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On the identity and distribution of *Atlanta inflata* Gray, 1850 (Gastropoda, Pterotracheoidea, Atlantidae) in the world's oceans

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We dedicate this paper to Louis François Auguste Souleyet (1811 - †1852), who collected, illustrated and described a number of new species of Atlanta, *but who in the end is no longer acknowledged as their author.*

Comparisons of the atlantid heteropod *Atlanta inflata* Gray, 1850, from the Pacific, Atlantic and Indian Oceans led to the conclusion that this species only occurs in the Pacific Ocean, while the populations in the Atlantic and Indian Oceans belong to a different species. Individuals from all three oceans are small (<2 mm) and have a keel that does not penetrate between the penultimate and last shell whorls, is tall with a truncate leading edge, and has a yellow-brown to brown keel base. Both taxa have a comparable range of spiral ridge ornament on the shell spire and share the same eye and opercular types. Characteristics that distinguish the two taxa are the number of whorls comprising the shell spire and the presence or absence of spire suture colouration. We conclude that the Atlantic/Indian Ocean taxon belongs to *A. selvagensis* De Vera & Seapy, 2006, described from the northeastern Atlantic Ocean. A lectotype is designated for *Atlanta inflata* Gray, 1850.

Key words: Gastropoda, Pterotracheoidea, *Atlanta inflata, Atlanta selvagensis*, morphology, distribution, lectotype designation.

INTRODUCTION

In addition to a number of other species in the genus, most authors over the past 1.5 centuries have regarded *Atlanta inflata* as having been introduced by Louis François Auguste Souleyet. In his 1852 (p. 378) paper, a rather extensive description was given for this species under the heading '*Atlanta inflata*, nobis', with reference to a plate 19 figs 21-28. These illustrations, however, refer to a separate atlas, published in folio size already several years earlier (presumably in 1841, see References) under the authorship of Eydoux & Souleyet. In this atlas, in an explanation to plate 19, the species was indicated only with its vernacular name 'Atlante renflée'; it was only in the 1852 publication that Souleyet latinized this name to *Atlanta inflata*.

Prior to the release of Souleyet's final text in 1852, however, Maria Emma Gray (1842-1857) published a five-volume iconography that contained a collection of illustrations 'etched for the use of students' and all copied from the then-existing literature. Part of the illustrations included in her volume 3 (dated 1850) were copied from the Eydoux & Souleyet atlas of 1841. In the 'Explanation of the plates' (volume 4, 1850: 46), her husband

John Edward Gray referred to Eydoux & Souleyet's vernacular names (although 'Atlante' was incorrectly cited as 'Atalante'). Unfortunately for Souleyet (but apparently unnoticed by him), J.E. Gray (vol. 4, 1850: 101) also had latinized the vernacular names. In doing so, he formally became the author of Souleyet's illustrated, but yet undescribed taxa. Most probably Souleyet never found out about this because he passed away as a victim of yellow fever in Martinique in the same year that his 1852 paper was published in Paris. A nice portrait of M.E. and J.E. Gray can be found on the website: http://www.npg.org.uk/collections/search/person.php?LinkID=mp54539. Unfortunately we have not been able to trace a portrait of Souleyet.

Following earlier authors (*e.g.*, Smith, 1888), Van der Spoel (1976: 137) wrote in his introduction to the family Atlantidae: 'As a commonly accepted rule, the names given by Gray (1850) are not used for taxa in this family in favor to those proposed by Souleyet (1852) though these are junior synonyms. This rule is also followed in this paper in favour to stability in nomenclature'. This procedure, however, is not supported by the ICZN Code, and therefore the names given by Gray must be given priority.

Several of the Latin names of J.E. Gray (1850) differ from the much more commonly applied ones given by Souleyet two years later. *Atlanta fusca* Souleyet, 1852 (latinized from 'Atlante brune') became an objective junior synonym of *A. brunnea* Gray, 1850. For *A. quoyana* Souleyet, 1852 (latinized from 'Atlante de Quoy') the older, valid name must be *A. quoyi* Gray, 1850, and *A. helicinoidea* Gray, 1850, became the valid name for *A. helicinoides* Souleyet, 1852. Since Mrs Gray's illustrations were copied from, and gave reference to Eydoux & Souleyet's atlas, the illustrated specimens and the material described by Souleyet (1852) remain syntypes on the basis of which the species have to be interpreted. In addition, *A. inflata* now also has to go under the authorship of J.E. Gray, 1850. Syntypical material of these taxa is housed in BM(NH), London (Gray, 1855, see below; Tesch, 1906: 1) and in MNHN, Paris (see Tesch, 1908: 2; Van der Spoel, 1976: 207-209). The latter author designated lectotypes for several of Souleyet's 1852 taxa (namely for *Atlanta gaudichaudi*, *A. lesueuri, A. inclinata*, *A. helicinoides* and *A. fusca*) in the Paris collection. Van der Spoel (p. 209) referred to two syntypes of *A. inflata* 'with desolved shell of which separation is impossible'.

Gray (1855) listed 'type and illustrated' specimens that were received at BM(NH) from 'the Executors of the late M. Souleyet', which included material from the voyage of La Bonite. Curiously, in January 1855 Gray wrote in the Preface to this list 'The text of the Zoological part of the "Voyage" has not yet been published', and he refers to the explanation of the plates in Eydoux & Souleyet (1841). Furthermore, he stated that he used as the Latin names in his list those given 'by M. Souleyet, …. in a small MS. list which accompanied the Collection, as being that which he had intended to have used if he had lived to publish the descriptions'. Among the species listed were *Atlanta fusca* and *A. helicinoides*, which indeed are Souleyet's names, but also *A. quoyi* instead of Souleyet's name *A. quoyana*. Gray (1855) did not refer to his earlier latinization of these names.

As a note of possible interest to the reader, the name *Atlanta inflata* Gray, 1850, is a junior homonym of *Atlanta inflata* d'Orbigny, 1834, a shelled pteropod in the family Limacinidae that is currently indicated as *Heliconoides inflata*. Janssen & Seapy (2009) submitted an application to the ICZN to place the name *A. inflata* Gray, 1850, on the Official List of Specific Names in Zoology, with the endorsement that it is not invalid by reason of its being a junior primary homonym of *A. inflata* d'Orbigny.

Atlanta inflata Gray, 1850, was described by Souleyet (1852: 378), based on specimens collected from the western North Pacific in Chinese seas ('les mers de la Chine') during the Bonite Expedition of 1836/1837. In a monograph on the Heteropoda collected by the

Siboga Expedition in the Indonesian Archipelago, *A. inflata* was among the species characterized by Tesch (1906: 55). For this paper he also studied the syntype material of Souleyet, deposited in BM(NH), London. Then, in 1908, Tesch undertook a revision of the Atlantidae based on material from the Indian Ocean, North Atlantic, and the type material of Souleyet (1852) deposited in MNHN, Paris. He made no distinction between *A. inflata* collected from the different oceans, assuming that the species was cosmopolitan. In his monograph on the heteropods from the circumglobal Dana Expedition of 1928-1930, Tesch (1949) did not include any distributional information on *A. inflata*.

