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Systematic revision of the genus *Scaphander* (Gastropoda, Cephalaspidea) in the Atlantic Ocean, with a molecular phylogenetic hypothesis

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The genus *Scaphander* (Gastropoda, Cephalaspidea) is a group of predominantly deep-sea, soft-bottom snails with extant species distributed worldwide from the Arctic to the Antarctic. There are approximately 45 species described worldwide, of which about 18 are considered to be valid. The systematics of *Scaphander* has traditionally been shell-based, but shell characters often show high intraspecific variability, and this led to a high number of nominal names available of unclear taxonomic status. The main objectives of this article are to revise the systematics of the Atlantic species of *Scaphander*, and to produce an identification key and a molecular phylogeny to aid with species delimitation. The validity of species was assessed following an integrative approach combining the study of type material and original descriptions, shells, morpho-anatomical characters, and molecular phylogenetics. Anatomical structures were documented by drawings, macro-photography, and scanning electron microscopy (SEM). Two mitochondrial (*COI* and *16S* rRNA) and one nuclear (*28S* rRNA) genes were sequenced, and Bayesian molecular phylogenetic hypotheses were produced. Representatives of the Cephalaspidean genera *Bulla* and *Haminoea* were included to test the monophyly of *Scaphander*. Eight species of *Scaphander* were recognized in the Atlantic Ocean. Three species are restricted to the western Atlantic (*Scaphander clavus*, *Scaphander darius*, and *Scaphander watsoni*), one is distributed only in the eastern Atlantic (*Scaphander lignarius*), one is endemic to the Azores (*Scaphander gracilis*; this species is only known from shells), and three have amphi-Atlantic distributions (*Scaphander bathymophilus*, *Scaphander nobilis*, and *Scaphander punctostriatus*). Shell characters and the morphology of the male reproductive system were found to be the best diagnostic characters for species recognition. The molecular phylogeny confirms the monophyly of *Scaphander*, and is largely congruent with species delimitation based on morpho-anatomical characters.

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ADDITIONAL KEYWORDS: Atlantic Ocean – biogeography – Cephalaspidea – deep-sea – Gastropoda – phylogeny – *Scaphander* – systematics.

INTRODUCTION

DEFINITION OF *SCAPHANDER* AND TAXONOMIC PLACEMENT

Scaphander is a genus of predominantly deep-sea gastropods, with extant species distributed worldwide from the Arctic to the Antarctic (Keen, 1971; Bouchet, 1975). There are approximately 45 species described worldwide, of which about 18 are considered to be valid (Valdés, 2008; OBIS, 2012; Rosenberg, Bouchet & Gofas, 2012). Alone, the Atlantic Ocean harbours over 50% of the global diversity, with ten recognized species (Marcus, 1974; Bouchet, 1975). *Scaphander* species have a strong shell and a cephalic shield that covers the mantle cavity when they burrow in soft sediments (see Fig. 1). The shell of *Scaphander* is pyriform to globose, with a large aperture, sunken spire, and punctuated grooves. The animal cannot

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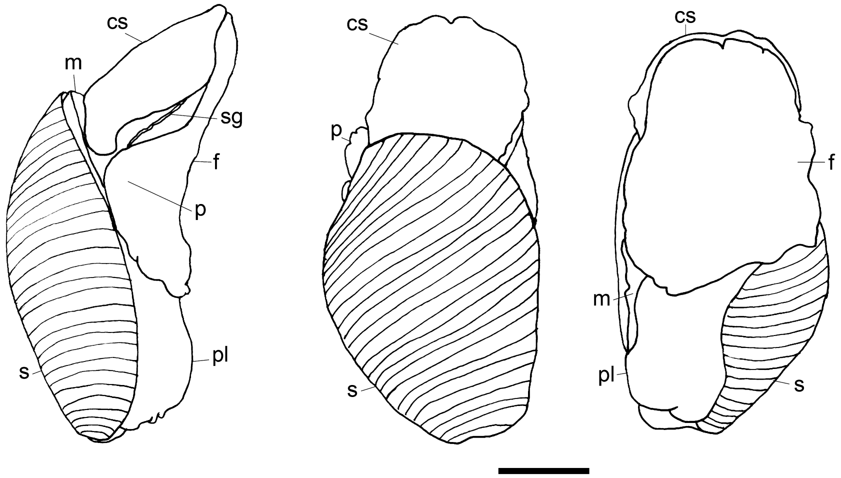

Figure 1. External morphology of *Scaphander*; cs, cephalic shield; f, foot; m, mantle; p, parapodia; pl, pallial lobe; s, shell; sg, seminal groove. Scale bar: 5 mm.

retract completely into the shell and lacks operculum (Burn & Thompson, 1998).

The genus *Scaphander* belongs to the clade ('Order') Cephalaspidea (Heterobranchia; class Gastropoda), and is often placed in the superfamily Philinoidea (including families Philinidae, Retusidae, Cylichnidae, Gasteropteridae, and Aglajidae), characterized by similarities in the radula and lack of spines in the gizzard (Burn & Thompson, 1998; Mikkelsen, 2002; Bouchet & Rocroi, 2005), but Malaquias *et al*. (2009a) and Göbbeler & Klussmann-Kolb (2011) did not retrieve this group as monophyletic in a molecular phylogenetic analysis of the Cephalaspidea. Sars (1878) introduced the family Scaphandridae for *Scaphander* only, but later Fischer (1887) assigned several other genera to it, such as *Sabatia*, *Smaragdinella*, *Atys*, *Cylichna*, and *Amphisphyra*. In more recent times *Scaphander* has often been ascribed to the family Cylichnidae, together with *Cylichna*, based on several morpho-anatomical potential synapomorphies (e.g. a strong external shell, shape of lateral radular teeth, and lack of distinct parapodia; Mikkelsen, 1996; Burn & Thompson, 1998; Mikkelsen, 2002; Bouchet & Rocroi, 2005). The family name Scaphandridae has seldom been used (e.g. McGinty, 1955; Thompson & Brown, 1984), but Malaquias *et al*. (2009a) found that Cylichnidae (represented by *Cylichna* and *Scaphander*) is not monophyletic, and reinstated Scaphandridae as the valid family name for the genus *Scaphander*.

BIOLOGY OF *SCAPHANDER*

Members of the genus *Scaphander* live at depths of 16–4255 m, with some species having a shallower bathymethric distribution, and some living only in deeper waters (Marcus, 1974; Pequegnat, 1983). They burrow into the sediment aided by ciliary movement on the cephalic region that sends small particles over the dorsal side (Hurst, 1956). Observations of gut content indicate that *Scaphander* ingest mud and sand with diatom frustules, foraminifers, and small animals like bivalves, young sea urchins, polychaetes, scaphopods, gastropods, and gastropod shells containing sipunculids (Hurst, 1956; Yonge & Thompson, 1976). *Scaphander* are simultaneous hermaphrodites, but very little is known about their reproductive biology and larval development. This is clearly demonstrated by Schaefer (1996) in his summary of cephalaspidean reproduction, where the only data on *Scaphander* is the spawning period of *Scaphander lignarius* (January–February near Plymouth, and April near the Isle of Man; Thompson & Brown, 1984). The information available on the reproduction and development in Cephalaspidea is very uneven, with some genera and families more studied than others (e.g. *Haminoea* and *Philine*, see Schaefer, 1996), but planktotrophy appears to be most common (Schaefer, 1996).

Scaphander lignarius is known to produce secondary metabolites, lignarenone A and lignarenone B, which are probably alarm pheromones used to warn conspecifics of predators, but this has not been possible to test because of the deep bathymetric distribution of these snails (Cimino, Spinella & Sodano, 1989). The biosynthetic pathways of these metabolites have been studied by Cutignano *et al*. (2008).

AIMS

The main objective of this work is to revise the systematics of the Atlantic species of *Scaphander* and to produce a molecular phylogeny to aid in species delimitation. Furthermore, we aim to establish the morphological characters that distinguish between species, the geographical distribution of each species, and to create a dichotomous key to facilitate species identification.

MATERIAL AND METHODS

Sampling, type material, synonymies, and geographic distributions

Specimens for anatomical and molecular work have been assembled from natural history museums (see list of institutional abbreviations below). Sampling cruises were undertaken along the coast of Norway under the research project MAREANO.

Original descriptions for all nominal names of Atlantic *Scaphander* (valid names and synonyms) were assembled, as well as more recent works on *Scaphander* species, including re-descriptions. Type specimens for nearly all nominal species were studied and photographed. Specimens were checked against literature and types. Synonymies attempt to be as complete as possible.

Geographical distributions have been inferred from the study of museum material, newly collected specimens, and reliable literature records, and were plotted using ArcMap (ESRI, 2011). When geographical coordinates were not available they were estimated from locality descriptions. If identification was uncertain or single specimens occurred outside the range set by reliable observations, the record was included, but labelled with a question mark (?).

Bathymetric distributions were established using a conservative approach: for species where both empty shells and live specimens were known, depth information was collected only from the latter. When depth was known as a range, then the average between the maximum and minimum depth was used.

Abbreviations

ARC, Atlantic Reference Centre, St Andrews, New Brunswick, Canada; FLMNH, Florida Museum of Natural History, Gainseville, FL, USA; H, shell height; MCZ, Museum of Comparative Zoology, Harvard University, Boston, MA, USA; MNHN, Muséum national d'Histoire naturelle, Paris, France; MZUSP, Museu de Zoologia da Universidade de São Paulo, Brazil; NHMUK, Natural History Museum, London, UK; RMNH, National Museum of Natural History (Naturalis), Leiden, the Netherlands; SEM, scanning electron microscopy; sh., shell(s); SMNH, Naturhistoriska Riksmuseet, Stockholm, Sweden; spc(s), preserved animal(s); USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA; ZMBN, Natural History Collections, University Museum of Bergen, Norway.

Anatomical characters

For the species where complete animals were available, between three and 16 specimens were dissected to establish the morphological characters that characterize the species, and to understand intraspecific variability. Drawings of the male reproductive system and digestive tract were made using a dissecting microscope fitted with a drawing tube. Shells and gizzard plates were photographed with a camera equipped with macro lens. Radulae, penial papillae, and gizzard plates were mounted for SEM. The radulae and gizzard plates were cleaned with commercial bleach and an ultrasonic machine to remove tissue prior to mounting on SEM stubs. Penial papillae were critical-point dried before mounting in order to maintain the shape of the structures. The SEM stubs were coated with a gold–palladium mixture and then photographed at low magnification to obtain a general view of the entire structures, and then at higher magnification for the details. For the species where only shells were available, species status was assessed by comparing shells with original descriptions and other relevant literature.

DNA extraction, amplification, and sequencing

DNA was extracted from tissue samples from the foot or head shield using the QIAGEN DNeasy Blood and Tissue Kit, following the manufacturer's protocol (spin-column protocol; QIAGEN). For difficult specimens that did not yield a satisfactory polymerase chain reaction (PCR) product, new extractions were performed using the EZNA Mollusc DNA Kit, following the manufacturer's protocol. The genetic markers used were cytochrome oxidase *c* subunit I (*COI*) and *16S* rRNA (two primers each, see Table 1), and nuclear *28S* rRNA (four primers, see Table 1). For *28S* rRNA, two primers (in bold font in Table 1) were used for amplification and an additional two internal primers were used for the sequencing. The PCR reaction volume was 50 µL for the three genes. For *COI* and *16S* rRNA, 17.5 µL Sigma-Aldrich water, 5 µL buffer, 5 µL dNTP, 10 µL Q solution, 7 µL $MgCl_2$, 2 µL of each of the primers, 0.5 µL TAQ, and 1 µL DNA were used, whereas for the *28S* rRNA only 2 µL of $MgCl_2$ was added, and the Sigma-Aldrich water volume used was 22.5 µL; all other items were the same for *COI* and *16S* rRNA. For each of the genetic markers, optimization PCRs with annealing temperatures of 43–55 °C (*COI*) and 48–60 °C (*16S* and *28S*) were run to establish the optimum annealing temperature. PCR thermal cycles for *COI*, *16S* rRNA, and *28S* rRNA were the same, but with specific annealing temperatures. An initial

Table 1. Sequencing primers for polymerase chain reactions

	Name	Sequence 5′ → 3′	Source
COI	LCO1490 (F)	GGTCAACAAATCATAAAGATATTGG	Folmer *et al*. (1994)
	HCO2198 (R)	TAAACTTCAGGGTGACCAAAAAATCA	
16S	16S ar-L	CGCCTGTTTATCAAAAACAT	Palumbi *et al*. (1991)
	16S br-H	CCGGTCTGAACTCAGATCACGT	
28S	**LSU5-F**	TAGGTCGACCCGCTGAAYTTAAGCA	Littlewood, Curini-Galletti & Herniou (2000)
	900-F	CCGTCTTGAAACACGGACCAAG	Olson *et al*. (2003)
	LSU1600-R	AGCGCCATCCATTTTCAGG	Williams, Reid & Littlewood (2003)
	ECD2S-R	CTTGGTCCGTGTTTCAAGACGG	Modified from Littlewood *et al*. (2000)

denaturation of 3 min at 95 °C, followed by 39 cycles with denaturation of 45 s at 94 °C, with annealing for 45 s at 45.0 °C (*COI*), 51.5 °C (*16S*), or 52.0 °C (*28S*), and with an extension for 2 min at 72 °C. The final extension was achieved by 10 min at 72 °C. One positive and one negative control were included in each run to check for a successful amplification reaction and to rule out contamination.

The quality of PCR products was assessed using gel electrophoresis imaging. PCR product (5 μL) was mixed with 2 μL of loading buffer and run on a 1.2% agarose gel based on half-strength TAE buffer (Tris base, acetic acid, and EDTA) and containing the staining agent GelRed (Biotium, Hayward, CA, USA). pGEM marker (5 μL; Promega, Madison, WI, USA) was used to quantify and estimate the length of amplified DNA fragments. The gel was run at 80–100 V for 40–60 min and analysed under UV light. GeneSnap (SynGene) was used to capture images. In cases were gel electrophoresis imaging revealed double bands, the total PCR product was run on a new gel (same specifications as above) for 90–120 min, the individual bands were then cut out from the gel with a sterile scalpel blade and placed individually in sterile 1.5-mL tubes. Gel extraction was performed using QIAquick Gel Extraction Kit (QIAGEN) following the manufacturer's protocol. PCR products were quantified using manual band quantification in GeneTools (SynGene).

Successful PCRs were purified using Exonuclease 1 (EXO, 10 U μL^{-1}) and shrimp alkaline phosphatase (SAP, 10 U μL^{-1}, USB®) in 25-μL reactions (EXO 0.25 μL, SAP 2.5 μL, Sigma-Aldrich water = 2.25 μL, PCR product 20 μL). Samples were incubated at 37 °C for 15 min followed by an inactivation step at 80 °C for 15 min. The purified PCR products were sequenced using an Automatic Sequencer 3730XL.

ALIGNMENT OF DNA SEQUENCES AND PHYLOGENETIC ANALYSES

SEQUENCHER 4.10.1 (Gene Codes Corp.) was used to assemble the forward and reverse strands, and to assess the quality of the sequences, which were edited by careful examination of chromatograms, and verified by forward and reverse comparisons. The sequences were blasted in GenBank to check for potential contamination and aligned using ClustalX (Thompson *et al*., 1997), with a gap-opening penalty of 60 and a gap-extension penalty of 30. The alignments were then optimized by eye using MacClade 4.06 (Maddison & Maddison, 2000), trimmed to the longest sequence, and missing data at the ends were coded with question marks (?). The sequences have been deposited in GenBank (see Table 2), and the concatenated alignment and consensus tree is listed in TreeBASE (study no. 13753).

