeography based on mtCO1 phylogeny and supported by ABGD analysis.

Clade	North Atlantic gyre	Equatorial Atlantic	South Atlantic gyre	North Indian Ocean	South Indian Ocean	SW Pacific Ocean	SE Pacific Ocean	North Pacific Ocean
Atlanta brunnea	X			X		X		
Atlanta brunnea form B							X	
Atlanta turriculata form A				X		X		
Atlanta ariejansseni			X			X		
Atlanta californiensis								X
Atlanta helicinoidea form A	X	X	X	X	X		X	
Atlanta helicinoidea form B				X	X	X		X
Atlanta inflata				X		X		
Atlanta selvagensis	X	X						
Atlanta lesueurii		X		X				
Atlanta oligogyra form A				X	X	X	X	X
Atlanta oligogyra form B			X	X	X	X		
Atlanta fragilis		X	X		X		X	X
Atlanta frontieri				X		X		
Atlanta peronii form A	X		X	X				X
Atlanta peronii form B	X				X	X	X	
Atlanta peronii form C		X					X	
Atlanta rosea form A1					X	X		
Atlanta rosea form A2							X	
Atlanta rosea form B	X		X					
Atlanta rosea form C1						X	X	
Atlanta rosea form C2	X		X					
Atlanta echinogyra				X			X	X
Atlanta gaudichaudi					X			
Atlanta plana				X	X	X		X
Atlanta inclinata		X		X				X
Atlanta tokiokai	X			X	X	X	X	X
Atlanta gibbosa				X				X
Atlanta meteori form A				X		X		
Atlanta meteori form B	X		X					
Protatlanta sculpta	X	X	X					
Protatlanta souleyeti	X		X			X	X	X
Oxygyrus inflatus form A1	X							
Oxygyrus inflatus form A2						X	X	
Oxygyrus inflatus form B		X						
Oxygyrus inflatus form C				X		X		X

continued study of this group and its inclusion in future molecular (particularly metabarcoding) and zooplankton research. The ability to identify specimens reliably using molecular techniques will allow us to expand this field of research, learning more about the largely unknown ecology of atlantids, including swimming mechanisms, predatory behaviour, migration and reproduction.

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Author contributions

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Alice K. Burridge: Specimen collection and contributed considerably to manuscript preparation.

Erica Goetze: Specimen collection and contributed considerably to manuscript preparation.

Frank R. Stokvis: Molecular and data analysis. Contributed to manuscript preparation.

Arie W. Janssen: Specialist in taxonomy, contributed to manuscript preparation.

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Christopher W. Smart: Contributed to manuscript preparation and provided funding.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2017.11.004.

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