Most taxonomic studies published on species of *Atlanta* since 1949 have been based on material from the North Atlantic Ocean, inclusive of the Mediterranean, and, secondarily, the Indian Ocean. Richter (1961) characterized distinctive radular, eye and opercular morphological types among the atlantids, based upon specimens collected from the Mediterranean Sea. He reported that the shell spire of *A. inflata* from the Mediterranean lacked the spiral ridges present on shells from the North Atlantic, and that his Mediterranean specimens corresponded to *A. quoyana* Souleyet (1852: 383), which Tesch (1908) suggested was a synonym of *A. inflata*. In his 1968 study on heteropods from the Gulf of Naples, Richter included drawings (p. 351, figs 1, 2) of *A. inflata* shells that represented the extremes in spiral ridge ornament. Six years later, Richter (1974) characterized and illustrated (using scanning electron micrographs) *A. inflata* from the northern Indian Ocean. In his 1976 book, Van der Spoel (p. 149, fig. 149) included a description of *A. inflata* and illustrated the species with drawings of a shell (attributed to Richter) that bore prominent spiral ridge ornament on the spire. He also gave a complete listing of the species' synonyms. In comparisons of species pairs that were very similar in appearance, Richter (1987) included a series of eight scanning electron micrographs (pl. 3 figs 17-24) that illustrated the range of spire ornament development in *A. inflata*. Lastly, in a paper on the Heteropoda of the South Atlantic Ocean, Richter & Seapy (1999: 635-6, fig. 6B) characterized *A. inflata* and illustrated the shell with scanning electron micrographs and a transmitted light photograph.

Taxonomic papers on Atlantidae from the Pacific Ocean have been far fewer, and the earlier studies are problematical. Tokioka (1955a, b) described and illustrated *A. inflata* from Japanese waters. His drawings of the right side of the shell were essentially in agreement with that of Souleyet (1852: pl.19 fig. 21; reproduced here in fig. 2) in terms of the number of whorls comprising the spire and the presence of a tall, truncated keel. However, his drawings of shells in apertural view showed two different spire shapes. Also, in the 1955b paper, which was based on a much larger sample size (29 versus 3 specimens), the range in shell diameters was 1.6-2.5 mm. This range exceeds the maximal diameter of 1.5 mm reported for *A. inflata* from Hawaiian waters and mostly exceeds the largest (1.8 mm) of the Souleyet syntypes (see Results). A possible explanation for the discrepancies in maximal size and shell spire shapes is that Tokioka appears to have included individuals that belonged to another species, i.e. *A. echinogyra* Richter, 1972, that was described seventeen years later. This suggestion is supported by the facts that (1) the maximal size of *A. echinogyra* is 2.5 mm (Richter, 1987), (2) Tokioka (1955b: 249) described the spire as 'purplish or purplish brown in colour and tall and wide, with the apical angle 84°-125°, 107° on average', and (3) Tokioka's drawings (1955a: fig. 4X'; 1955b: fig. 7A') of larval and adult shells in apertural views show conical spires in agreement with his 1955b description of the spire's shape.

The opercula of eight atlantid species were described and illustrated by Tokioka (1961), based on material from the eastern tropical Pacific. He characterized (p. 286) the operculum of *Atlanta inflata* as "possessing a row of craw-like ornaments around the central portion of the gyre". This gyre morphology is absent, however, in the opercula of *A.*

inflata from Hawaiian waters (Seapy, 1990a). These seemingly contradictory findings were resolved by Richter (1972), who identified the "echinate" gyre morphology identified by Tokioka as a defining character of his newly described species, *A. echinogyra*.

In 1964, Zhang described (in Chinese) and illustrated the shells of atlantids from waters off China. Zhang included *Atlanta inflata*, although this appears to be a misidentification for two reasons: (1) in the illustrated specimen (p. 197) the keel inserts between the penultimate and last shell whorls, which has never been reported by any other authors; (2) the reported shell diameters (3.0 to 6.5 mm) are far in excess of the maximal shell diameter of 1.8 mm recorded for *A. inflata* from the Souleyet collections in the western North Pacific (see Results).

It was not until 1990 that two studies employed scanning electron micrographs to provide details of shell morphology of atlantids from the Pacific Ocean. The first paper (Seapy, 1990a) characterized 13 species of atlantids, including *Atlanta inflata*, from Hawaiian waters. The second, a Ph.D. thesis by Newman (1990), provided descriptions of 14 atlantid species, including *A. inflata* that was collected in low numbers from eastern Australian and New Guinean waters.

Following the taxonomic revisions of the genus *Atlanta* by Tesch (1908, 1949), *A. inflata* has been widely recognized as a cosmopolitan species from tropical to subtropical latitudes in the world's oceans. In addition, most taxonomic studies (prominently those of Richter cited above) have been based upon animals collected from the Atlantic Ocean and, secondarily, the Indian Ocean. With an absence of comparable studies from the Pacific Ocean until 1990, the Atlantic and Indian Ocean studies have served to characterize the species. In this paper we compare *Atlanta inflata* from the Pacific, Atlantic and Indian Oceans using its syntype material from the western Pacific, as well as published and unpublished data, and scanning electron micrographs of shells.

METHODS

The shell characteristic that first led us to suspect that *Atlanta inflata* in the Pacific Ocean was not the same species as that in the Atlantic Ocean was the number of whorls comprising the shell spire. In the adult shell the location where the first adult whorl is produced following larval metamorphosis is indicated by a rapid increase in whorl width. The whorl in which a rapid increase in width occurs differs among atlantid species, as was reported by Seapy (1990a: table 1) for *Protatlanta souleyeti* (Smith, 1888) and eleven species of *Atlanta*. Seapy used this character to separate groups of species in a dichotomous key (pp. 128-129). As a taxonomic character this is obviously a substantial improvement over reports by earlier authors of the total number of whorls comprising the adult shell, which increases with shell growth and becomes less and less predictive in the larger species (*e.g.*, the largest atlantid, *A. peronii*, reaches a diameter of 10 mm).

In a subsequent paper, Seapy (in Richter & Seapy, 1999) modified this character to specify the location, to the nearest ¼ whorl, of the rapid increase in whorl width. In turn, this defined the number of whorls comprising the shell spire, *i.e.*, the larval portion of the adult shell (protoconch). Based on examination of scanning electron micrographs of shells from eleven species of Hawaiian atlantids in Seapy (1990a, and unpublished) and published papers for the remaining seven species, the number of spire whorls was reported in Richter & Seapy (1999: table 4) for *Protatlanta souleyeti* and 18 species of *Atlanta*, with spire sketches (1999: fig. 1) for six of the species.

To count the number of whorls comprising the shell spire in a consistent manner, the following procedure was followed (see fig. 1). The shell is oriented under a dissection microscope with the nucleus of the embryonic shell (protoconch I) directed upward in the

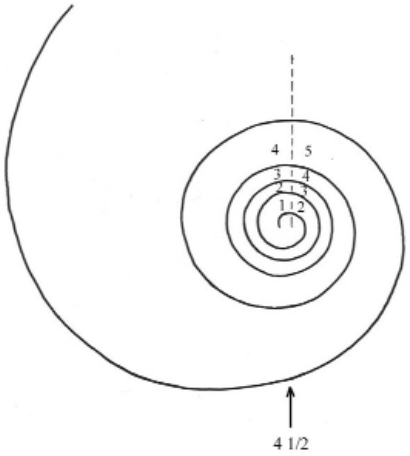

Fig. **1**. Sketch of *Atlanta inflata* shell whorls, illustrating the method of whorl counting employed by Richter & Seapy (1999) and herein. The dashed line originates at the midpoint of the embryonic shell cap, and the location where each whorl ends and the next whorl begins is indicated by the successive whorl numbers. The arrow at the bottom of the sketch denotes the approximate point where whorl width begins to increase rapidly and determines the number of whorls comprising the shell spire (here = 4½). Sketch modified from Seapy (1990a: fig. 6i).

field of view, and an imaginary line is drawn upwards from the center of the embryonic shell. Counting outwards, the ending of a whorl and beginning of the next one (1-2, 2-3, etc.) are then determined. In the case of *A. inflata* (fig. 1), the number of complete spire whorls is 4, followed by ½ of the fifth whorl; thus, the number of spire whorls is 4½.