Saturation was tested for each gene and for the first, second, and third codon positions of the *COI* gene by plotting general time-reversible (GTR) pairwise distances against total substitutions (transitions + transversions). Four individual gene analyses were performed (trees not shown): (1) *COI*; (2) *COI* (excluding the third codon positions); (3) *16S* rRNA; and (4) *28S* rRNA, as well as a complete concatenated data set (all taxa and all sequences included), with empty regions of the alignment coded as missing data (see Table 2 for complete list of specimens). Representatives of the genera *Bulla* and *Haminoea* were included to test the monophyly of *Scaphander*. All analyses were rooted with *Diaphana* because it represents the most basal lineage of Cephalaspidea (Malaquias *et al*., 2009a; Jörger *et al*., 2010).

The best-fitting models of evolution (see Table 3) were selected using Akaike's information criterion (Akaike, 1974) implemented in MODELTEST 3.7 (Posada & Crandall, 1998). Distances and substitutions were calculated in PAUP* (Swofford, 2003) and plotted in R (R Development Core Team, 2012). The phylogenetic analyses were performed in MRBAYES (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), with three parallel runs of 2 million generations for the single-gene data sets and 5 million generations for the concatenated data set, with sampling every 100 generations. The con-

Table 2. Taxa set used for molecular phylogenetics with locality, voucher numbers, and GenBank accession numbers

Species	Seq no.	Locality	Voucher no.	*COI*	*16S*	*28S*
Scaphander lignarius	1	Spain	ZMBN 87998		KC351524	KC351543
Scaphander lignarius	2	Bergen, Norway	ZMBN 87999	KC351562	KC351525	KC351544
Scaphander lignarius	12	Celtic Sea	MNHN, IM-2009-29694		KC351523	
Scaphander lignarius	19	Spain	MCZ 371884	KC351561	KC351522	
Scaphander lignarius	37	Bergen, Norway	ZMBN 88000	KC351563	KC351526	KC351545
Scaphander lignarius	51	Norway	ZMBN 88001	KC351564	KC351527	
Scaphander lignarius	GB1	Algarve, Portugal	NHMUK 20060325	DQ974663	DQ923454	DQ927221
Scaphander lignarius	GB2	Algarve, Portugal	NHMUK 20060114	DQ974664		DQ927212
Scaphander lignarius	GB3	Blanes, Spain				EF489372
Scaphander punctostriatus	3	60°09′ N, 05°19′ E	ZMBN 88002	KC351568	KC351532	KC351549
Scaphander punctostriatus	4	Newfoundland	MNHN, IM-2009-29695	KC351566	KC351531	KC351548
Scaphander punctostriatus	34	Norway	ZMBN 88006	KC351571	KC351536	KC351553
Scaphander punctostriatus	35	Norway	ZMBN 88005	KC351570	KC351535	KC351551
Scaphander punctostriatus	36	Skagerrak	ZMBN 88004	KC351569	KC351534	KC351552
Scaphander punctostriatus	38	Norway	ZMBN 88003	KC351567	KC351533	KC351550
Scaphander watsoni	5	Brazil	MZSP 34644		KC351540	
Scaphander watsoni	8	Brazil	MZSP 86804		KC351541	
Scaphander watsoni	15	Gulf of mexico	USNM 1151226	KC351575	KC351542	KC351557
Scaphander watsoni	17	Gulf of Mexico	USNM 1151240	KC351576		KC351558
Scaphander nobilis	9	Bay of Biscay	MNHN, IM-2009-29696		KC351530	
Scaphander bathymophilus	13	Azores	RMNH unnr.	KC351559	KC351520	
Scaphander bathymophilus	52	Puerto Rico	MZSP 75708		KC351519	
Scaphander darius	21	Brazil	MZSP 29016	KC351560	KC351521	
Scaphander mundus	29	Philippines	MNHN, IM-2009–4319	KC351565	KC351529	KC351547
Scaphander mundus	31	Philippines	MNHN, IM-2009–4318		KC351528	KC351546
Scaphander sp. A	30	New Caledonia	MNHN, IM-2009–4317	KC351572	KC351537	KC351554
Scaphander sp. B	32	New Caledonia	MNHN, IM-2009–4371	KC351573	KC351538	KC351555
Scaphander subglobosus	33	Philippines	MNHN, IM-2009–4339	KC351574	KC351539	KC351556
Haminoea orbignyana		Naples, Italy	ZMBN 81714	KC404964	KC404959	KC404961
Haminoea orteai		Faial, Azores	NHMUK 20070459	KC404963	KC404960	KC404962
Bulla occidentalis		Florida	NHMUK 20030779/1	DQ986543	DQ986603	DQ986666
Bulla striata			NHMUK 20030784/3	DQ986566	DQ986631	DQ986693
Diaphana sp.				EF489394.1	EF489325.1	EF489373.1

Table 3. Best-fit model and estimated parameters for phylogenetic analyses

Parameter	COI	16S	28S
No. specimens	25	28	23
No. characters	698	465	1514
Best-fit model	TVM+I+G	TVM+I+G	GTR+I+G
Frequency A	0.2853	0.3097	0.1922
Frequency C	0.1504	0.1564	0.3221
Frequency G	0.1543	0.2110	0.2613
Frequency T	0.4100	0.3229	0.2245
Gamma shape	0.8877	0.6974	1.3875
Prop. inv. sites	0.5582	0.4077	0.7717
R-matrix [A-C]	0.1855	0.3500	2.9100
R-matrix [A-G]	9.4538	7.7476	17.4542
R-matrix [A-T]	0.5056	4.8052	3.6316
R-matrix [C-G]	0.5378	0.0000	1.6120
R-matrix [C-T]	9.4538	7.7476	2.9827
R-matrix [G-T]	1.0000	1.0000	1.0000

Prop. inv. sites = proportion of invariant sites.

vergence of runs was assessed using TRACER 1.5 (Rambaut & Drummond, 2007) and the burn-in was set to 10%. Consensus phylograms were generated in MRBAYES, annotated and converted to graphics in FIGTREE 1.3.1 (Morariu *et al*., 2008), and final adjustments were made in ADOBE ILLUSTRATOR CS6.

RESULTS

Systematic descriptions

Genus *Scaphander* de Montfort, 1810

Charta Martini, 1769: 283, 284, pl. 21, figs 194, 195. Type by monotypy *Charta convoluta* [= *Scaphander lignarius* (Linnaeus, 1758)]. *Nomen oblitum* following International Commission on Zoological Nomenclature (ICZN), article 53.9.

Gioeni Gioeni, 1783: 5–36, pl. 1, figs 1–13. Type by subsequent designation *Tricla gioeni* Philipsson, 1788 [= *Scaphander lignarius* (Linnaeus, 1758)]. *Nomen oblitum* following ICZN article 53.9.

Tricla Philipsson, 1788: 8; Winckworth, 1932: 232. Type by monotypy *Tricla gioeni* Philipsson, 1788 [= *Scaphander lignarius* (Linnaeus, 1758)]. Suppressed by ICZN (1954: opinion 287).

Gioenia Bruguière, 1792: 12, 502–504. Type by monotypy *Gioenia sicula*. Supressed by ICZN (1954: opinion 287).

Scaphander de Montfort, 1810: 334, pl. 84. Type by monotypy *Scaphander lignarius* (Linnaeus, 1758). *Nomen protectum* following ICZN, article 53.9.

Bulla (*Scaphander*) Adams, 1855: 574; Weinkauff, 1862: 336.

Scaphander (*Sabatia*) Dall, 1889a: 86, pl. 17, figs 9, 9b; Dall, 1889b: 53, 54, pl. 17, figs 9, 9b.

Scaphander (*Sabatina*) Dall, 1908: 240, 241. Type by original designation *Scaphander* (*Sabatina*) *planeticus*: Dall, 1908.

Assula Schumacher, 1817: 258. Type by monotypy *Assula convoluta* [= *Scaphander lignarius* (Linnaeus, 1758)].

Sabatia (*Sabatina*) Dall, 1927: 25.

Bulla (*Bullocardia*) Nordsieck, 1972: 29, pl. 7, fig. 25. Type by original designation *Bulla millepunctata* Locard, 1897 (= *Scaphander nobilis* Verill, 1884).

Bucconia Dall, 1890: 16, 17, pl. 10, fig. 9; Habe, 1955: 69; Bullis, 1956: 2, 3, pl. 2, figs A,B,D,E. Type by original designation *Scaphander nobilis* Verill, k1884: 209, 210, pl. 32, figs 18, 18a–d.

Eoscaphander Habe, 1952: 75–77, figs 7, 8. Type by monotypy *Eoscaphander fragilis*.

Nipponoscaphander Kuroda & Habe in Kuroda, Habe & Oyama, 1971: 292, pl. 64, fig. 27. Type by original designation *Scaphander japonicus* Adams, 1962.

Taxonomic history

The first species of *Scaphander* to be described (*S. lignarius*) was originally placed in the genus *Bulla*, as defined by Linnaeus (1758). *Bulla* was redefined during the 19th century (reviewed in Malaquias & Reid, 2008), and the name *Scaphander* was introduced by de Montfort (1810) to include *Bulla lignaria* Linnaeus, 1758. Martini (1769) described a shell resembling a roll of paper ('Das eingerollte papier') and named it *Charta convoluta*. His figure shows the shell of *Scaphander lignarius*, and he also mentions *Bulla lignaria* Linnaeus, 1758 as a synonym. This overlooked publication contains the oldest available putative synonym of *Scaphander* de Montfort, 1810. Schumacher (1817) proposed a new genus, *Assula*, for the species *Charta convoluta* Martini, 1769, without any justification of this change.

According to ICZN (1999; article 23.9), the precedence of names can be reversed if the senior synonym has not been used as valid after 1899 and the junior synonym has been used as valid in at least 25 publications, by at least ten different authors, in the immediately preceding 50 years, and encompassing a span of no less than 10 years. To our best knowledge, the name *Charta* has not been used as valid since its publication in 1769, and the junior synonym (*Scaphander* de Montfort, 1810) is used as valid in at least the following publications: Marcus & Marcus (1967), Marcus (1971), Keen (1971), Marcus (1974), Bouchet (1975), Yonge & Thompson (1976), D'Angelo & Gargiullo (1978), Pequegnat (1983), Thompson & Brown (1984), Cimino *et al*. (1989), Poppe & Goto (1991), Mikkelsen (1996), Schaefer

(1996), Burn & Thompson (1998), Mikkelsen (2002), Cutignano *et al*. (2008), Klussmann-Kolb *et al*. (2008), Valdés (2008), Malaquias *et al*. (2009a), Malaquias, Berecibar & Reid (2009b), Segers, Swinnen & de Prins (2009), Rios (2009), Poppe (2010), Daccarett & Rossio (2011), and Gofas, Moreno & Salas (2011). Therefore, *Scaphander* de Montfort, 1810 is here validated as a *nomen protectum* and *Charta* Martini, 1769 is considered a *nomen oblitum*. Gioeni (1783) found a gizzard of *S. lignarius* and described it as if it was a complete animal and named the new taxon *Gioeni* (of unspecified rank). Philipsson (1788) regarded *Gioeni* as the species epithet and gave the supposed animal the binominal name *Tricla gioeni*, whereas Bruguière (1792) considered it the genus epithet and gave it the name *Gioenia sicula*. The true nature of the 'animal' was exposed by Draparnaud (1800), and the names *Tricla* and *Gioenia* were not used until Winckworth (1932) introduced *Tricla* as a generic name for *S. lignarius* in his 'British Marine Mollusca'. He was followed by a few other authors until *Tricla* and *Gioenia* were suppressed by ICZN (1954: opinion 287), following an application by Lemche. *Gioeni* Gioeni, 1783 was never invalidated by the ICZN because it is a uninominal name, and Lemche considered it not available; however, as pointed out by Valdés (2008), ICZN (1999: article 11.4.1) states that 'A published work containing family-group names or genus-group names without associated nominal species is accepted as consistent with the Principle of Binominal Nomenclature in the absence of evidence to the contrary'. *Gioeni* Gioeni, 1783 has, to the best of our knowledge, not been used as valid after 1899, and as shown above, *Scaphander* de Montfort, 1810 fulfils the conditions of ICZN (1999: article 23.9.1). *Gioeni* Gioeni, 1783 is therefore here considered a *nomen oblitum*, and *Scaphander* de Montfort, 1810 is maintained as a *nomen protectum*.

Adams (1855) considered *Scaphander a* subgenus of *Bulla*, where he included the species *Bulla lignaria* Linnaeus, 1758 and *Bulla puncto-striata* Mighels & Adams, 1842, along with three other species later assigned to the genera *Philine* and *Johania* (CLEMAM, 2012).

Dall (1890) divided the genus *Scaphander* into two subgenera: *Scaphander* and *Bucconia*. He defined *Scaphander* based on the pyriform shape of the shell of the type species *S. lignarius*, and *Bucconia* by a more globose shape of the shell and a 'posterior pillar extended backward and supporting an expansion of the outer lip', where he included the species *Scaphander nobilis* Verill, 1884. Dall (1890) also transferred the fossil species *Scaphander grandis* to the subgenus *Bucconia*. The subgenus was adopted by Bullis (1956) and Habe (1955), who gave it generic status, but Bouchet (1975) found no consistent anatomical differences supporting the subgenus *Bucconia*, and Valdés (2008) came to the same conclusion from examining Pacific specimens of Scaphandridae.

The species *Scaphander bathymophilus* (Dall, 1881) was originally described as an *Atys* (Dall, 1881), but a few years later Dall assigned it to *Sabatia* (Bellardi, 1876) and made this a subgenus of *Scaphander* (Dall, 1889a, 1889b). *Sabatia* (Bellardi, 1876) is based on a Pliocene fossil, which later led Dall (1908) to propose the name *Sabatina* to separate the recent species from the fossil group. Valdés (2008) suggested that *Sabatina* should be considered a synonym of *Sabatia* based on the presence of a parietal callus as a synapomorphy, but stressed that the taxonomic validity of the genera/subgenera *Scaphander*, *Bucconia*, *Sabatia*, and *Sabatina* needed further work. In the present study neither anatomical differences nor phylogenetic evidence were found to support the division of Scaphandridae in different genera (see Discussion).

Habe (1952) described a new genus, *Eoscaphander*, and a new species, *Eoscaphander fragilis*. The author claimed that his species differs from the type species of *Scaphander* in the radular characters, but gave no details about these differences. Valdés (2008) compared the anatomy of *E. fragilis* with *Scaphander* species from the West Pacific and found no sound anatomical differences. *Eoscaphander* is therefore considered a synonym of *Scaphander*. Kuroda *et al*. (1971) assigned *Scaphander japonicus* to a new genus *Nipponoscaphander* defined by a smaller and more ovoid shell than typical *Scaphander* species. Valdés (2008) reviewed *S. japonicus* and found no anatomical or shell differences that separate this species from other *Scaphander*, and therefore *Nipponoscaphander* is here considered a synonym of *Scaphander*. *Bullocardia* was described as a subgenus of *Bulla* with *Bulla millepunctata* Locard, 1897 as the type species. *Bulla millepunctata* is a synonym of *S. nobilis* (see systematic description of *S. nobilis*), and therefore *Bullocardia* is considered a synonym of *Scaphander*.

Diagnosis

Shell external, usually solid, pyriform to ovoid, with only one visible whorl. Shell sculpture composed of spiral grooves, usually punctuated. Aperture as long as shell; spire sunken. Animal can only partially withdraw into shell; operculum absent. Large head shield without posterior lobes, parapodial lobes present, not concealing the shell. Eyes absent. Radular formula $N \times 1.1.1$ or $N \times 1.0.1$, rachidian teeth, when present, small and fragile, probably vestigial. Flexible, non-muscular crop, gizzard large with three calcified gizzard plates (two large paired and one smaller unpaired), bound together by muscular fibre. Reproductive system monaulic, penis armed or unarmed.