Independently, and unknown to each other until in recent years, we have used this taxonomic character for the adult shell in extant (RRS) and fossil (AWJ) atlantid species. The method of counting spire whorls devised by AWJ for gastropod shells in general (*in* Janssen & De Vogel, 1965; Gittenberger & Janssen, 1998; Janssen, 2007) is slightly different: the imaginary line extending outward begins at the base of the embryonic shell cap and is oriented 90˚ clockwise to the line used by RRS. The result is that the total number of whorls is ¼ whorl *less* than that using the method of RRS. In the present paper the RRS method of whorl counting is applied without exception. We consider this taxonomic character to be of particular importance to workers who study fossil shells and shells collected from bottom samples because body remains are lacking and characteristics of the soft parts (*e.g.*, the types of eyes, opercula and radulae) and any colouration of soft parts, whorl sutures and the keel base, if present in life, have disappeared completely.

The following abbreviations are used: BM(NH) - The Natural History Museum, London (UK); MNHN - Muséum national d'Histoire naturelle, Paris (France); RGM - National Natural History Museum *Naturalis*, fossil Mollusca (formerly Rijksmuseum van Geologie en Mineralogie), Leiden (The Netherlands); RMNH - National Natural History Museum *Naturalis*, recent Mollusca (formerly Rijksmuseum van Natuurlijke Historie), Leiden (The Netherlands); SMF - Senckenberg Museum, Frankfurt am Main (Germany); TFMC - Museo de Ciencias Naturales de Tenerife (Canary Islands). For the authors, the abbreviations RRS and AWJ are used.

RESULTS

While working on the identification of a large collection of holoplanktonic gastropods from the eastern Mediterranean, AWJ expected to find the species of *Atlanta* that have been recorded commonly from the Mediterranean; viz. *Atlanta brunnea* Gray, 1850 (in literature usually found as *A. fusca* Souleyet, 1852), *A. inflata* Gray, 1850, *A. lesueurii* Gray,

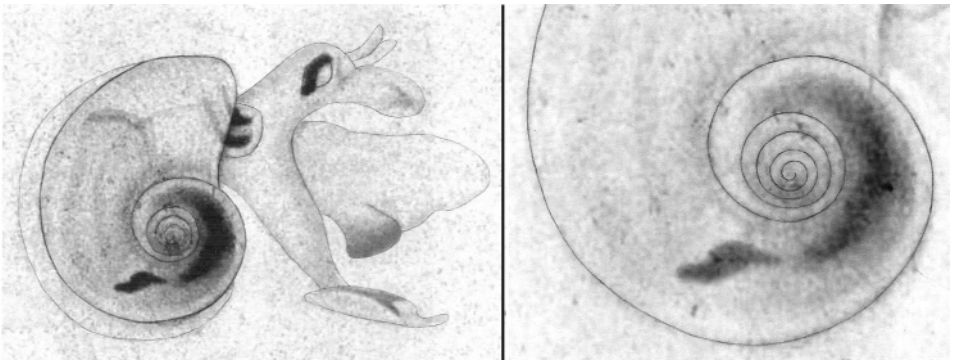

Fig. **2**. Drawing of a complete specimen (left), with an enlarged view of the spire region (right) of *Atlanta inflata* Gray, 1850 (from Eydoux & Souleyet, 1841: pl. 19 fig. 21). Drawing scanned by RRS from an original colour transparency of the Eydoux & Souleyet figure taken by AWJ. The resultant images were converted from colour to black and white, and tracings were added for clarification. In this drawing the initial whorls seem to increase more regularly in diameter than in the lectotype (fig. 4), but the number of larval whorls is identical.

1850 and/or *Atlanta peronii* Lesueur, 1817. Identifications were made using the dichotomous key in Seapy (1990a), resulting in the satisfactory recognition of three of the above four taxa. Most of the remaining specimens had small shells that were less than 2 mm in diameter and appeared to belong to *A. inflata*, although most had spires with ¾ to 1 fewer whorls than recorded by Seapy for North Pacific *A. inflata*.

A closer look at Richter's 1968, 1974 and 1987 drawings and photographs of *Atlanta inflata* shells from the Mediterranean, North Atlantic and Indian Oceans revealed that most of these shells had spires of 3½ or 3¾ whorls instead of the 4½ whorls in Hawaiian *A. inflata*. In addition, the Mediterranean specimens examined by AWJ displayed the same range in expression of spiral ridge development as the ones studied by Richter (1987), varying from near absence to fully developed. These observations were supported by further examination of specimens from the Atlantic and Indian Oceans identified as *A. inflata* and deposited in the SMF collections by G. Richter. Importantly, none of these specimens reached the number of spire whorls shown by Seapy in Hawaiian *A. inflata*. The strong suspicion then developed that the Atlantic, Mediterranean and Indian Ocean specimens represented a different species than that identified from the Pacific, and that the species was closely related to, if not identical with, *Atlanta selvagensis* De Vera & Seapy, 2006, from the northeastern Atlantic. To decide whether or not the above observations and interpretations were correct, we carried out an extended correspondence that ultimately resulted in the present paper.

Our first objective was to determine which of the two forms of *Atlanta inflata* (Pacific Ocean or Atlantic/Indian Oceans) was before Souleyet (1852) when he described and illustrated the species. In the drawing of *A. inflata* in Eydoux & Souleyet (1841: pl. 19 fig. 21; reproduced here in fig. 2), the spire whorl that expands rapidly is the fifth and the number of spire whorls is 4½ (in agreement with the shell sketch and scanning electron micrographs of *A. inflata* in Seapy (1990a: figs 6I, 11A-D).

Additionally, thanks to the much appreciated cooperation of Ms Kathie Way and Mrs Amelia MacLellan of BM(NH), one of us (AWJ) was able to study the remaining syntypes of *Atlanta inflata*. Two samples were available, with 3 (BMNH 1854.7.24.308) and 11

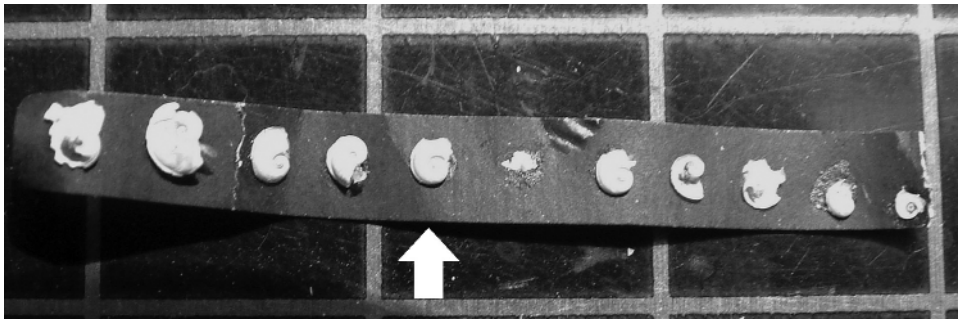

Fig. **3**. Syntypes of *Atlanta inflata* Gray, 1850 (sample BMNH 1854.7.24.69). Grid size of background is 10 mm. Arrow indicates the lectotype specimen illustrated in fig. 4.

(BMNH 1854.7.24.69) specimens, respectively. An interesting detail is that according to the labels, these samples were purchased from a certain 'E. Parzudaki', a fact not mentioned by Gray (1855). The sample of 3 specimens includes dried out soft parts without any shell remaining. The eleven specimens in the other sample are glued to a strip of paper (fig. 3).