Remarks

The presence or absence of rachidian teeth in the radula of *Scaphander* has been a matter of debate. In several publications (e.g. Sars, 1878; Marcus & Marcus, 1967) a rachidian tooth is depicted, but Bullis (1956) stated that this must be a mistake and that he did not find rachidian teeth in the species he examined. Valdés (2008) did not find rachidian teeth in the *Scaphander* species from the south-west Pacific. In this study rachidian teeth were found to be very small and fragile, and easily lost during the preparation of the radula. Rachidian teeth in *Scaphander* are vestigial, and may not serve any function, but this study proves their presence in all of the Atlantic species studied. The fragile nature of these teeth is likely to be the reason for the misunderstanding, but careful preparation of the radula might show them to be present in all species in the genus.

Valdés (2008) defined *Scaphander* as having a penis that can be 'armed or not'. The penis is unarmed in all Atlantic species for which the male reproductive system is known. Based on Valdés' (2008) diagnosis of *Scaphander*, the genus is here defined as potentially having an armed penis, as we could not confirm this for the Indo-Pacific species.

SCAPHANDER BATHYMOPHILUS (DALL, 1881)

Atys bathymophila Dall, 1881: 98 (Yucatan Strait; types seen, 2 syntypes, MCZ 6990, *H* = 4.9, 5.4 mm, Gulf of Mexico (24°1′N, 88°58′W); 1 syntype MCZ 6987, *H* = 15 mm, Yucatan; 3 syntypes, USNM 95198, *H* = 3.6, 4.9, 8.3 mm).

Scaphander (*Sabatia*) *bathymophila* Dall, 1889a: 86, pl. 17, figs 9, 9b; Dall, 1889b: 53, 54, pl. 17, figs 9, 9b; Pilsbry, 1893: 256, pl. 32, figs 27, 28; Johnson, 1934: 147.

Sabatia bathymophila Maury, 1922: 49; Thiele, 1931: 391.

Roxania (*Sabatia*) *bathymophila* Thiele, 1925: 244; Zilch, 1959–60: 27.

Sabatia (*Sabatina*) *bathymophila* Dall, 1927: 25.

Sabatia bathymophilus: Bullis, 1956: 2; Clarke, 1962: 40.

Scaphander (*Sabatina*) *bathymophilus* Dall, 1908: 241; Marcus, 1974: 341–345, figs 67–82.

Scaphander punctostriatus var. *clavus* Dall, 1889b: 52 (in part; specimen from Barbados).

Scaphander loisae Bullis, 1956: 8, figs 2G, H (Barbados, Caribbean Sea; type seen, holotype USNM 95188, *H* = 17.2 mm).

Taxonomic history

Dall (1881) first proposed the name *Atys bathymophila* for shells from the Yucatan Strait, casting doubts, however, on the generic assignment. Later, Dall (1889a, 1889b) placed the species in the subgenus *Sabatia* Bellardi, 1876. For discussion of this subgenus, see the taxonomic history of *Scaphander*. The anatomy of *S. bathymophilus* was studied by Marcus (1974), and shows great similarity to that of other *Scaphander* species. This study confirms these similarities, and *Atys bathymophila* Dall, 1881 is here considered a member of the genus *Scaphander*. Bullis (1956) examined the two specimens of *S. punctostriatus* var. *clavus* described by Dall (1889b) and found them to be two distinct species. The specimen from Barbados was chosen as the type specimen of a new species, namely *Scaphander loisae*. This species is only known from the type specimen, and nothing is known of the anatomy. The type specimen of *S. loisae* was examined, and it has the characteristic tuberculate callus of *S. bathymophilus*. The outline of the shell is also identical to the latter species (see Fig. 2: 12). Continuous striations, as seen in *S. loisae*, are not an uncommon intraspecific variation (e.g. *S. clavus*), and can also be present in some sections of the shell in a specimen with otherwise punctuated striations. *Scaphander loisae* Bullis, 1956 is here considered a synonym of *S. bathymophilus* (Dall, 1881).

Diagnosis

Shell solid, ovoid, white or cream. Striations punctuated by round, interconnected depressions. Parietal wall covered by thick, tuberculate, white callus. Body white. Lateral radular teeth with complex denticulation, rachidian teeth rectangular, with two posterolateral, triangular extensions. Prostate cylindrical, rounded at the end. Prostatic duct separating prostate and penial chamber, penial chamber cylindrical, extended where prostatic duct attaches. Penial papilla short with smooth surface. Type locality: Yucatan strait.

Material examined

Yucatan strait, 2 sh., MCZ 66690, *H* = 4.9, 5.4 mm; Gulf of Mexico (24°1′N, 88°58′W), 1 sh. MCZ 6987, *H* = 15 mm; Cape Hatteras, 32°50′N, 77°00′W, 1 spc. dissected, *H* = 17.4 mm; locality unknown, 3 sh., USNM 95198, *H* = 3.6, 4.9, 8.3 mm; locality unknown, 1 sh., USNM 836689, *H* = 24.6 mm; Puerto Rico, 1 spc. dissected, MZSP 75708, *H* = 30.5 mm; Azores, 2 spcs dissected, RMNH unnumbered, *H* = 19.2, 19.8 mm.

Shell (Fig. 2: 6–9, 11, 12): Maximum *H* = 37.5 mm (Marcus, 1974). Shell solid and ovoid, aperture very narrow posteriorly, extended anteriorly. Posterior edge of outer lip rounded, protruding beyond apex. A thin, white, or cream periostracum sometimes visible,

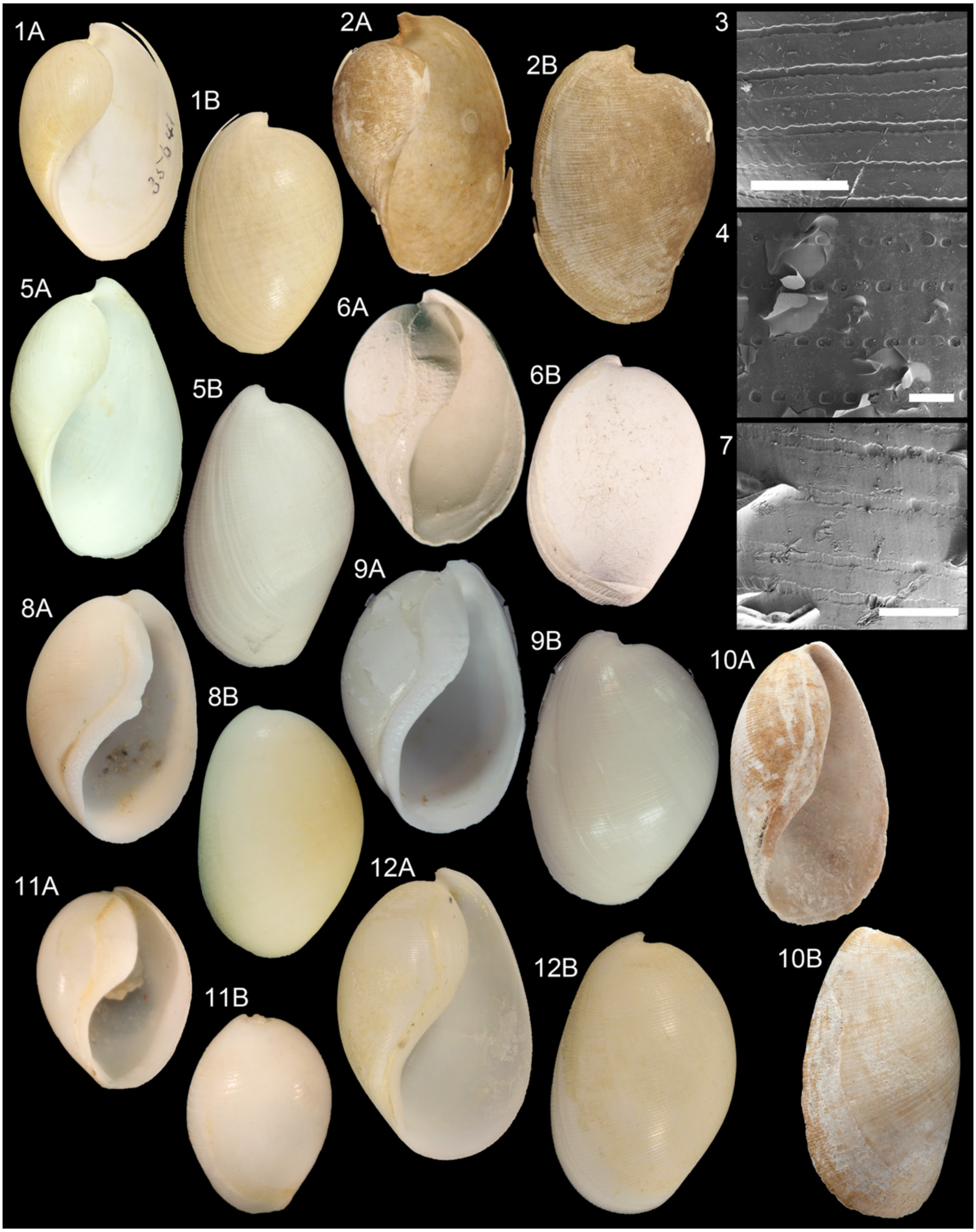

Figure 2. Shells and SEM images of the shell scuplture of *Scaphander nobilis* (1–5), *Scaphander bathymophilus* (6–9, 11, 12), and *Scaphander gracilis* (10); 1, holotype, Delaware Bay, USA (USNM 35641, $H = 34.2$ mm); 2, *Scaphander stigmaticus*, holotype, Gulf of Mexico (USNM 95196, $H = 35.4$ mm); 3, surface structure of shell, Georges Bank, USA (USNM 45562, $H = 11.3$ mm); 4, surface structure of shell, Bay of Biscay (MNHN, IM-2009-29696, $H = 31.9$ mm); 5, Bay of Biscay (MNHN, IM-2009-29696, H = 31.9 mm); 6, syntype, Yucatan, Mexico (MCZ 6987, $H = 15.0$ mm; 7, surface structure of shell, Cape Hatteras (MCZ 364990, $H = 12$ mm); 8, Azores (RMNH, unnumbered, $H = 19.8$ mm); 9, Cape Hatteras (MCZ 364990, $H = 12$ mm); 10, São Miguel I., Azores, syntype (NHMUK 1887.2.9.2187-8, $H = 13.0$ mm; image courtesy of the NHMUK photographic unit); 11, Yucatan Strait, syntype (MCZ 6990, $H = 5.4$ mm); 12, Barbados, holotype *Scaphander loisae* (USNM 95188, $H = 17.2$ mm). Scale bars: 500 µm.

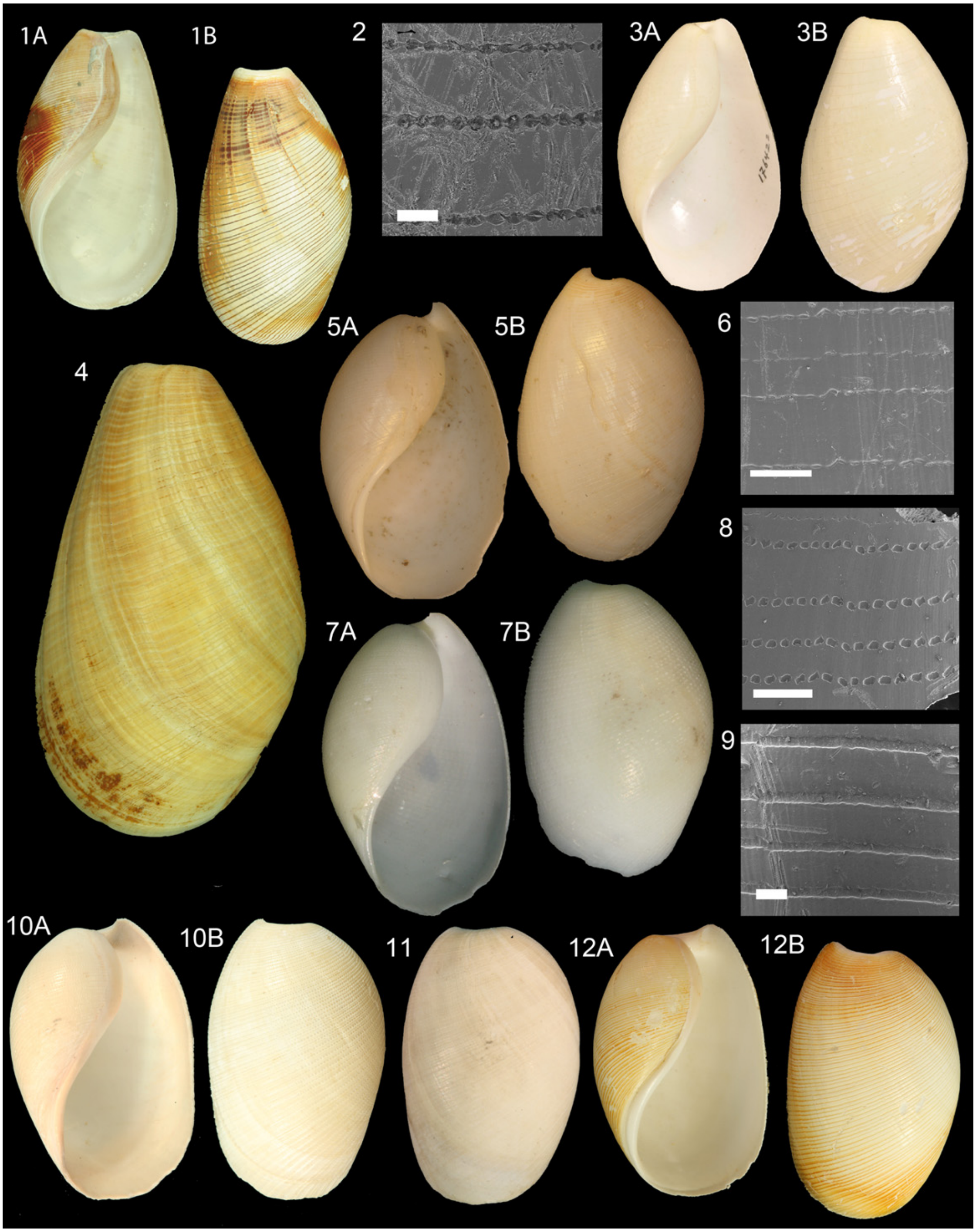

Figure 3. Shells and SEM images of the shell scuplture of *Scaphander lignarius* (1–4), *Scaphander punctostriatus* (5–8), and *Scaphander clavus* (9–12); 1, Høylandssundet, Hardangerfjord, Norway (ZMBN 62008, $H = 33.0$ mm); 2, surface structure of shell, Norway (ZMBN 17883, $H = 23.7$ mm); 3, syntype, *Scaphander lignarius* var. *alba*, Shetland Islands (USNM 176422, $H = 37.4$ mm); 4, Dublin Bay, Ireland (RMNH, unnumbered, $H = 70$ mm); 5, syntype, *Scaphander librarius*, Finnmark, Norway (SMNH 8039, $H = 16.2$ mm); 6, surface structure of shell, South Newfoundland (MNHN, IM-2009-29695, $H = 33.2$ mm); 7, neotype, locality unknown (MCZ 177003, $H = 11.0$ mm); 8, surface structure of shell, East of Norfolk, Virginia, USA (USNM 757101, $H = 12$ mm); 9, surface structure of shell, Suriname (USNM 836676, $H = 25.5$ mm); 10, Panama (MZSP 75.943, $H = 17.5$ mm), 11, lectotype, *Scaphander punctostriatus clavus*, Louisiana, USA (MCZ 6981, $H = 16.7$ mm); 12, Suriname (USNM 836676, $H = 25.5$ mm). Scale bars: 2, 100 μm; 6, 8, 500 μm; 9, 200 μm.