For some specimens no more than fragments remain, while other specimens are severely damaged or are glued with their apical side downward. All in all just 4 specimens are present in which the number of larval whorls and other characteristics of the early whorls can be observed. The shells range from 1.20 to 1.80 mm, all have reasonably strong spiral ornament on the spire whorls, and in each of them the whorl expanding rapidly is the fifth (table 1).

Specimen number	Shell diameter (mm)	Number of spire whorls
3	1.80	4½
5	1.56	4¾ (lectotype)
7	1.48	4¾
10	1.20	4¼

Table **1**. Shell diameters and the number of spire whorls of four syntypes of *Atlanta inflata*. Specimen numbers and data are taken from fig. 3. (counting from left to right). In specimen 10, with the lowest number of larval whorls, an irregularity occurs in whorl 4; apparently a repaired damage or similar growth interruption.

As the syntype specimens are extremely delicate, no SEM images could be made. One of the better specimens (no. 5, arrow in fig. 3) clearly shows the boundary between the larval shell and the teleoconch (reproduced as a camera-lucida drawing here in fig. 4). We herewith designate this specimen as the lectotype of *Atlanta inflata* Gray, 1850.

The following characteristics are shared between *Atlanta inflata* from the Pacific Ocean and the taxon (hereafter referred to as *A. inflata*?) from the Atlantic and Indian Oceans:

(1) Adult shell diameter, excluding the keel, small (<2.0 mm). Regional variability in maximal size appears to exist in both the Pacific and Atlantic taxa. In the Pacific, shell size in *A. inflata* is best known from the specimens collected in two opening-closing net studies off leeward Oahu, Hawaii (Seapy, 1990b, 2008). In the first study (based on 352 specimens) the largest shell was 1.46 mm, with only 15 shells (or 4.3%) between 1.40 and 1.49 mm. In the second study, which included fall and spring sampling periods (with 314 and

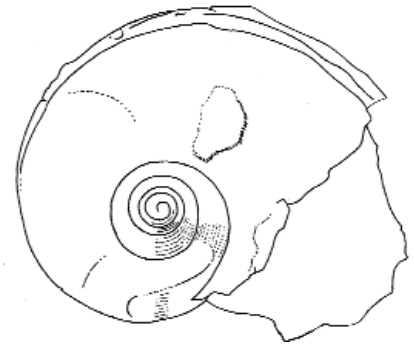

Fig. **4**. Lectotype of *Atlanta inflata* Gray, 1850. Leg. Eydoux & Souleyet, 1836-1837, Chinese Sea. BM(NH) 1854.7.24.69.

550 specimens of *A. inflata*, respectively), shell diameters were determined and are summarized here in Table 2.

In the fall, the largest shell was 1.27 mm, while in the spring the largest was 1.48 mm (with only 4 shells, or 0.7% of the total in the 1.40-1.49 mm size class). Most shells, however, were smaller than 1.20 mm; only 8 shells (1.5% of the total) were 1.30-1.39 mm and 20 (3.6%) were 1.20-1.29 mm. Combining the two sampling periods, only 12 of the 864 specimens (1.4%) had shell diameters of 1.30 mm or larger.

From the western Pacific, the syntype shells of *Atlanta inflata* (fig. 3) included one that

	0.60-0.69	0.70-0.79	0.80-0.89	0.90-0.99	1.00-1.09	1.10-1.19	1.20-1.29	1.30-1.39	1.40-1.49
September	58 (18.5)	71 (22.6)	66 (21.0)	39 (12.4)	38 (12.1)	28 (8.9)	14 (4.5)	-	-
April	54 (9.8)	158 (28.7)	162 (29.5)	77 (14.0)	51 (9.3)	16 (2.9)	20 (3.6)	8 (1.5)	4 (0.7)
Combined	112 (13.0)	229 (26.5)	228 (26.4)	116 (13.4)	89 (10.3)	44 (5.1)	34 (3.9)	8 (0.9)	4 (0.5)

Table **2**. Shell diameters of *Atlanta inflata* expressed as numbers of specimens and percentages (in parentheses) in 0.09 mm size classes, collected off leeward Oahu, Hawaii during the months of September (n = 314) and April (n = 550) (see Seapy, 2008).

Location	Coll.	No. samples	No. shells	Size range (mm)	No. of spire whorls (%)			
					3¼	3½	3¾	4
Trop. Atlantic	RGM	3	58	0.49-1.47	6.9	37.9	50.8	1.7
E. Atlantic	RMNH	23	51	0.86-1.80	17.6	51.0	44.4	-
E. Med.	SMF	23	106	0.68-1.92	20.8	46.2	33.0	-
E. Med./Med.	RGM	3	54	0.98-1.96	13.2	50.9	35.8	-
Caribbean	RGM	1	15	0.42-1.68	-	13.3	86.7	-
Indian	SMF	3	44	0.49-1.47	6.8	4.5	81.8	6.8

Table **3**. Range of shell diameters and numbers of spire whorls (expressed as percentages) in *Atlanta inflata*? from the tropical mid-Atlantic (Meteor Expeditions; plankton), eastern Atlantic (CANCAP Expeditions; benthos), eastern Mediterranean (Meteor ME-25 Expedition; benthos); eastern Mediterranean & Mediterranean (Meteor Expeditions; benthos), Caribbean (Atlantis Expedition; benthos), and Indian Ocean (Meteor Expeditions; plankton).

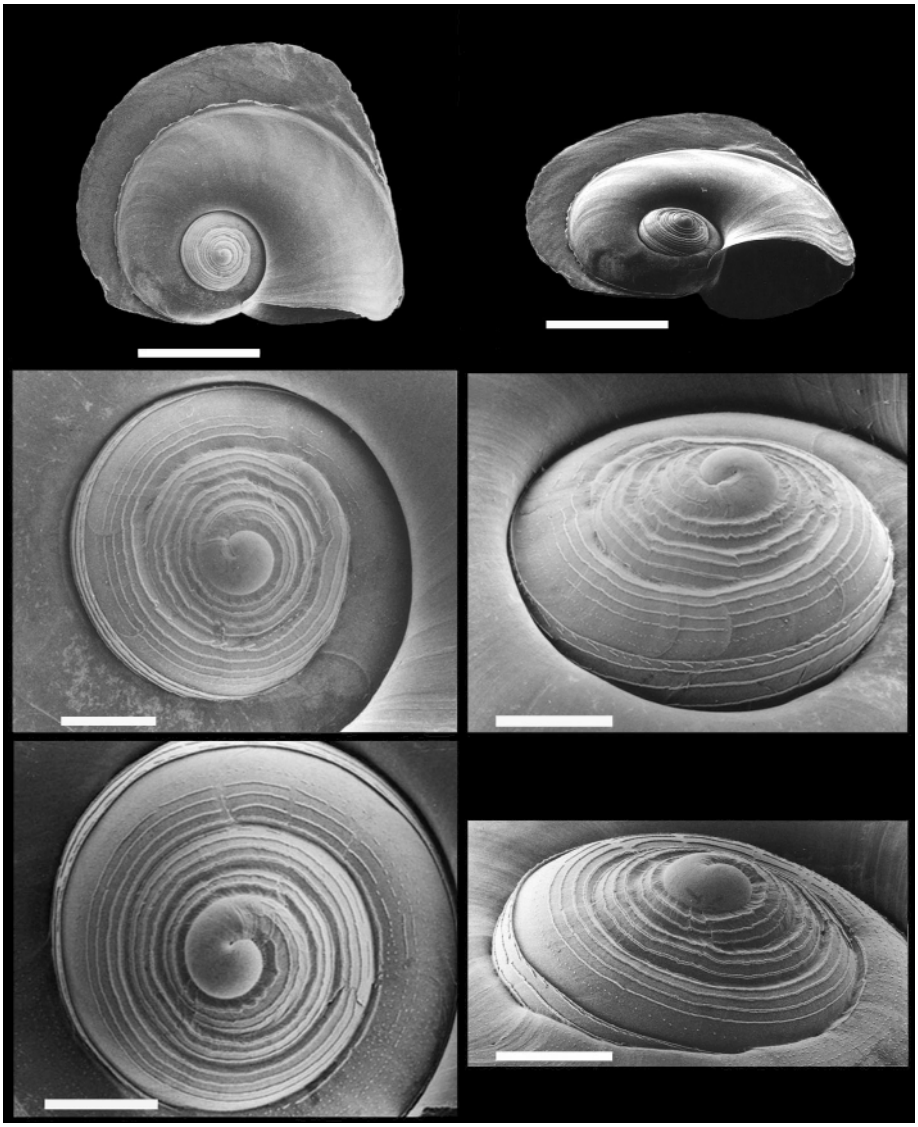

Fig. **5**. Shells of *Atlanta inflata* Gray, 1950, from Hawaiian waters. Top and middle images of a 1.22 mm shell; bottom images of a 0.9 mm shell. Left and right image pairs are from the right side and at a 60° tilt, respectively. Specimens collected with paired, opening-closing 70-cm BONGO nets, 0-50 m, off leeward Oahu, Hawaii, 21° 15′ N 158° 20′ W. Scale bars = 500 μm (top left and right) and 100 μm (middle and bottom).

measured 1.80 mm; 0.3 mm larger than the largest specimen recorded from Hawaiian waters. One of the syntypes (second from left in Fig. 3) measures 2.49 mm, but this specimen was glued apex downward and cannot be identified as *A. inflata* with certainty.

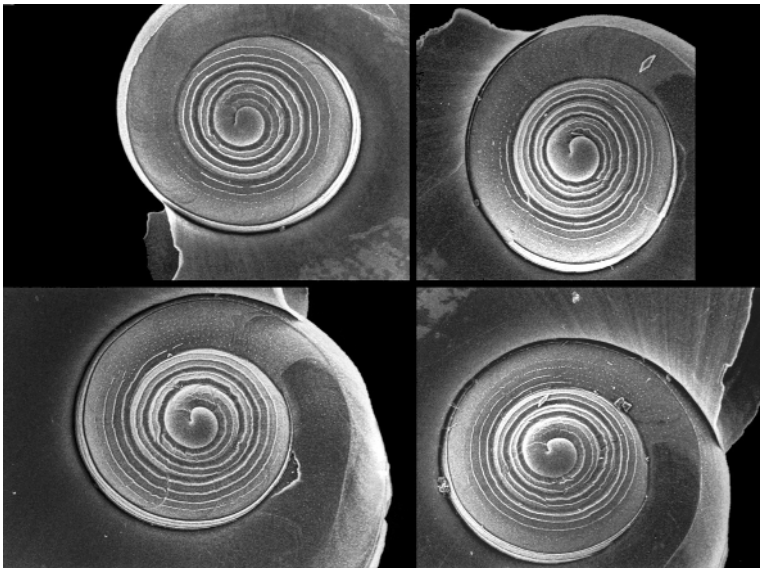

Fig. **6**. Shell spires of *Atlanta inflata* Gray, 1950, from Hawai-ian waters, illustrating the range of spiral ridge development, ending just past 3½ whorls (top left) to 4 whorls (bottom right). Specimens collected off leeward Oahu; collection data not available.

Among the 330 shells of *Atlanta inflata*? examined by AWJ from the Atlantic and Indian Oceans (Table 3), the two largest ones measured 1.96 and 1.92 mm, respectively. Individuals larger than 1.5 mm were not uncommon; 66 of the 330 specimens (20%) exceeded 1.5 mm in diameter.

(2) Keel tall, with a truncate leading edge (figs 5, 8; top left in each). The two shells used in the above figures were unusual in possessing keels that are nearly intact. In the vast majority of cases, the thin and fragile keel is damaged to varying degrees, with the result that the true shape of the keel and its leading edge often cannot be determined. Typical examples of shells with keel damage are seen here in specimens collected by plankton nets (fig. 9) and bottom samplers (figs 10, 11).

(3) Keel does not penetrate between the penultimate and last shell whorls (figs 5, top left; 7, top left; and 9-11).

(4) Spire ornament of raised spiral ridges, ranging from fully developed to limited or absent and varying geographically in the strength of expression. In Hawaiian waters of the North Pacific, spiral ornament is well developed in most specimens (fig. 5), and is associated (see below) with those individuals having mottled yellow- to red-brown spires (due to underlying tissues), but has reduced expression (fig. 7) in those with purple spires. In those shells with well-developed spire ornament, variability is limited to the location on the fourth whorl (between whorls 3½ and 4) where the spiral ridges end (fig. 6). In the purple colour morph (fig. 7), a single spiral ridge begins in the second half of the second whorl, with the ridges ending early on the fourth whorl (after about ¼ whorl). In eastern Australian waters, Newman (1990) reported a wide range of spiral ridge development,

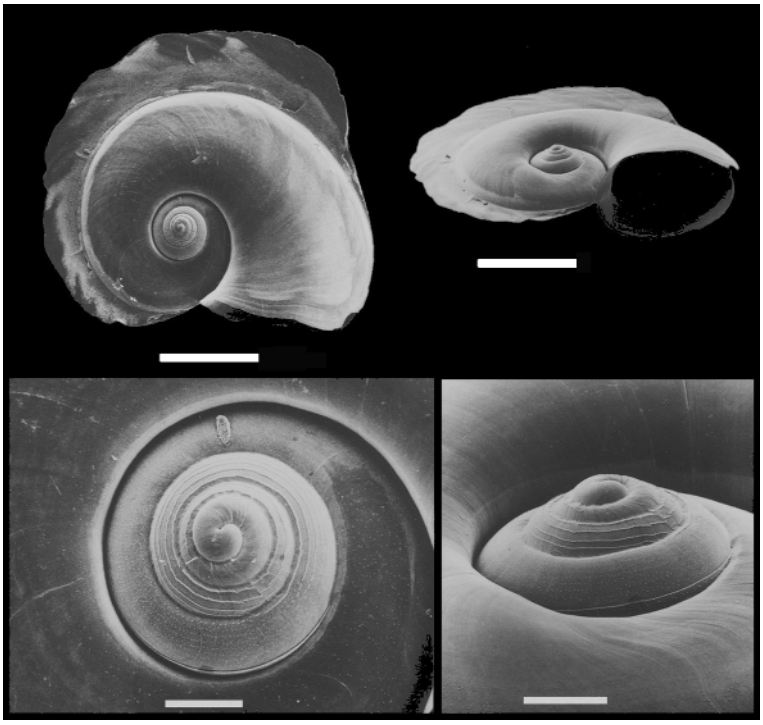

Fig. 7. Shell of *Atlanta inflata* Gray, 1850, with a purple spire from Hawai-ian waters. Shell from right side (top left) and tilted (top right); spire from right side (bottom left) and tilted (bottom right). Specimen collected with paired, opening-closing 70-cm BONGO nets, 0-50 m, off leeward Oahu, Hawaii, 21° 15′ N 158° 20′ W. Scale bars = 500 μm (top) and 100 μm (bottom).

from well developed (her fig. 3.7E), as seen in most Hawaiian shells, to a greatly reduced ornament limited to one or two thin ridges on the second and third whorls (her figs 3.7F,G). In the syntypes of *A. inflata* from the Chinese seas (fig. 3), the spiral ornament is well developed. In the lectotype (fig. 4), the part of the fifth whorl just in front of the boundary with the teleoonch has finer, but more numerous spiral ridges; probably because the protoconch is situated a bit obliquely. The ornament continues, however, until the boundary. Souleyet (1852: 383) described a second species, *A. quoyana*, that lacked the spire ornament. Tesch (1908) regarded this as possibly a junior synonym of *A. inflata* (see Discussion).