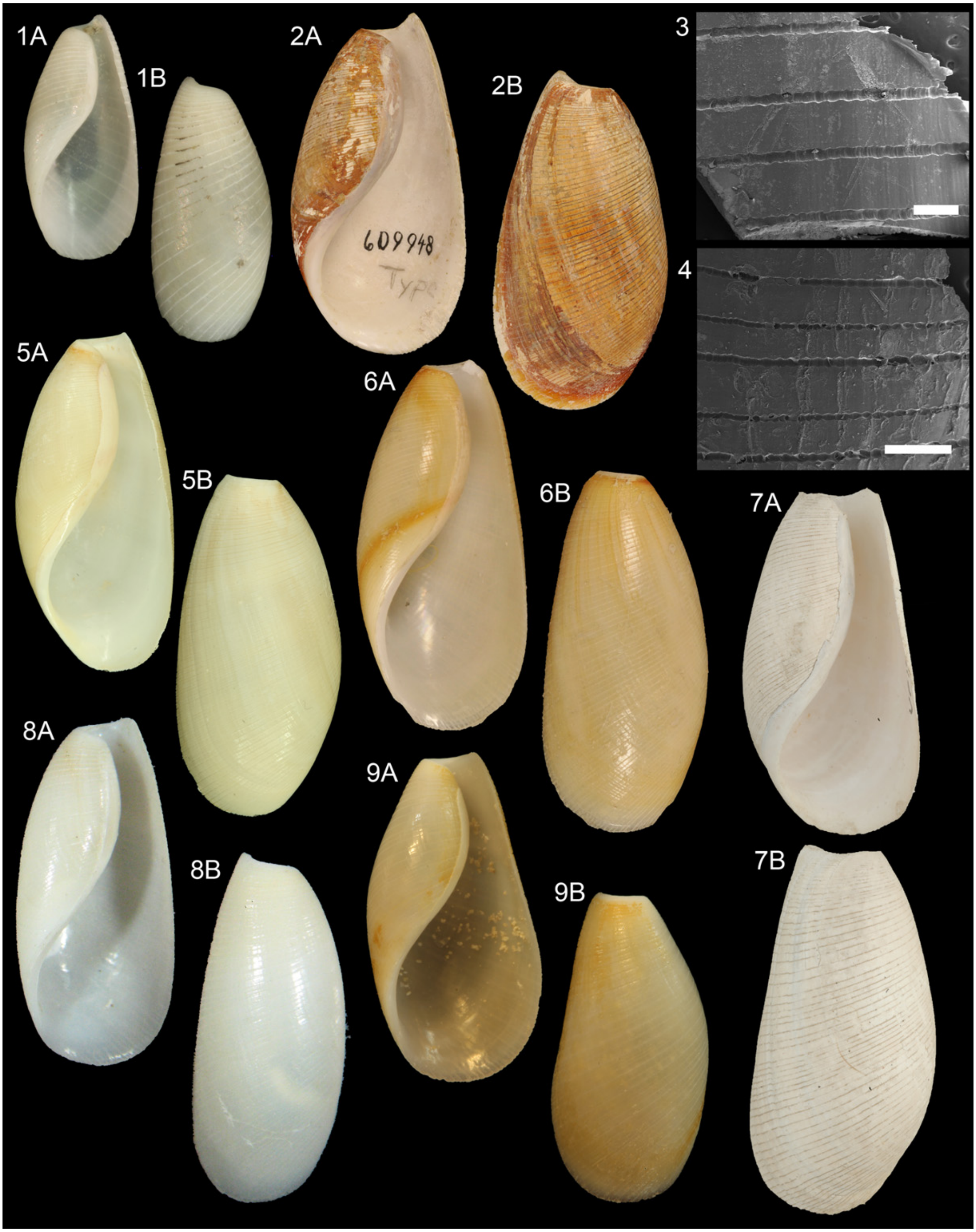

Figure 4. Shells and SEM images of the shell sculpture of *Scaphander watsoni* (1–5), *Scaphander darius* (6, 8–9), and *Scaphander pilsbryi* (7); 1, syntype, off Sombrero Island (MCZ 6982, $H = 8.1$ mm); 2, *Scaphander watsoni rhederi*, holotype, Gulf of Mexico (USNM 609948, $H = 39.3$ mm); 3, surface structure of shell, Gulf of Mexico (USNM 1151226, $H = 31.5$ mm); 4, surface structure of shell, off Florida, Gulf of Mexico (USNM 855168, $H = 13.1$ mm); 5, Santos, Brazil (USNM 34644, $H = 31.9$ mm); 6, holotype, off Colombia and Panama (USNM 679054, $H = 15.5$ mm); 7, holotype (FLMNH 174325, $H = 30.6$ mm); 8, Colombia, paratype (MZSP 76266, $H = 12.0$ mm); 9, off Florida, Gulf of Mexico (USNM 855168, $H = 13.1$ mm). Scale bars: 500 µm.

shell white under periostracum. Striations with round, interconnected punctuations. Parietal wall covered by a thick, tuberculate, white callus, sometimes forming an extension into the aperture (see Fig. 2: 8).

Radula (Fig. 5A–D): Lateral teeth are curved, with a broad base and weak denticulation on inner edge, consisting of several rows of denticles flattened along the side of the teeth. Rachidian teeth rectangular, with two posterolateral, triangular extensions.

Digestive tract (Fig. 5G, H): Salivary glands very long, flattened, with uneven, glandular surface. Paired gizzard plates kidney shaped to subtriangular.

Male reproductive system (Fig. 5E, F): Prostate cylindrical, rounded at the end and filled with spongy tissue. Prostatic duct separating prostate and penial chamber, penial chamber cylindrical, extended where prostatic duct attaches. Penial papilla short with smooth surface.

Ecology

Feeds on foraminiferans. Depth range: 805–1609 m.

Distribution (Fig. 12)

From Delaware Bay, USA (Pilsbry, 1893) to Caribbean Sea, Azores (present study).

Remarks

Dall (1927) reports 'numerous young specimens' of *S. bathymophilus* collected near Georgian and Fernandina (Florida, USA), and also specimens from the Yucatan Strait and around Cuba. He gives a depth range of 1342–5130 m, but does not indicate if the specimens consisted of shells only or live specimens, or what the depth ranges of individual dredgings were. Thus, it is possible that the depth range of *S. bathymophila* is much deeper than considered in this work (see Ecology).

SCAPHANDER CLAVUS DALL, 1889B

Scaphander punctostriatus var. *clavus* Dall, 1889b: 52; Pilsbry, 1893: 246; Dautzenberg & Fischer, 1896: 401, 402 (Gulf of Mexico, off Louisiana, USA; type seen, 1 lectotype, MZC 6981, *H* = 16.7 mm.

Scaphander clavus Bullis, 1956: 8, fig. 2I; Marcus & Marcus, 1967: 599, figs 1–4; Marcus, 1974: 333, 334, figs 34, 81, 85; Pequegnat, 1983: 159.

Taxonomic history

The name '*clavus*' was suggested by Dall (1889b) to describe two shells found in the Gulf of Mexico. He considered them a variety of *S. punctostriatus*, differing from that species by a more blunt apex and a 'more *Bulla*-like form'. Bullis (1956) raised this variety to specific status and gave a more detailed description of the shell morphology, and which characters separate this species from *S. punctostriatus* (mainly the shell shape and details of the striation). At this time no live specimens were known. Marcus & Marcus (1967) recorded the first living specimen of this species and depicted the radular teeth, apex, and male genital system, including the penial papilla. They noted that the shape of the shell and striations agreed perfectly with the description by Bullis (1956) and images of the type specimen. Marcus (1974) described the anatomy of another specimen from Surinam, and the description and figures agree with that of Marcus & Marcus (1967). Bouchet (1975) concluded that *S. clavus* Dall, 1889b is nothing more than a geographical variety of *S. punctostriatus*. Bouchet (1975) stated that there are differences in shell morphology and radular characters, but he believed these differences were not enough to justify specific status. Bouchet (1975) did not comment on the characters of the male reproductive system of *S. clavus* and *S. punctostriatus*, because he believed the specimens he examined to be sexually immature, and therefore had no material to compare with the figure in Marcus & Marcus (1967). The specimens of *S. punctostriatus* dissected here showed that the species has no penial papilla at any life stage, and adding this anatomical difference to the shell and radular characters it is clear that *S. clavus* and *S. punctostriatus* are two valid species.

Diagnosis

Shell solid, subrectangular, white to orange. Striations closely set with quadrate punctuations separated by short spaces. Body white. Lateral radular teeth with simple denticulation on outer edge, trilobed rachidian teeth with rounded lobes. Prostate tapering towards a short prostatic duct, connecting to the penial chamber. Penial papilla bulbous with a flagellate extension, the bulbous base of the papilla and the tip of the flagellum is covered with warts. Type locality: Gulf of Mexico.

Material examined

Gulf of Mexico, off Louisiana, USA, 1 sh., MCZ 6981, *H* = 16.7 mm; Colombia, Cartagena, 1 sh., MZSP 75941, *H* = 25 mm; Panama, 3 sh., MZSP 75943, *H* = 17.5, 22.3, 23 mm; Colombia, Isla Fuerte, 1 sh., MZSP 75433, *H* = 23 mm; Suriname, 1 spc. dissected (anterior part of digestive tract and male reproductive system were missing because of a previous dissection), USNM 836676, *H* = 25.50 mm.

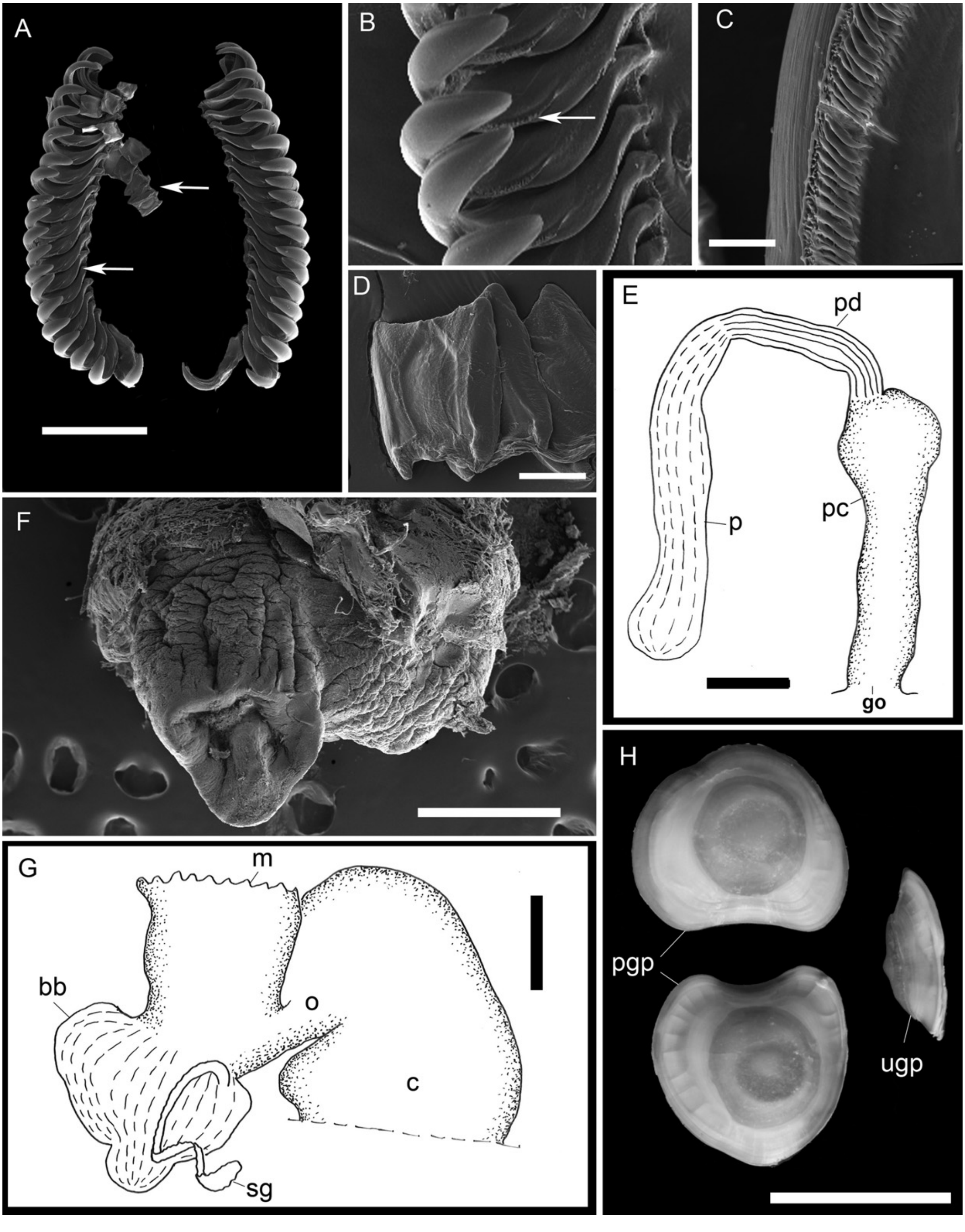

Figure 5. Anatomical details of *Scaphander bathymophilus*: A, radula, arrows point to location of rachidian teeth and details of lateral teeth; B, details of lateral teeth, arrow points to location of denticulation; C, denticulation of the outer edge of lateral teeth; D, rachidian teeth; E, male reproductive system; F, penial papilla; G, anterior part of digestive tract; H, gizzard plates; bb, buccal bulb; c, crop; go, genital opening; mo, mouth; o, oesophagus; p, prostate; pc, penial chamber; pd, prostatic duct; pgp, paired gizzard plates; sg, salivary gland; ugp, unpaired gizzard plate. Scale bars: A, 200 μm; B, 50 μm; C, 25 μm; D, 50 μm; E, 1 mm; F, 500 μm; G, 1 mm; *H* = 5 mm.

Shell (Fig. 3: 9–12): Maximum $H = 30$ mm. Shell thick and subrectangular in outline. Posterior edge of outer lip rounded, protruding slightly beyond apex. Periostracum sometimes visible, colour white to orange. Shells white under periostracum. Thick, closely set striations, some specimens with coloured striations (see Fig. 3: 12). Punctuations quadrate, separated by a short space. Sometimes fused together forming a continuous line (see Fig. 3: 9). Parietal wall covered by white callus.

Radula: Lateral teeth are curved with a broad base and simple denticulation on inner edge. Rachidian teeth with square base and three anterior lobes (based on Marcus & Marcus, 1967).

Digestive tract: Paired gizzard plates subtriangular, with a strongly calcified, yellow centre, and more porous edges, as in the other species (present study, data not shown). Shape of anterior part of digestive tract (in front of the gizzard, including salivary glands) not known.

Male reproductive system: Prostate tapering towards a short prostatic duct, connecting to the penial chamber. Penial papilla bulbous with a flagellate extension, base of papilla and the tip of flagellum is covered with warts. Walls of the penial chamber harbours a long ridge (Marcus & Marcus, 1967; Marcus, 1974).

Ecology

Marcus & Marcus (1967) found isopods and calcareous algae in the crop of one specimen from the Caribbean Sea. Depth range: 595–1056 m.

Distribution (Fig. 14)

Gulf of Mexico (Pequegnat, 1983), Caribbean Sea (Marcus, 1974), and Suriname (present study).