In *Atlanta inflata*? from the Atlantic Ocean, the range in spire ornament expression is continuous (fig. 9), from weak, and limited to a few incomplete spiral ridges on the second whorl (top, fig. 9; fig. 10), to strongly developed on the second, third and fourth whorls (bottom, fig. 9; fig. 11). This range of expression was illustrated nicely with a series of eight spire SEMS by Richter (1987, figs 17-24).

(5) Keel with a brown to yellow-brown base. Colour photographs are limited to Seapy (1990a, fig. 5f) for *A. inflata* and De Vera & Seapy (2006: figs 3a-c) for *A. selvagensis*. Richter (1987) described the keel base in *A. inflata*? as dark).

Fig. 8. Shell (top left), tilted (bottom), and spire (top right) of *Atlanta inflata*? from the Indian Ocean. Modified from Richter (1974, plate 1, fig. 4) with added scale bars. Scale bars = 500 μm (top left, bottom) and 100 μm (top right).

(6) Eyes type a and operculum type c (Richter, 1961, 1974, 1987; Seapy, 1990a; Richter & Seapy, 1999).

The following two characteristics distinguish the shells of *Atlanta inflata* in the Pacific Ocean from *A. inflata*? in the Atlantic and Indian Oceans:

(1) With 4¼-4½ whorls (figs 7 and 5, respectively), the number of whorls comprising the shell spire (protoconch) is greater in *Atlanta inflata*, than in *A. inflata*?, with 3¼-4 whorls (table 3). In *A. inflata*? the maximal number of 4 whorls was only recorded in 4 (1.2%) of the 328 shells examined, while 45 (13.7%) had 3¼ whorls, 128 (39.0%) had 3½ whorls, and 150 (45.7%) had 3¾ whorls. If geography is taken into consideration, most (79-95%) of the shells from the Atlantic had spires with 3½ or 3¾ whorls, except in the Caribbean Sea, where 87% had 3¾ whorls. Similar to the Caribbean, 82% of the shells from the Indian Ocean had 3¾ whorls. If one combines all the collection data, 278 (or 85%) of the shells had 3½ or 3¾ spire whorls, which is ¾ to 1 whorl less than in the Hawaiian *A. inflata*.

(2) Shell spire sutures transparent in *Atlanta inflata* (Seapy, 1990a: fig. 5F; Seapy, in prep.). We are unaware of any descriptions or colour photographs of suture pigmentation in the literature for *A. inflata*?, although the sutures in *A. selvagensis* were consistently reddish-purple (magenta) (De Vera & Seapy, 2006: fig. 3a and unpublished observations), a feature also diagnostic of *A. plana* from the Indo-Pacific (Seapy, 1990a).

One final character that may or may not differ between the Pacific and Atlantic/Indian taxa is spire colouration, due to underlying tissues and the presence or absence of any pig-

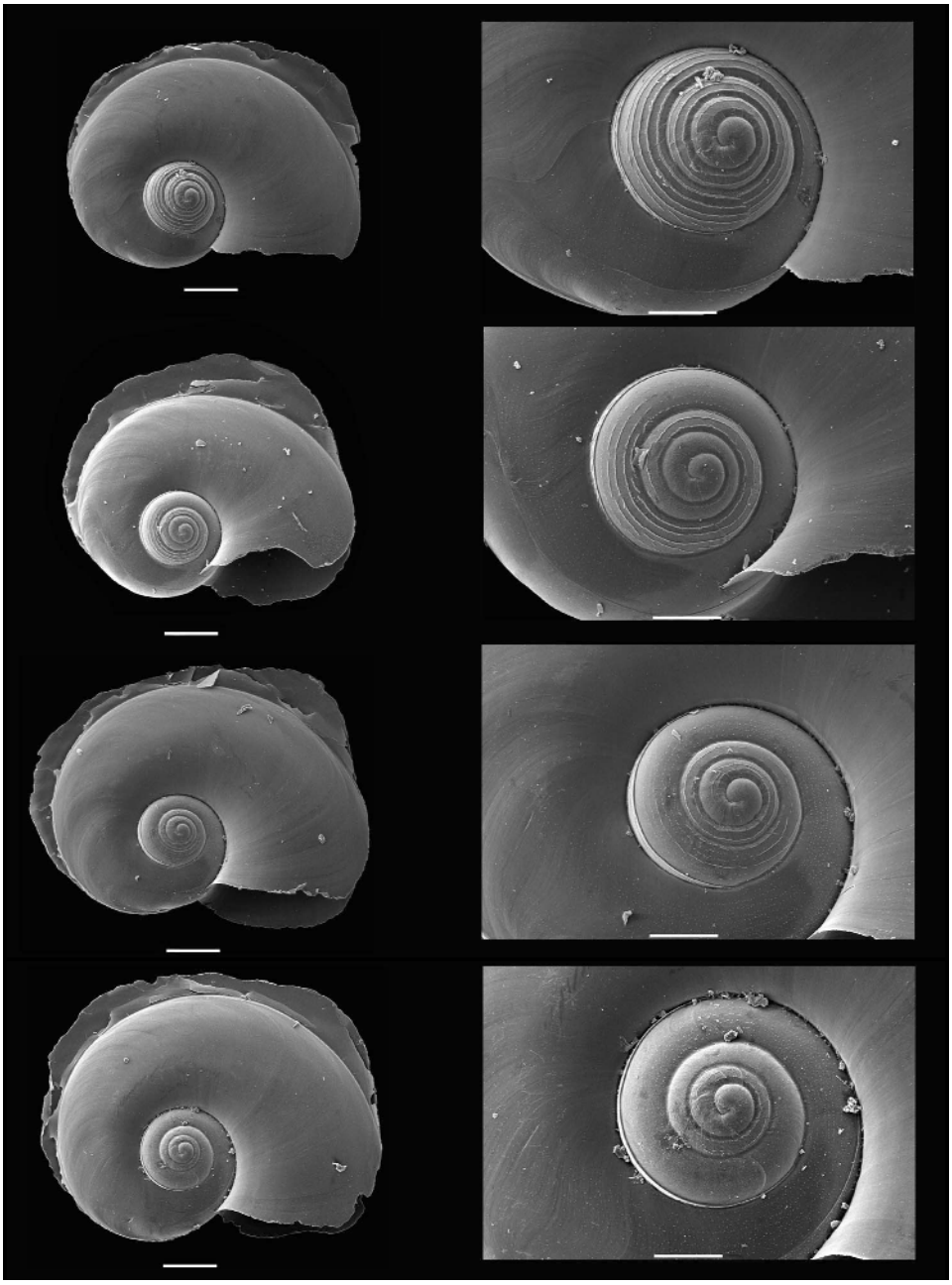

Fig. **9**. Shells of *Atlanta inflata*? from the tropical mid-Atlantic. Views of right side of shells at low (left) and high (right) magnification, illustrating the range of spiral ornament from greatest (top) to least (bottom). Meteor Expedition M51-43MC, 01˚44.900′ N 021˚59.700′ W, 30-50 m, 8 February 1979. SMF 324214.

Scale bars = 200 μm (left) and 100 μm (right). All specimens identified as *A. inflata* by G. Richter.

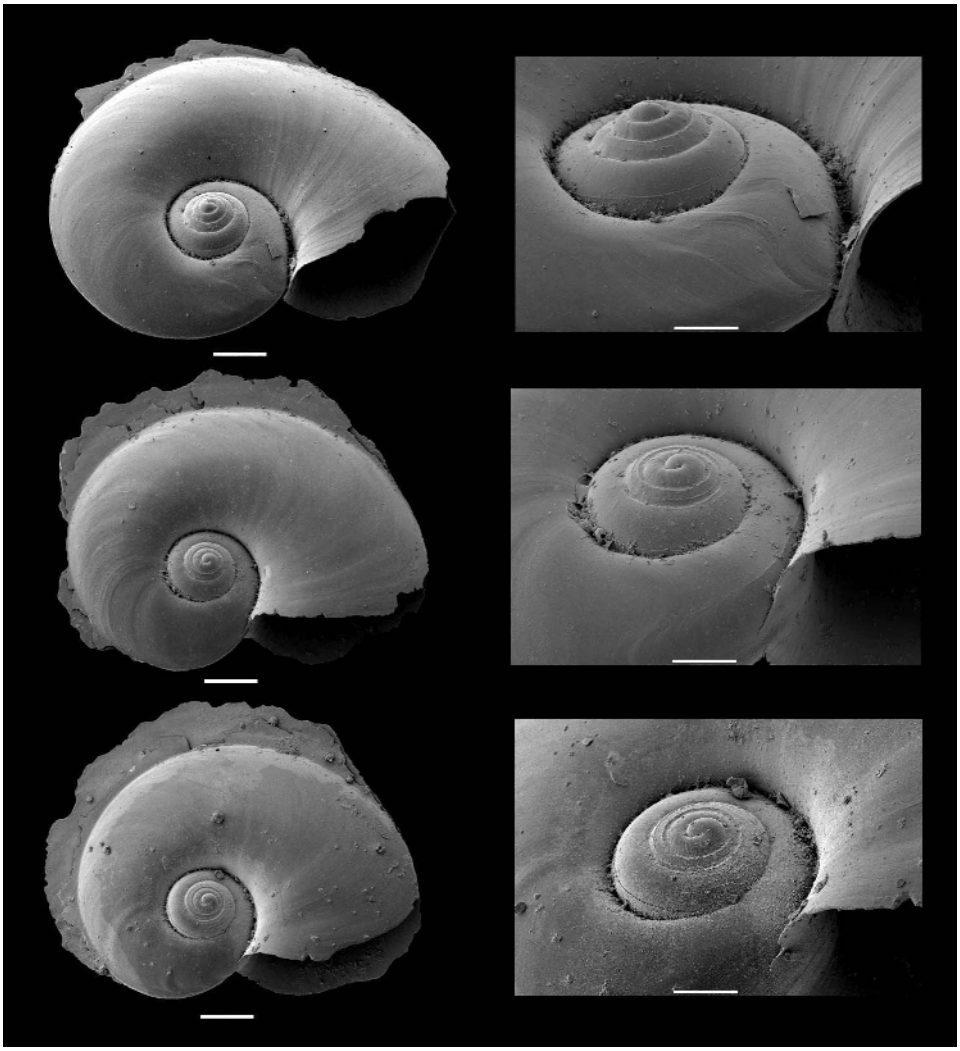

Fig. **10**. Shells of *Atlanta inflata*? from the eastern Mediterranean, illustrating weak spire ridge ornament. Views of right side of shells at low (left) and high, tilted (right) magnifications, Meteor expedition, box core sample Me25-37 Kg1, coll. RGM 541 611. Scale bars = 200 μm (left) and 100 μm (right).

mentation pattern. In Hawaiian *A. inflata* two colour morphs were observed by Seapy (1990a) that were attributable to the digestive gland and/or gonadal tissues; the first, mottled and ranging from light to dark yellow-brown to red-brown, was seen in most specimens, while the second, was uniform light purple. As described above, these two colour morphs were accompanied by different degrees of spire ornaments (figs 5 and 6, respectively). Newman (1990) described the spire colouration as pink or purple. Although only limited descriptions are available, spire colouration could also be dimorphic in *A. inflata*? Richter (1987, 1974) described the spires of *A. inflata*? from the North Atlantic as violet or

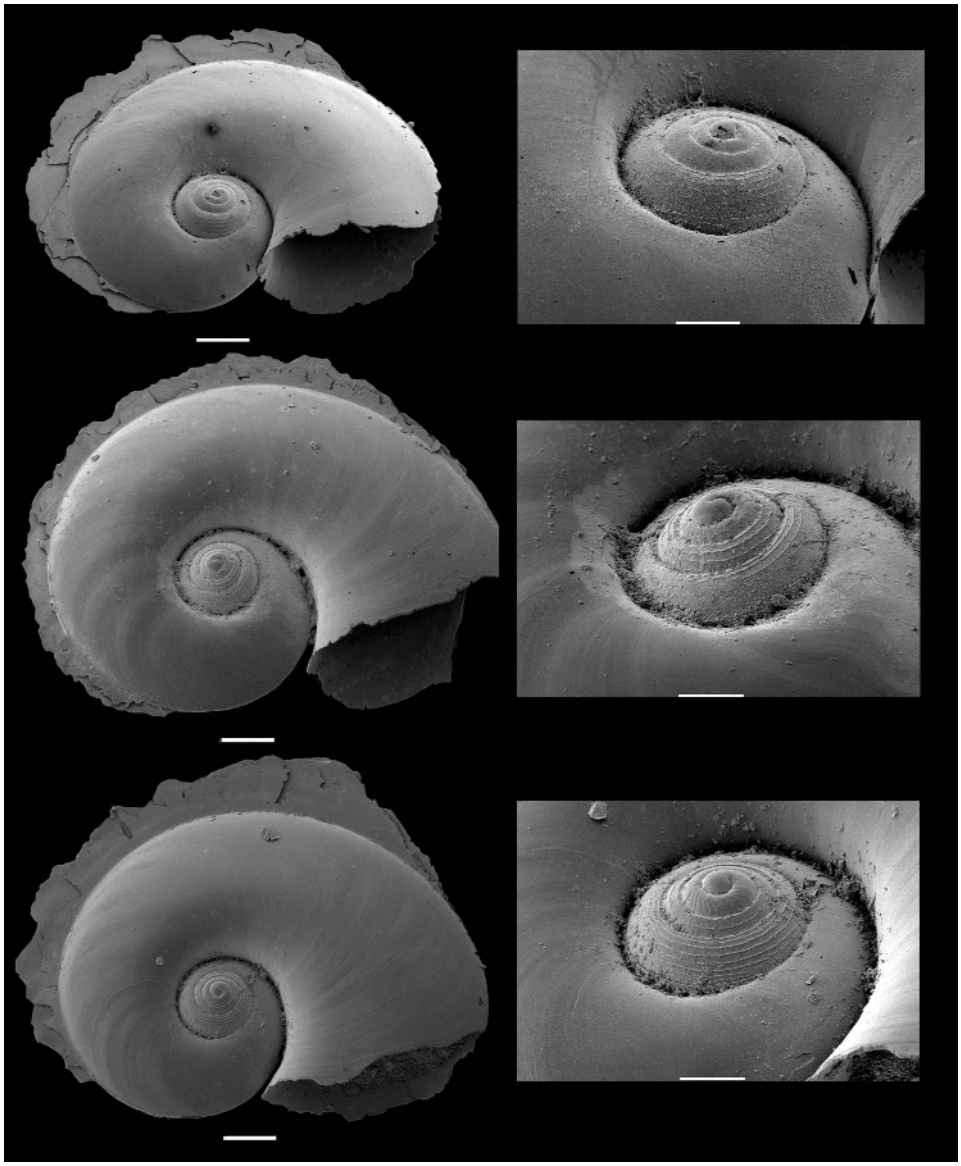

Fig. **11**. Shells of *Atlanta inflata*? from the eastern Mediterranean, illustrating strong spire ornament. Views of right side of shells at low (left) and high, tilted (right) magnifications, Meteor expedition, box core sample Me25-37 Kg1, coll. RGM 541 611. Scale bars = 200 μm (left) and 100 μm (right).