Remarks

Only one specimen was available for dissection, and it had already been dissected by someone else. The anterior part of the digestive tract (anterior to the gizzard) and the male reproductive system were missing. Dautzenberg & Fischer (1896) reported finding *S. punctostriatus* var. *clavus* Dall, 1889b around the Azores, and they described the specimens as heavy shells with less attenuation at the top. With this little information about the specimens, and no figures or pictures to confirm the identification, this record is not considered reliable. Knowing the variability of shell morphology found in *S. punctostriatus*, it might as well be that species, which is common around the Azores.

SCAPHANDER DARIUS MARCUS & MARCUS, 1967

?*Scaphander pilsbryi* McGinty, 1955: 82, 83, pl. 2, fig. 8 (Pensacola, Florida, USA; type images seen, FLMNH 174325, $H = 30.6$ mm).

Scaphander darius Marcus & Marcus, 1967: 603, 604, figs 10–17; Marcus, 1971: 925; Marcus, 1974: 336–340, figs 57–66, 81, 86 (Caribbean Sea, off Colombia and Panama; type seen, holotype, USNM 679054, $H = 15.5$ mm; type images seen, MZSP 76266, 2 paratypes, $H = 12.0$, 15.3 mm.

Taxonomic history

Scaphander darius was described by Marcus & Marcus (1967), who commented on its morphological similarity to both the eastern Atlantic *Scaphander lignarius* and the western Atlantic *Scaphander watsoni*, with the latter being so similar that one could not separate between the two species without examining the male copulatory apparatus (Marcus, 1974).

Diagnosis

Shell thin or solid, pyriform, white to light brown. Striations punctuated by round interconnected punctuations. Parietal wall often covered by thin, white callus. Body white. Lateral radular teeth with simple denticulation on both edges, rachidian teeth trilobed. Prostate short, cylindrical; prostatic duct separating prostate and penial chamber. Penial chamber bulbous, penial papilla bulbous, covered with warts. Type locality: off Colombia and Panama, Caribbean Sea.

Material examined

Caribbean Sea, off Colombia and Panama, 1 sh., USNM 679054, $H = 15.5$ mm; 9°31.3′N, 76°15.4′W, 2 sh., MZSP 76266, $H = 12.0$, 15.3 mm; off Florida, 25°16′54″N, 83°43′11″W, 1 spc. dissected, USNM 855168, $H = 13.1$ mm; Guarapari, Brazil, 1 spc. dissected, MZSP 29016, $H = 12.0$ mm.

Shell (Fig. 4: 6, 8, 9): Maximum $H = 23$ mm. Shell thin or solid, pyriform, anterior of aperture only very slightly extended. Posterior edge of outer lip sometimes pointed, protruding slightly beyond apex. Periostracum often visible, colour white to light brown. Shell white under periostracum. Thick punctuated striations. Punctuations are round and interconnected along the striae. Grooves are separated by gaps much wider than the grooves themselves.

Radula (Fig. 6A–D): Lateral teeth curved with a broad base, one row of denticulation on both edges.

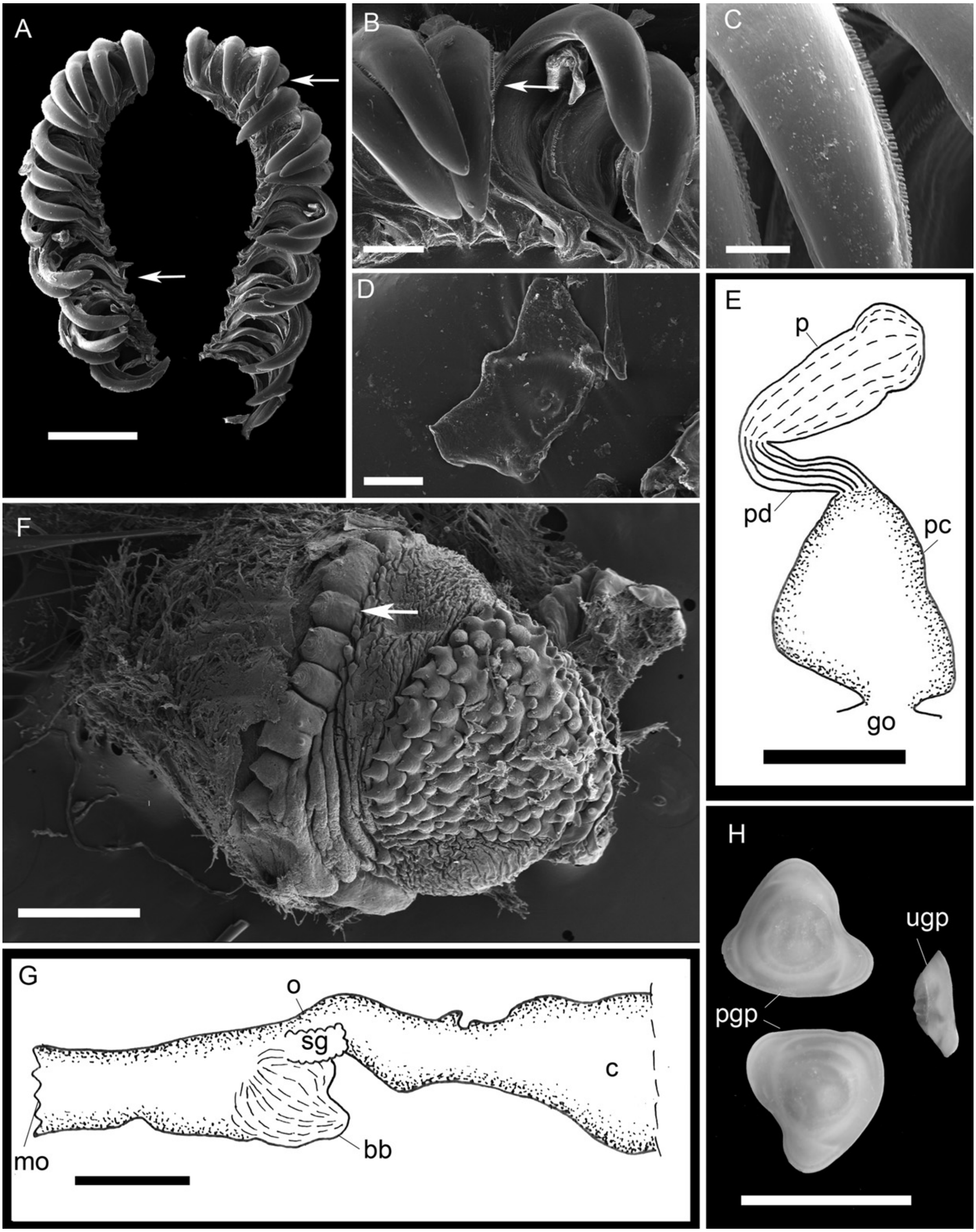

Figure 6. Anatomical details of *Scaphander darius*: A, radula, arrows pointing to location of rachidian teeth and details of lateral teeth; B, details of lateral teeth, arrow points to location of denticulation; C, denticulation of the outer edge of lateral teeth; D, rachidian tooth; E, male reproductive system; F, penial papilla, arrow pointing to circle of large warts; G, anterior part of digestive tract; H, gizzard plates; bb, buccal bulb; c, crop; go, genital opening; m, muscle; mo, mouth; o, oesophagus; p, prostate; pc, penial chamber; pd, penial duct; pgp, paired gizzard plates; sg, salivary gland; upg, unpaired gizzard plate. Scale bars: A, 500 μm; B, 100 μm; C, 20 μm; D, 50 μm; E, 5 mm; F, 200 μm; G, 2 mm; H, 5 mm.

Rachidian teeth wider than long, base square, anterior end trilobed with triangular lobes.

Digestive tract (Fig. 6G, H): Salivary glands short with uneven surface. Paired gizzard plates subtriangular. Central area of gizzard plates often yellowish and thicker than lateral area, which is porous and thinner.

Male reproductive system (Fig. 6E, F): Prostate cylindrical, rounded at distal end, prostatic duct separating prostate and penial chamber. Prostate filled with spongy tissue. Penial chamber bulbous, penial papilla bulbous, with a circle of large warts around the base, and papilla covered with small warts.

Ecology
Feeds on foraminiferans. Depth range: 16–97 m. Punctuations are round and interconnected along the striae. Grooves are separated by gaps much wider than the grooves themselves.

Distribution (Fig. 13)
Gulf of Mexico, Caribbean Sea, and Brazil (Marcus & Marcus, 1967; Marcus, 1971; Marcus, 1974).

Remarks
Scaphander pilsbryi McGinty, 1955 was described based on a single shell from Pensacola, Florida. Images of the type shell (FLMNH 174325, $H = 31$ mm) have been examined (Fig. 9: 7), and although the posterior end is more open compared with typical *S. darius* and *S. watsoni*, this feature falls within the variation of shell morphology seen in the latter two species. It is, however, impossible to say to which of these two species the shell of *S. pilsbryi* belongs, because, as discussed earlier, these species are only distinguishable by their internal anatomy.

SCAPHANDER GRACILIS WATSON, 1883

Scaphander gracilis Watson, 1883: 345, 346; Watson, 1886: 645, 646, pl. 47, figs 4a–c; Pilsbry, 1893: 247, 248, pl. 31, figs 19, 20; Dautzenberg & Fischer, 1896: 402; Locard, 1897: 47–49, pl. 1, figs 15–18; Bouchet, 1975: 338, pl. 3, fig. i (Western Azores, south of Flores Island; types seen, 4 syntypes, NHMUK 1887.2.9.2183–6, $H = 8.8$, 5.1, 11.3, 13.5 mm. south of São Miguel Island, Azores; 2 syntypes, NHMUK 1887.2.9.2187–8, $H = 13.0$, 14.4 mm).

Scaphander gracilis var. *minor* Locard, 1897: 47–49.

Scaphander gracilis var. *major* Locard, 1897: 47–49.

Taxonomic history
The name *Scaphander gracilis* was first used by Watson (1883) for shells found in the Azores during the 'Challenger' expedition. Watson (1883) compared the shells with *S. punctostriatus*, but differences in the shape and form of the callus and striations separate them from the latter species. Shells of this species have later been found around the Azores (the only known locality; Locard, 1897), but complete specimens have never been observed. Locard (1897) described a variety *major*, larger and more pyriform than the variety *minor*, with a more pronounced callus on the total length of the parietal wall. This most likely represents intraspecific variability correlated with the size of the animal, but it is difficult to assess the status of these varieties without any information on the anatomical characters of the animal. They are here considered synonyms of *Scaphander gracilis* Watson, 1883.

Diagnosis
Shell thin or solid, pyriform to ovoid, and white or yellow. Striations with round punctuation separated by short spaces. Anatomical characters not known. Type locality: archipelago of the Azores (south of São Miguel and Flores islands).

Material examined
West of the Azores, 4 sh., NHMUK 1887.2.9.2183–6, $H = 8.8$, 5.1, 11.3, 13.5 mm; San Miguel, Azores, 2 sh., NHMUK 1887.2.9.2187–8, $H = 13.0$, 14.4 mm.

Shell (Fig. 2: 10): Maximum $H = 24$ mm (Locard, 1897). Shell thin or solid, pyriform with anterior of aperture extended very little. Posterior edge of outer lip pointed, protruding beyond apex. Periostracum often visible, colour white to yellow. Shell white under periostracum. Medium, thick, punctuated striations. Punctuations are round, separated by short spaces. Striations are separated by gaps wider than the grooves themselves. Parietal wall covered by thick, white callus, sometimes forming a tooth-like projection in the anterior half of the aperture.

Radula: Unknown.

Digestive tract: Unknown.

Male reproductive system: Unknown.

Ecology
Feeding habits unknown. Depth range: 1299–2995 m.

Distribution (Fig. 14)

Azores (Watson, 1883; Dautzenberg & Fischer, 1896; Locard, 1897; Marcus, 1974; Bouchet, 1975).

Remarks

Marcus (1974) reported two shells of *S. gracilis* from the Caribbean Sea (12°55′N, 71°55′W). The author expressed uncertainty about the taxonomic identity of the shells, and admitted they could belong to *S. punctostriatus*, a common species in the area. Amphi-Atlantic distributions are known for several species of *Scaphander* (*S. nobilis*, *S. punctotriatus*, and *S. bathymophilus*) but because of a lack of sound evidence, *S. gracilis* is here considered restricted to the Azores. The depth distribution is based on shells only, and is therefore not entirely reliable because shells can be moved by currents and animals such as crustaceans.

SCAPHANDER LIGNARIUS (LINNAEUS, 1758)

Bulla lignaria Linnaeus, 1758: 727; da Costa, 1778: 26–28, pl. 1, fig. 9; Schröter, 1783: 175; Humphrey, 1794: 15, pl. 2, figs 1–8; Montagu, 1803: 205; Maton & Rackett, 1807: 125; Pennant, 1812: 254, pl. 63, fig. 2; Turton, 1819: 19, figs 3, 4 (gizzard plates); Blainville, 1825: 626, pl. 45, fig. 8; Payraudeau, 1826: 95; Costa, 1829: 75; Requien, 1848: 41; Petit, 1852: 81; Scacchi, 1857: 10 (Sicily and Adriatic Sea; type image seen, image reference: G-M 0010160, The Linnean Collections Online [http://www.linnean-online.org/16898/]).

Scaphander lignarius de Montfort, 1810: 334; Lovèn, 1846: 142; Leach, 1852: 39; Jeffreys, 1867: 443, pl. 8, fig. 6; Hidalgo, 1870: 2, pl. 9, figs 1, 2; Monterosato, 1878: 111; Sars, 1878: 292, pl. 18, fig. 7 (shell), pl. 26, fig. 4 (whole animal), pl. 11, fig. 13a–h (digestive tract, radula); Vayssière, 1879–80: pl. 10, figs 85–94 (head shield, digestive system, radula), pl. 11, figs 99–102 (nervous system); Bucquoy, Dautzenberg & Dollfus, 1882: 536–539, pl. 63, figs 1–3; Monterosato, 1884: 144; Locard, 1886: 69; Pilsbry, 1893: 245, pl. 31, figs 17, 21–23, pl. 32, figs 24 (whole animal), 25 (gizzard), pl. 61, figs 33–37 (gizzard), 39, 40 (radula); Locard, 1896: 207; Locard, 1897: 42; Friele & Grieg, 1901: 112; Sykes, 1904: 34; Perrier & Fisher, 1911: 72–126; Lemche, 1948: 59, 86, 87; Marcus, 1974: 325, fig. 31; Bouchet, 1975: 340; Yonge & Thompson, 1976: 116; Thompson & Brown, 1984: 125, figs 63, 64; Cutignano *et al*., 2008; Valdés, 2008: 667–668.

Bulla (*Scaphander*) *lignaria* Adams, 1855: 574, pl. 121, fig. 47; Weinkauff, 1862: 336.

Scaphander lignarius var. *alba* Jeffreys, 1867: 444; Pilsbry, 1893: 245 (Scotland; types seen, five syntypes USNM 176422, *H* = 31.7, 37.4, 7.6, 6.1, 3.6 mm).

Scaphander lignarius var. *curta* Jeffreys, 1867: 444; Pilsbry, 1893: 245 (Scotland; types seen, 2 syntypes, USNM 176430, *H* = 18.2, 17.7 mm).

Scaphader lignarius var. *hidalgoi* Bucquoy, Dautzenberg & Dollfus, 1882: 536–539; Hidalgo, 1870: 2, pl. 9, fig. 3.

Scaphander lignarius var. *brittanica* Monterosato, 1884: 144; Pilsbry, 1893: 245, pl. 31, fig. 17.

Scaphander lignarius var. *minuscula* Monterosato, 1884: 144; Pilsbry, 1893: 245.

Scaphander lignarius var. *targionia* Monterosato, 1884: 144; Pilsbry, 1893: 243.

Tricla lignaria Winckworth, 1932: 232.

Charta convoluta Martini, 1769: 283, pl. 21, figs 194, 195.

Assula convoluta Schumacher, 1817: 258.

Tricla gioeni Philipsson, 1788: 8.

Gioenia sicula Bruguière, 1792: 12, 502–504.

Scaphander giganteus Risso, 1826: 51, pl. 2, fig. 12.

Scaphander targionius Risso, 1826: 51, pl. 2, fig. 13.

Bulla zonata Turton, 1834: 352, 353.

Scaphander librarius Lovèn, 1846: 142 (in part; 1 syntype, SMNH 8039, *H* = 9.5 mm, remaining syntypes are *S. punctostriatus*).

Scaphander brownii Leach, 1852: 40.

Tricla lignaria brownii Fisher, 1935: 172.

Taxonomic history

This species was first described as *Bulla lignaria* by Linnaeus (1758). Linnaeus (1758) does not refer to a type locality, but Gmelin (1791), in the 13th edition of *Systema Naturae*, places the type locality in the western Mediterranean Sea (Sicily and Adriatic Sea). *Charta convoluta* Martini, 1769 is a senior synonym of *S. lignarius*, but precedence is here reversed in favour of *Scaphander* de Montfort, 1810 (see the taxonomic history of *Scaphander*). *Assula convoluta* Schumacher, 1817 is a synonym of *Charta convoluta* Martini, 1769, and therefore a synonym of *S. lignarius*. Gioeni (1783) described the gizzard of *S. lignarius* as a new animal, but the names *Gioeni* Gioeni, 1783, *Tricla lignaria* Philipsson, 1788, and *Gioenia sicula* Bruguière, 1792 given to this ‘stomach-animal’ are not valid today (see the taxonomic history of *Scaphander*). de Montfort (1810) introduced the genus *Scaphander* to include the species *S. lignarius* (Linnaeus, 1758). Adams (1855) placed *Scaphander* as a subgenus of *Bulla*, but by the end of the 1800s the genus *Scaphander* was widely accepted. Towards the end of the 19th century several variations of *S. lignarius* were described (e.g. Jeffreys, 1867; Monterosato, 1884), based on shell characters like variations in size, colour, and striations. *Scaphander lignarius* var. *hidalgoi* was described by Bucquoy, Dautzenberg & Dollfus, 1882 based on a figure by Hidalgo (1870) of a small *S. lignarius* with a uniform brown colour. In the present study none of these shell variations have correlated with variations in the anatomy of the animal, and they should be considered nothing more than part of the intraspecific variability of the species. *Scaphander brownii* Leach, 1852 and *Bulla zonata* Turton, 1834 were described from young *S. lignarius*. Lovèn (1846) described *S. librarius* from Finnmark, Norway, but this is a synonym of *S. punctostriatus* (Mighels & Adams, 1842). However, examination of the syntypes revealed that one of them is *S. lignarius* (SMNH 8039, *H* = 9.5 mm).

Scaphander lignarius is a well-known species in both scientific and amateur malacological/conchological communities, and the literature available is vast. It was therefore not feasible to provide a comprehensive list of literature for this species, and only a selection of considered key works have been included. For a more complete list of literature prior to 1948 see Lemche (1948).

Diagnosis
Shell solid, pyriform, and white to brown. Striations punctuated with round, usually interconnected depressions. Body white, yellow, or brown. Lateral radular teeth with simple denticulation on outer edge, trilobed rachidian teeth. Prostate tapering toward penial chamber, no penial papilla, inside of penial chamber covered with soft, wart-like structures. Type locality: Sicily and Adriatic Sea (Mediterranean Sea).

Material examined
Scotland, UK, 5 sh., USNM 176422, *H* = 3.6, 6.1, 7.6, 31.7, 37.4 mm; Scotland, UK, 2 sh., USNM 176430, *H* = 18.2, 17.7 mm; Bergenfjorden, Norway, 2 spcs dissected, ZMBN 28436, *H* = 35.5, 36.1 mm; Høylandssundet, Norway, 2 spcs dissected, MZBN 62008, *H* = 18.2, 33 mm; Halsnøy, Hardangerfjorden, Norway, 2 spc. dissected, ZMBN 62007, *H* = 20.1, 21.3 mm; Barcelona, Spain, 1 spc. dissected, MCZ 371885, *H* = 40.0 mm; Celtic Sea (48°39′N, 09°46′S), 1 spc. dissected, MNHN, IM-2009-29694, *H* = 30 mm.

Shell (Fig. 3: 1–4): Maximum *H* = 70 mm. Shell solid, pyriform with anterior of aperture extended. Posterior edge of outer lip rounded, usually not protruding beyond apex. Periostracum often visible, colour white to brown. Shell white under periostracum. Thick punctuated striations, some specimens with coloured striations (see Fig. 3: 1). Punctuations are round and usually interconnected along the striae. Groves are separated by gaps much wider than the grooves themselves. Major growth lines present and common.

Radula (Fig. 7A–D): Lateral teeth curved with broad base and simple denticulation (one row) on outer edge or on both edges. Rachidian teeth with quadrate base, anterior end trilobed with two rounded lobes and one pointed lobe in the centre.

Digestive tract (Fig. 7G, H): Salivary glands short with uneven surface. Paired gizzard plates subtriangular to trilobed. Central area of gizzard plates often yellowish and thicker than lateral area, which is porous and thinner.

Male reproductive system (Fig. 7E, F): Prostate cylindrical, rounded at the end, and tapering towards penial chamber. Prostate filled with spongy tissue. Penial chamber cylindrical. No penial papilla, the inside of the penial chamber is covered with soft warts.

Ecology
Feeds on foraminiferans, bivalves, gastropods, scaphopods, and occasionally sipunculids. Produces secondary metabolites, probably alarm pheromones (Cimino *et al*., 1989). Depth range: 70–630 m.

Distribution (Fig. 14)
East Atlantic; from Finnmark (Norway) to the British Isles, Europe, and the Mediterranean Sea (Gmelin, 1791; Locard, 1897; Hidalgo, 1917; Bouchet, 1975; present study). Canaries (Hernàndez *et al*., 2011) and Madeira (Nordsieck & Garcia-Talavera, 1979).

Remarks
Vayssière (1879–80) described the presence of a nipple-shaped protrusion – 'mammillae' – covered with cartilaginous cones in the penial chamber of *S. lignarius* located around the opening of the prostate. A swelling similar to the structure described by Vayssière was found in some specimens during this study; however, the cone-shaped warts covering the inner walls of the penial chamber are not cartilaginous, but are instead made of soft tissue. Marcus & Marcus (1967) mentioned the unpublished thesis of Lloyd (1952), who described the penial papilla of *S. lignarius* as hammer-shaped, but no distinct papilla has been found in any of the specimens dissected in this study.

SCAPHANDER NOBILIS VERILL, 1884

Scaphander nobilis Verill, 1884: 209, 210, pl. 32, fig. 18a–d; Dall, 1889a: 86; Dall, 1889b: 53, pl. 64., fig. 106; Pilsbry, 1893: 249, 250, pl. 32, figs 31, 32; Maury, 1922: 49; Dall, 1927: 26; Johnson, 1934: 147; Clarke, 1962: 40; Bouchet, 1975: 335, 336, figs 7A–C, pl. 3, figs a–c, map 5 (Delaware Bay; type seen, holotype, USNM 35641, *H* = 34.2 mm).

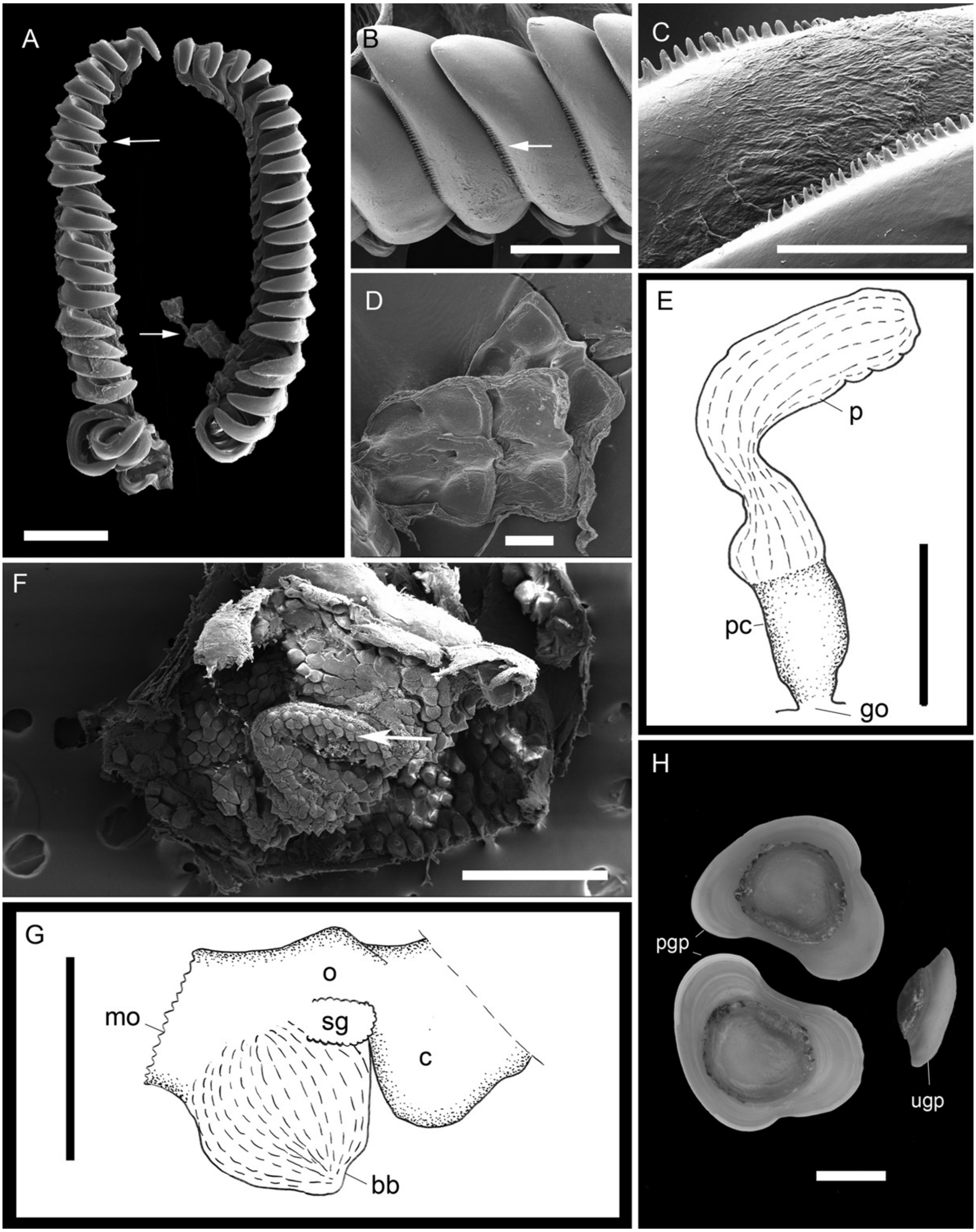

Figure 7. Anatomical details of *Scaphander lignarius*: A, radula, arrows point to location of rachidian teeth and details of lateral teeth; B, details of lateral teeth, arrow points to location of denticulation; C, denticulation of the outer edge of lateral teeth; D, rachidian teeth; E, male reproductive system; F, penial chamber turned inside out, arrow pointing to warts covering the inside of the chamber; G, anterior part of digestive tract; H, gizzard plates; bb, buccal bulb; c, crop; go, genital opening; mo, mouth; o, oesophagus; p, prostate; pc, penial chamber; pgp, paired gizzard plates; sg, salivary gland; ugp, unpaired gizzard plate. Scale bars: A, 500 μm; B, 100 μm; C, 50 μm; D, 50 μm; E, 5 mm; F, 500 μm; G, 5 mm; H, 1 mm.

Scaphander (*Bucconia*) *nobilis* Dall, 1890: 16, 17, pl. 10, fig. 9; Thiele, 1925: 319; Bullis, 1956: 6, figs 2A,B.

Scaphander stigmatica Dall, 1927: 26 (Gulf of Mexico; type seen, holotype, USNM 95196, *H* = 35.4 mm).

Scaphander (*Bucconia*) *stigmatica* Bullis, 1956: 6, figs 2D,E.

Scaphander stigmaticus Marcus, 1974: 334, figs 51–56.

Bulla millepunctata Locard, 1897: 52, 53.

Atys millepunctatus Martens & Thiele, 1903: 15, pl. 5, fig. 20.

Taxonomic history

This species was first described by Verill (1884), based on specimens from the New England coast (USA). Dall (1889a, 1889b) reported finding *S. nobilis* in the Gulf of Mexico, but later described this shell as a new species, namely *Scaphander stigmatica* (Dall, 1927). Locard (1896) described the species *Bulla millepunctata* and reported its occurrence on the west coast of Africa and the Azores (Locard, 1897). Martens & Thiele (1903) transferred this species to the genus *Atys*. Bouchet (1975) compared the types of *B. millepunctata* Locard, 1896 and *S. stigmatica* Dall, 1927 with the figures of the type of *S. nobilis* Verill, 1884 in Bullis (1956), and concluded that they represent variation in the shell morphology of *S. nobilis*. In the present study the types of *S. nobilis* and *S. stigmatica* were studied and compared with the figure of *Atys millepunctatus* in Martens & Thiele (1903), and the same conclusion was reached.

Diagnosis

Shell thin, ovoid, and white. Striations with round punctuations separated by short spaces or interconnected. Body white. Lateral radular teeth with weak denticulation on the inner edge, rachidian teeth rectangular. Prostate tapering toward penial chamber, penial papilla flagellate, covered with warts. Type locality: Delaware Bay, USA.

Material examined

Delaware Bay, USA, 1 sh., USNM 35641, *H* = 34.5 mm; South of Cuba, 1 sh., USNM 95196, *H* = 35.4 mm; Georges Bank, USA, 1 spc. dissected, USNM 45562, *H* = 11.3 mm; Bay of Biscay, 2 spcs dissected, MNHN, IM-2009-29696, *H* = 26.2, 31.9 mm.

Shell (Fig. 2: 1–5): Maximum *H* = 40 mm. Shell thin and ovoid, aperture wide. Posterior edge of outer lip pointed, protruding well beyond apex. A thin, translucent periostracum visible, shell white. Striations punctuated by small, round punctuations separated by short spaces or interconnected (see Fig. 2: 3, 4)

Radula (Fig. 8A–D): Lateral teeth curved with broad base and weak denticulation on inner edge. Rachidian teeth rectangular, longer than wide, anterior end pointed in the centre.

Digestive tract (Fig. 8G, H): Salivary glands medium long, uneven surface. Paired gizzard plates kidney shaped. Central area of gizzard plates orange in specimens from Bay of Biscay, thicker than lateral area, which is porous and thinner.

Male reproductive system (Fig. 8E, F): Prostate round, tapering towards penial chamber, and filled with spongy tissue. Penial chamber cylindrical and covered with soft warts on the inside, also in juvenile specimens without a developed penial papilla. Penial papilla with bulbous base and flagellum covered with warts.

Ecology

Feeds mainly on foraminiferans ingested along with sand. One specimen from the Bay of Biscay had empty polychaete tubes, coccoliths, and faecal pellets containing small foraminiferans in the crop. Depth range: 1493–4255 m.

Distribution (Fig. 15)

From Martha's Vineyard, MA, USA (Dall, 1927), the Gulf of Mexico (Bullis, 1956), and from the Caribbean Sea to south Brazil (Marcus, 1974). Bay of Biscay, the Azores (Bouchet, 1975), and the north-west coast of Africa from the Canaries to Senegal (Locard, 1897; Marcus, 1974).