yellow-brown and from the Indian Ocean as yellowish or weak violet. The spire tissues in *A. selvagensis* from the northeastern Atlantic lacked any distinctive colouration (De Vera & Seapy, 2006: fig. 3A). However, the specimens were stored in 70% ethanol solution after initial preservation in formalin-sea water solution, and pigmentation of the spire tissues

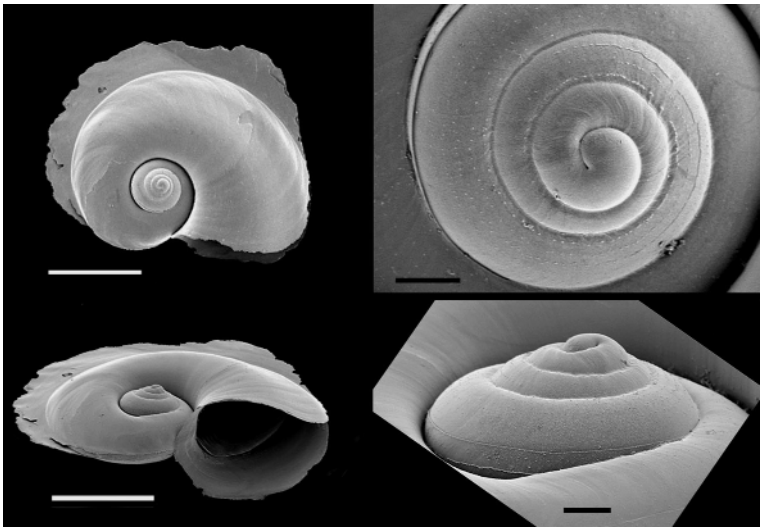

Fig. 12. Shell of *Atlanta selvagensis* De Vera & Seapy, 2006, paratype 3, from the right side (upper left), tilted (lower left), and spire from right side (upper right) and tilted (lower right). Images modified from De Vera and Seapy (2006: fig. 2b, e, a, and d, respectively) by addition of scale bars and 45° clockwise rotation of lower right image. Northeastern Atlantic, Selvagens Islands, 30°05′45″ N 15°51′12″W, 0-1,000 m vertical tows. Oceanographic Vessel Taliarte, 26.ix.2000. TFMCBMZP/02919; HT/0042. Scale bars = 500 μm (left) and 50 μm (right).

could have been lost between the time of collection in September 2000 and examination by De Vera in 2005-2006.

The question remains as to whether or not an existing species possesses the attributes described above for *Atlanta inflata*? in the Atlantic and Indian Oceans. We conclude that the recently described species *A. selvagensis* De Vera & Seapy, 2006, satisfies these criteria. The species description was based on only five adult specimens, which could explain why the maximal shell diameter was 1.5 mm. Shell characters (fig. 12) include a tall keel with a truncated leading edge, a moderately low conical spire consisting of 3¾ whorls, spire ornament of weakly to moderately developed spiral ridges, reddish violet (magenta) spire sutures, type a eyes, and type c operculum (misidentified as type b).

The reason that the specimens were not identified as *Atlanta inflata* was that the species has long been recognized as cosmopolitan (as discussed in the Introduction), and that first-hand experience with this species by RRS was limited to specimens from Hawaiian waters. The identity of Selvagens Islands specimens as *A. inflata* was not even considered a possibility because of the lower number of spire whorls (3¾ instead of 4½) and the colouration of the spire sutures (reddish violet instead of unpigmented). The species deemed closest in appearance to the Selvagens Islands specimens (De Vera & Seapy, 2006) was the Indo-Pacific *Atlanta plana* Richter, 1972, which was abundant in the Hawaiian atlantid fauna (Seapy, 1990a,b). Similar to *A. selvagensis*, *A. plana* has a yellowish brown to brown keel base, a low conical spire of 3½ whorls, weakly developed spiral ridges on the second and third whorls of the spire, and spire sutures that are reddish violet. However, its operculum distinguishes it from all other species in the genus; the gyre has about 20 short, outwardly directed spines (Richter, 1972: fig. 4; 1974: fig. 7; and 1987: fig. 41; Seapy, 1990a: fig. 9B).

DISCUSSION

The variation in the expression of spiral ridge ornament on the shell spires reported here for both Pacific *Atlanta inflata* and Atlantic/Indian Ocean *A. inflata*? was probably responsible, at least in part, for the separate descriptions by Souleyet (1852) of *A. inflata* and *A. quoyana*. After examining Souleyet's type specimens in the Paris Museum and shells of *A. inflata*? from the Atlantic and Indian Oceans collected by Buitendijk and deposited in the Leiden Museum, Tesch (1908: 20) stated: 'Seen from above, the shells of the typical *A. inflata* with its characteristic spire (fig. 13) and that of '*A. quoyana*' (fig. 15) of Mr. Buitendijk agree entirely (except as regards the ornament, which is absent in the latter)'. The specimen used by Tesch in his fig. 15 was from the Indian Ocean, while the source of the shell drawn in his fig. 13 was not given. Tesch concluded that *A. quoyana* was probably a junior synonym of *A. inflata*, although he couldn't be certain because the type material for *A. quoyana* was missing from the Paris Museum collections. After examining specimens of *A. inflata*? from the Mediterranean Sea and Indian Ocean, Richter (1968, 1974) reported that shells with weak spiral ornament were present from both locations, and that *A. quoyana* should be regarded as a junior synonym of *A. inflata*. Because one of the two adult shells figured by Newman (1990) from eastern Australian waters showed weak spiral ridge development, it is entirely conceivable that shells like those described as *A. quoyana* by Souleyet are part of the range of spiral ridge development in Pacific *A. inflata*. Examination of *A. inflata* from other areas of the tropical to subtropical Pacific (particularly the western Pacific) should help to clarify the issue.

We conclude that the species previously identified as *Atlanta inflata* from the Atlantic Ocean, inclusive of the Mediterranean, and Indian Ocean, corresponds to *A. selvagensis* De Vera & Seapy, 2006. Both taxa are small (maximal size of <2.0 mm) and have keels that are tall with truncate leading edges and a yellowish-brown to brown keel base. The spire in the five type specimens of *A. selvagensis* consisted of 3¾ whorls, which was the most frequent whorl count obtained here from the shells of *A. inflata*? from the North Atlantic and Indian Oceans. The range of spire ornament seen in *A. selvagensis* overlaps with the lower end of the range reported for *A. inflata*? here and by Richter (1961, 1974). Lastly, type a eyes and type c opercula are found in both taxa.

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Note: The atlas was published undated and only vernacular names were given. Smith (1888) and Van der Spoel (1976, implicitly, see e.g. p. 207) referred to the atlas with the year 1841. According to Tesch (1908: 25, footnote) the atlas appeared in 1842. Sherborn & Woodward (1901: 391) mentioned as publication date '1846-1849?'. Also Bauchot et al. (1982) were not able to date the atlas with certainty. Dance (1986: 237) cited atlas + text together as 1841-1852. Here we maintain the date 1841, but with a query.

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