Remarks

Marcus (1974) reported finding a small specimen of *S. nobilis* in Brazil. The author pointed out that the rachidian tooth of the specimen was different from the drawings by Verill (1884). Verill's drawings have very few details, and it is unclear if the markings in the centre of the radula refer to rachidian teeth. Nevertheless, the rachidian teeth found in this study are of a different shape than the one drawn by Marcus (1974), but are similar to the tooth depicted by Bouchet (1975; see Fig. 6D). Variability in the shape of rachidian teeth is, however, not uncommon in *Scaphander* species (see Fig. 5). Yet, the description by Marcus (1974) of the male reproductive system of the Brazilian specimen, with a penial papilla covered with soft warts, coincides with our observations of *S. nobilis* specimens. Several reports on the occurrence of *Scaphander mundus* Watson, 1883 in the Atlantic Ocean have been published (Locard, 1897; Marcus & Marcus, 1966; Pequegnat, 1983), even though *S. mundus* is an Indo-West Pacific species, originally described from Aru Island,

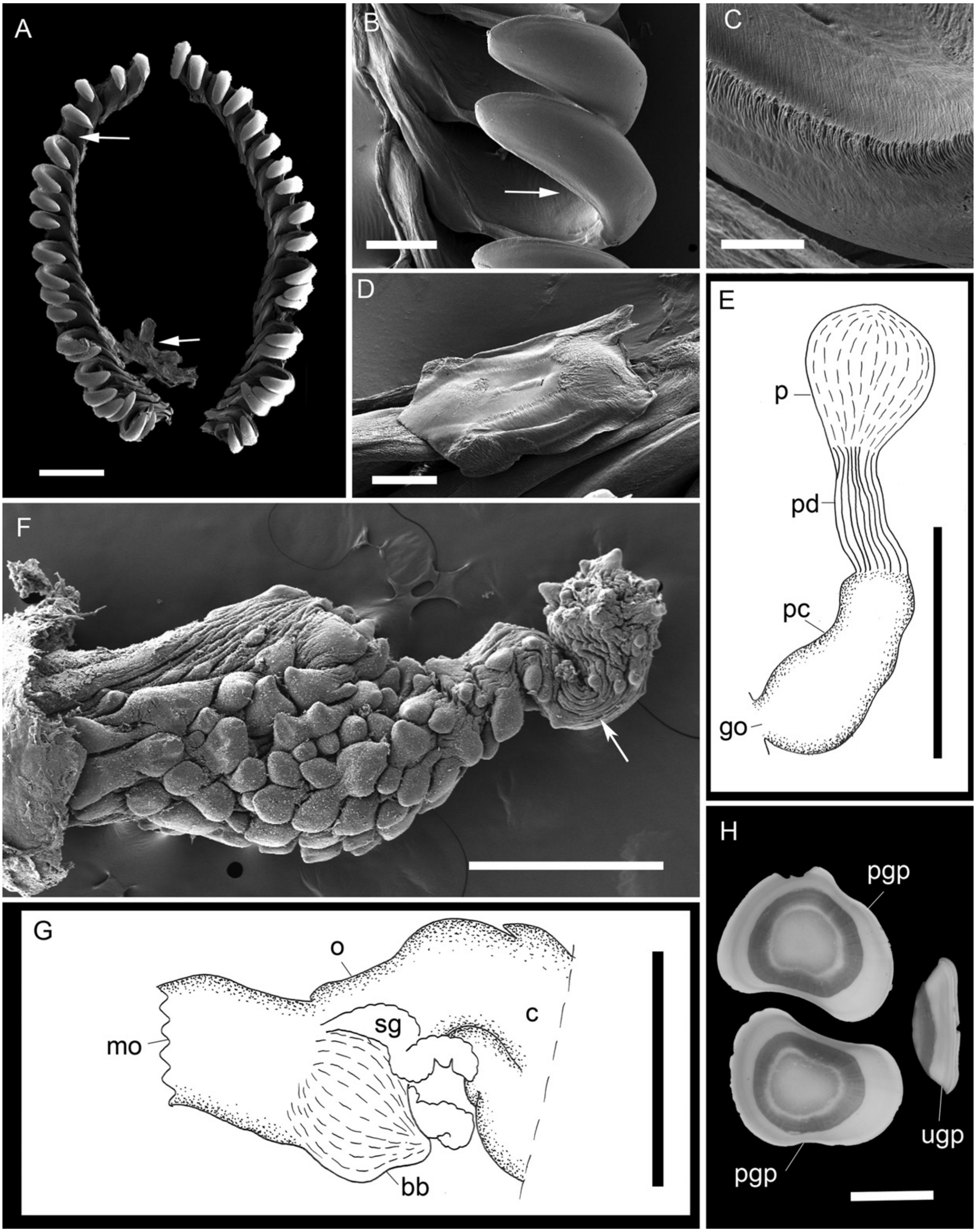

Figure 8. Anatomical details of *Scaphander nobilis*: A, radula, arrows point to location of rachidian teeth and details of lateral teeth; B, details of lateral teeth, arrow points to location of denticulation; C, denticulation of the outer edge of lateral teeth; D, rachidian teeth; E, male reproductive system; F, penial papilla, arrow pointing to flagellum; G, anterior part of digestive tract; H, gizzard plates; bb, buccal bulb; c, crop; f, flagellum; go, genital opening; mo, mouth; o, oesophagus; p, prostate; pc, penial chamber; pd, prostatic duct; pgp, paired gizzard plates; sg, salivary gland; ugp, unpaired gizzard plate. Scale bars: A, 500 µm; B, 100 µm; C, 20 µm; D, 50 µm; E, 5 mm; F, 500 µm, G, 5 mm; H, 5 mm.

West of Papua, Indonesia (Watson, 1883; Valdés, 2008). These observations in the Atlantic Ocean are probably based on misidentifications of *S. nobilis*, which is very similar in shell morphology to *S. mundus*. To test for this, one specimen of *S. mundus* from the Philippines was dissected (illustrations not shown), and the anatomy of the male reproductive system was confirmed to differ. Moreover, two specimens of *S. mundus* from the Philippines were included in the molecular phylogenetic analyses, which corroborated the morpho-anatomical results. Therefore, the records of *S. mundus* for the western Atlantic are here included in the distribution of *S. nobilis* (Fig. 13).

SCAPHANDER PUNCTOSTRIATUS (MIGHELS & ADAMS, 1842)

Bulla puncto-striata Mighels & Adams, 1842: 43, 44, pl. 4, fig. 10; Stimpson, 1851: 17, 18 (no locality; type seen, neotype, MCZ 177003, $H = 11$ mm).

Bulla (Scaphander) puncto-striata Adams, 1855: 575, pl. 121, fig. 50.

Scaphander puncto-striatus Gould, 1870: 215, fig. 505; Sars, 1878: 292, pl. 18, fig. 7, pl. 26, fig. 4; Friele & Grieg, 1901: 113.

Scaphander punctostriatus Watson, 1886: 642, 643; Locard, 1886: 70; Dall, 1889a: 86, pl. 72, fig. 4; Dall, 1889b: 52; Pilsbry, 1893: 246, pl. 31, fig. 16; Dautzenberg & Fischer, 1896: 401, 402; Locard, 1896: 208; Locard, 1897: 45; Sykes, 1904: 34; Maury, 1922: 49; Johnson, 1934: 146; Lemche, 1948: 59, 60, 87, 88; Bullis, 1956: 5, 6, figs 2 C, F; Marcus, 1974: 325, 326, fig. 33; Bouchet, 1975: 338–340, figs 8A–F, pl. 3, figs d–f, map 6; Thompson & Brown, 1984: 126, fig. 65.

Scaphander librarius Lovén, 1846: 142; Jeffreys, 1867: 445, 446; Monterosato, 1878: 111 (Finnmark, Norway; types seen, 1 syntype, SMNH 8039, $H = 16.2$ mm, 2 syntypes, SMNH 8040, $H = 7.6, 14.8$ mm).

Cryptaxis crebripunctatus Jeffreys, 1883: 298, pl. XLIV, figs 11, 11a–c; Pilsbry, 1893: 293, pl. 27,

Scaphander punctostriatus var. *intermedia* Locard, 1897: 45.

Scaphander punctostriatus var. *inflata* Locard, 1897: 45.

Scaphander punctostriatus var. *elongata* Locard, 1897: 45.

Clistaxis crebripunctatus Cossmann, 1895: 90.

Brocktonia crebripunctatus Iredale, 1915: 340.

Taxonomic history

The name *Bulla puncto-striata* was introduced by Mighels & Adams (1842) for a shell found in the stomach of a haddock in Casco Bay, Maine, USA. The original types were lost in a fire at the Portland Society of Natural History and a neotype was selected from C.B. Adams' collection (Johnson, 1949). A few years later Lovén (1846) described some shells from Finnmark, Norway, as *S. librarius*. The type specimens of the latter species were studied and found to correspond to *S. punctostriatus*, except one (SMNH 8039, $H = 9.5$ mm), which is *S. lignarius*. The species *Cryptaxis crebripunctatus* Jeffreys, 1883 was described based on small shells ($H = 5$ mm) found at around 1000 m depth between the Hebrides and the Faroe Islands. He grouped these shells together with *Cylichna parvula* in a new genus *Cryptaxis* based on the partial concealment of the spire. *Cryptaxis* Jeffreys, 1883 is, however, a junior homonym of *Cryptaxis* Lowe, 1854, and the new name *Clistaxis* Cossmann, 1895 was proposed for the genus. Iredale (1915) created another genus, *Brocktonia* Iredale, 1915, for the species *Clistaxis crebripunctatus*, with the argument that 'This species does not really fall into *Cryptaxis* Jeffreys, 1883'. From the original description by Jeffreys and the plates, it looks like the animals described are young *S. punctostriatus*, which was also the conclusion of Friele & Grieg (1901) and Lemche (1948).

Diagnosis

Shell usually solid, ovoid to pyriform, and white or yellow. Striations narrow, rounded or oblong punctuations separated by short spaces. Body white or yellow. Lateral radular teeth with or without denticulation, bilobed or trilobed rachidian teeth. Prostatic duct separating prostate and penial chamber, penial chamber usually with small blind sac near entrance of prostatic duct. No penial papilla. Original type locality: Casco Bay, Maine, USA; neotype locality: unknown.

Material examined

Locality unknown, 1 sh., MCZ 177003, $H = 11$ mm; locality unknown, 1 sh., MCZ 156451, $H = 5{,}4$ mm; Mudheim, Norway, 4 spcs dissected, ZMBN 62015, $H = 26.1$, 26.7, 27.3, 28.5 mm; South Newfoundland, 3 spcs dissected, MNHN, IM-2009-29695, $H = 26.7$, 28.9, 33.2 mm; Eidsfjorden, Norway, 1 spc. dissected, ZMBN 62022, $H = 24.1$; Samlafjord, Norway, 2 spcs dissected, ZMBN 62014, $H = 21.0$, 26.4 mm; Cape Cod, USA, 1 spc. dissected, MCZ 304991, $H = 24$ mm; Between Canary Is and Morocco (27°89′–27°85′N, 13°91′–13°88′W), north-west Africa, 1 spc. dissected, NHMUK 19980349, $H = 32$ mm; Between Canary Islands and Morocco (27°90′N, 13°90′W), north-west Africa, 1 spc. dissected, NHMUK 19980249, $H = 41.2$ mm; Cape Sable, Nova Scotia, 1 spc. dissected, MCZ 200802, $H = 28$ mm; Gulf of St Lawrence, 1 spec dissected, ARC 9460084, $H = 26$ mm.

Shell (Fig. 3: 5–8): Maximum $H = 41.2$ mm. Shell usually solid, pyriform to ovoid with anterior of aperture extended. Posterior edge of outer lip curves towards apex, forming a cup, usually not protruding much beyond apex. Periostracum often visible, colour white to yellow. Shell white under periostracum. Narrow, punctuated striations. Punctuations are oblong or round, with a short space between. Grooves are separated by gaps much wider than the grooves themselves. Growth lines present, but usually not major; thin to medium in thickness, white callus on parietal wall sometimes present.

Radula (Figs 9A–D, 10A–D): Lateral teeth curved with a broad base; denticulation present or absent, simple (one row of denticles) or in multiple rows (Fig. 9C, D). Base of rachidian teeth with posterolateral triangular extensions, anterior end bilobed or trilobed, with triangular or rounded lobes (see Fig. 10).

Digestive tract (Fig. 9G, H): Salivary glands medium long, surface uneven. Paired gizzard plates kidney-shaped to subquadrate.

Male reproductive system (Fig. 9E, F): Prostate cylindrical, rounded at the end and tapering towards a long prostatic duct. Prostate filled with spongy tissue; often positioned on the left side of the digestive tract with the prostatic duct running under the digestive tract, connecting to the penial chamber on the right side. Penial chamber cylindrical, usually with small, rounded blind sac where the prostatic duct opens into the penial chamber. Interior walls of penial chamber harbours soft, longitudinal ridges running lengthwise from prostatic duct to genital opening. Ridges fill up most of the space inside penial chamber.

Ecology

Feeds on foraminiferans, often ingested along with sand and mud. Depth range: 264–2730 m.

Distribution (Fig. 15)

East Atlantic: from Norway, Iceland, Faroe Islands, southwards to the British Isles and Mediterranean Sea (Dautzenberg & Fischer, 1896; Locard, 1897; Sykes, 1904; Lemche, 1929; Bouchet, 1975; Marcus, 1977). West Atlantic: from Greenland, east coast of North America, Antilles, and Sargasso Sea (Locard, 1897; Lemche, 1929; Marcus, 1974; present study).

Remarks

The radula of *S. punctostriatus* shows extensive variability in denticulation of the lateral teeth and shape of rachidians. In a specimen from Cape Cod (MCZ 304991, $H = 24$ mm) and one from Gulf of St Lawrence (ARC 9460084, $H = 26$ mm) the denticulation on the lateral teeth was formed by one row of long denticles on the inner edge of the teeth and a band of short denticles at the base (see Fig. 4C). One specimen from Norway (ZMBN 62015, $H = 26.1$ mm) has one row of denticles on the outer edge, and one specimen from East of Norfolk, Virginia (USNM 757101, $H = 12$ mm) has one row of denticles on the inner edge. Specimens from Nova Scotia (MCZ 200802, $H = 41.2$ mm), Norway (ZMBN 62015, $H = 27.3$, 26.76 mm), and Newfoundland (MNHN, IM-2009-29695, $H = 26.7$, 28.9, 33.2 mm) show no denticulation on the lateral teeth. The variability of the rachidian teeth of *S. punctostriatus* was depicted by Bouchet (1975), and can also be seen in Figure 5. This intraspecific variation does not follow a geographical pattern.

SCAPHANDER WATSONI DALL, 1881

Scaphander watsoni Dall, 1881: 99, 100; Dall, 1889a: 86, pl. 17, fig. 10; Dall, 1889b: 52, 53, pl. 17, fig. 10; Pilsbry, 1893: 248, 249, pl. 31, fig. 18; Maury, 1922: 49; Johnson, 1934: 147; Marcus, 1974: 326–328, figs 35–41, 81, 87; Pequegnat, 1983: 159 (Caribbean Sea, Sombrero Island; type seen, 1 syntype, USNM 95190, $H = 8.8$ mm, 2 syntypes, MCZ 6982, $H = 8.1$, 8.1 mm).

Scaphander (*Scaphander*) *watsoni watsoni* Bullis, 1956: 10, figs 3C,D.

Scaphander (*Scaphander*) *watsoni rhederi* Bullis, 1956: 13–15, figs 3A–D [Gulf of Mexico, off Mobile; type seen, holotype, USNM 609948, $H = 39.3$ mm. (29°10′N, 88°03′W); type seen, 1 paratype, MCZ 214372, $H = 40.8$ mm].

Scaphander watsoni rhederi Marcus & Marcus, 1967: 602, 603, figs 5–9.

?*Scaphander pilsbryi* McGinty, 1955: 82, 83, pl. 2, fig. 8 (Pensacola, Florida, USA; type images seen, FLMNH 174325, $H = 30.6$ mm).

Taxonomic history

Scaphander watsoni was first described by Dall (1881), based on a very small shell ($H = 8.8$ mm) from Sombrero Island, Caribbean Sea, probably a juvenile specimen, but adult shells (measuring up to 38 mm) were found later by Dall (1889a, 1889b). Bullis (1956) placed *S. watsoni* in the subgenus *Scaphander*, related in shape to the type species *S. lignarius*, and described a new subspecies, *Scaphander watsoni rhederi*, differing from *Scaphander watsoni watsoni* by a slightly higher width/height ratio and slightly more striae per length of shell surface. Bullis (1956) also mentioned a more ‘pinched together’ appearance of the unpaired gizzard plate. In the present study none of these characters have shown any correlation

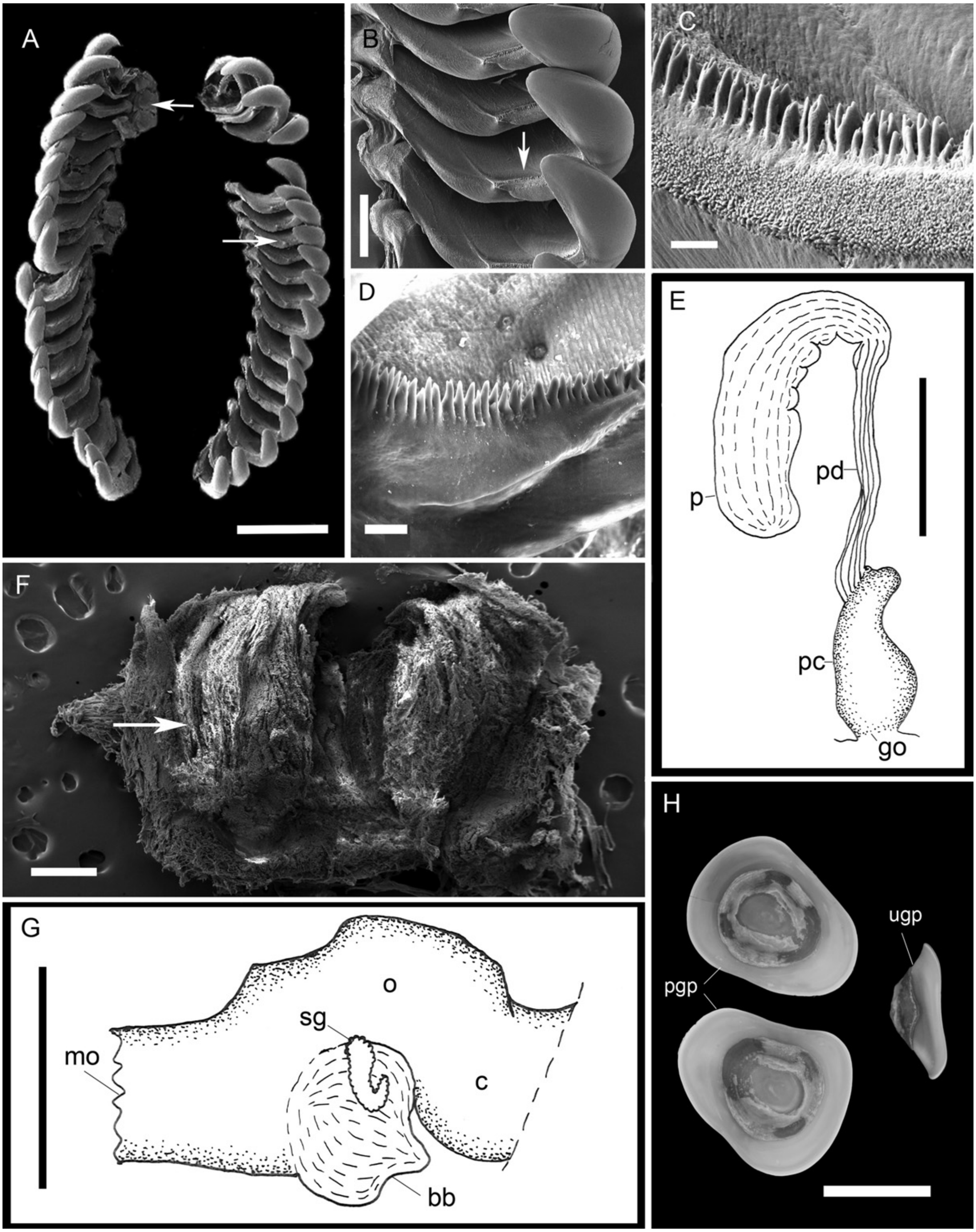

Figure 9. Anatomical details of *Scaphander punctostriatus*: A, radula, arrows point to location of rachidian teeth and details of lateral teeth; B, details of lateral teeth, arrow points to location of denticulation; C, denticulation of the outer edge of lateral teeth; D, variation of denticulation found in *S. punctostriatus*; E, male reproductive system; F, penial chamber opened, arrow pointing to ridges on the inside; G, anterior part of digestive tract; H, gizzard plates; bb, buccal bulb; c, crop; go, genital opening; mo, mouth; o, oesophagus; p, prostate; pc, penial chamber; pd, prostatic duct; pgp, paired gizzard plates; sg, salivary gland; ugp, unpaired gizzard plate. Scale bars: A, 500 μm; B, 100 μm; C, 5 μm; D, 5 μm; E, 5 mm; F, 500 μm; G, H, 5 mm.

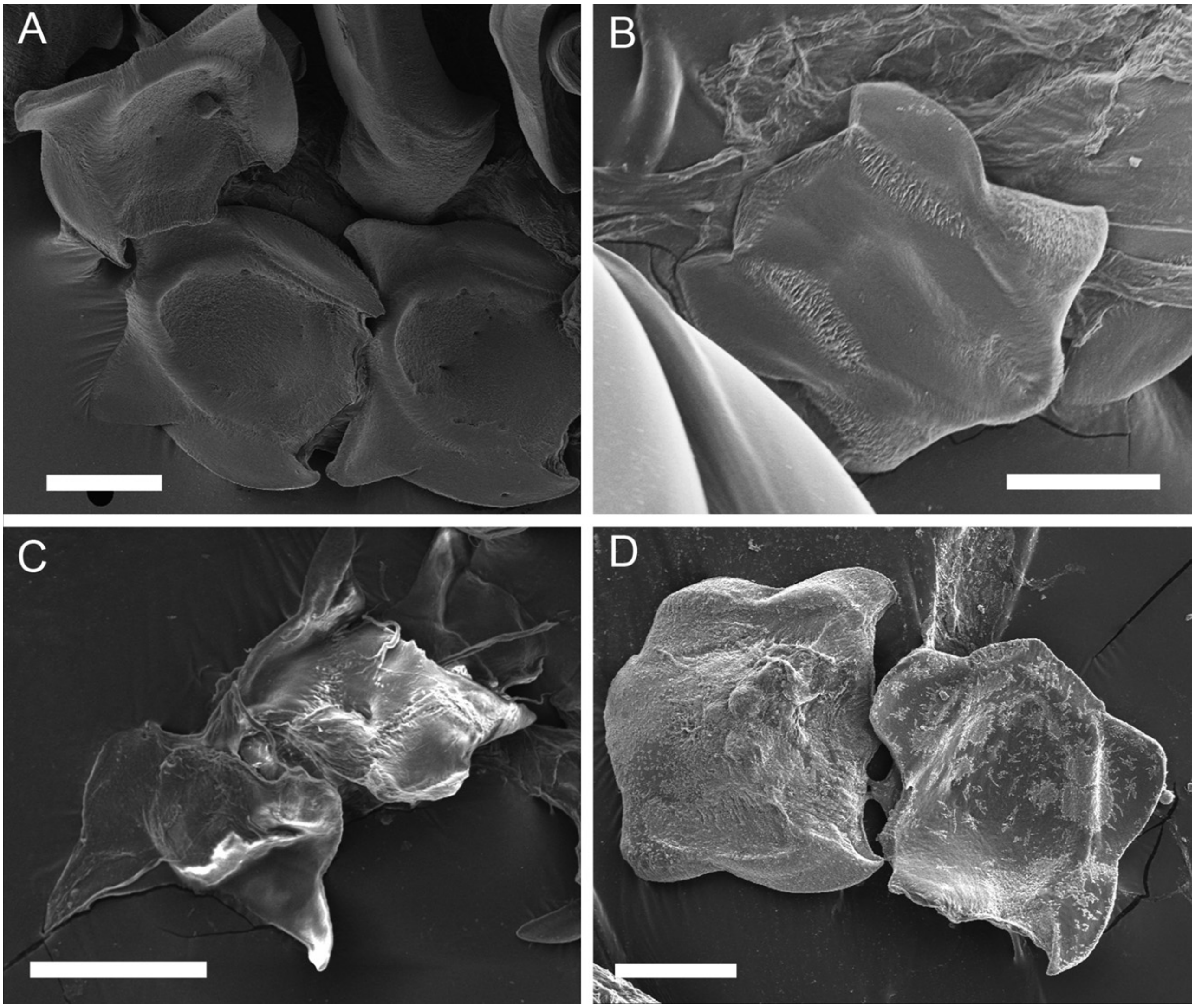

Figure 10. Variation in the rachidian teeth of *Scaphander punctostriatus*. A, Cape Cod, Massachusets, USA, MCZ 304991, $H = 24$ mm; B, off north-west Africa, 27°9′N, 13°9′W, NHMUK 19980249, $H = 41.2$ mm; C, East of Norfolk, Virginia, USA, USNM 757101, $H = 12$ mm; D, Mundheim, Norway, ZMBN 62015, $H = 27.3$ mm. Scale bars: 50 μm.

with variation in other anatomical features, and they are considered part of the intraspecific variability of *S. watsoni*. Marcus & Marcus (1967) depicted the penial papilla of *S. watsoni rhederi*, and this is identical to the papilla found in *S. watsoni* in the present study, supporting conspecificity.

Diagnosis

Shell solid, pyriform, white to brown. Striations with round interconnected punctuations. Parietal wall often covered by thin, white callus. Body white. Lateral radular teeth without denticulation, rachidian teeth trilobed. Prostate disc-shaped, prostatic duct separating prostate and penial chamber. Penial chamber cylindrical, penial papilla bulbous with flagellate extension. Type locality: Sombrero Island, Caribbean Sea.

Material examined

Sombrero Island, Caribbean Sea, 1 sh., USNM 95190, $H = 8.8$ mm; Gulf of Mexico, off Mobile, 1 sh., USNM 609948, $H = 39.3$ mm; off Louisiana, Gulf of Mexico (29°10′N, 88°03′W), 1 sh., MCZ 214372, $H = 16.7$ mm; Cabo Frio, Rio de Janeiro, Brazil, 2 spc. dissected, MZSP 86804, $H = 26.2$, 30.7 mm; Cabo Frio, Rio de Janeiro, Brazil, 1 spc. dissected, MZSP 32986, $H = 39.5$ mm; Santos, São Paulo, Brazil, 3 spc. dissected, MZSP 34644, $H = 31.3$, 31.4, 31.9 mm; Gulf of

Mexico, 1 spc. dissected, USNM 1151226, $H = 31.5$ m; Gulf of Mexico, 1 spc. dissected, USNM 1151240, $H = 33.8$ mm; Caribbean Sea, 1 spc. dissected, USNM 836700, $H = 32$ mm.

Shell (Fig. 4: 1–5): Maximum $H = 39.5$ mm. Shell solid, pyriform, anterior of aperture only very slightly extended. Posterior edge of outer lip often pointed, protruding well beyond apex. Periostracum often visible, colour white to brown. Shell white under periostracum. Thick, punctuated striations, some specimens with coloured striations (see Fig. 4: 2). Punctuations are round and interconnected along the striae. Groves are separated by gaps much wider than the grooves themselves. Major growth lines common.

Radula (Fig. 11A–D): Lateral teeth curved with a broad base, inner edge with a ridge, but no denticulation. Base of rachidian teeth square, anterior end trilobed with triangular lobes.

Digestive tract (Fig. 11G, H): Salivary glands short with uneven surface. Paired gizzard plates subtriangular to kidney-shaped. Central area of gizzard plates often yellowish and thicker than lateral area, which is porous and thinner.

Male reproductive system (Fig. 11E, F): Prostate disc-shaped, prostatic duct separating prostate and penial chamber. Prostate filled with spongy tissue; often positioned on the left side of the digestive tract, with the prostatic duct running under the digestive tract, connecting to the penial chamber on the right side. Penial chamber cylindrical, penial papilla bulbous, with flagellate extension, surface smooth.

Ecology

Feeds on foraminiferans, often very large species. Depth range: 110–476 m.

Distribution (Fig. 13)

Caribbean Sea (Marcus & Marcus, 1967; Marcus, 1974), Gulf of Mexico (Bullis, 1956; Pequegnat, 1983), and Brazil (present study).

Remarks

Marcus (1974) pointed out that it is impossible to distinguish between the shells of *S. watsoni* and *S. darius*: these species can only be separated by examining the male reproductive system, and this is confirmed by our results. This implies that records of *S. watsoni* in which identification is based on shells only are unreliable. Caution should be applied when identifying specimens of these species; our work shows that reliable identifications can only be achieved by either anatomical dissections or DNA barcoding. *Scaphander pilsbryi* is a synonym of either *S. watsoni* or *S. darius* (this is discussed under remarks for *S. darius*).

DNA SEQUENCE ANALYSES

Our data set included representatives of six Atlantic and four Pacific species (for a complete specimen list, see Table 2). Seven sequences from *S. lignarius* were downloaded from GenBank and included in the data set. The *COI* alignment was 704 bp, the *16S* alignment was 466 bp, and the *28S* alignment was 1514 bp in length. Most gaps were caused by the out-groups, and none of the alignments contained indel-rich regions, which made determination of homology problematic.

Uncorrected *p*-distances for *COI* ranged between 0.3–1.2% for species of *Scaphander* and 11.2–19.7% for all species (see Table 4); however, one specimen of *S. lignarius* from Barcelona, Spain (spc. 19) showed unusually high divergence from conspecific specimens (9.7–10.3%). The lineages recognized with the *COI* phylogeny confirmed the species identifications based on morpho-anatomical data. The sequencing success was highest for *16S*, and this data set was the most complete, with 25 *Scaphander* specimens representing six species (one species more than in the *COI* data set, and three more than in the *28S* data set). For the species where *COI* sequences were not available, molecular species status was assessed by comparison of *16S* distances between the already established species (based on *COI* data) and the remaining specimens. Uncorrected *p*-distances varied in the *16S* gene between 0–1.6% within species and 1.0–5.3% between species (see Table 5). Clearly the separation of species based on *16S* is more difficult, as there is overlap between the ranges of distances observed within and between species. The overlap, however, was caused by just a few specimens: *S. lignarius* from the Celtic Sea (seq. 12), and from Barcelona, Spain (seq. 19), that showed high divergence (0.46–1.9%, Table 5) from the conspecifics; and *S. darius* from Brazil that shows low divergence from *S. watsoni* from Brazil (1–1.2%, Table 5). *Scaphander bathymophilus* from Puerto Rico (not included in the *COI* analysis) differs from *S. bathymophilus* from the Azores by 0.23% in *16S*, which supports conspecificity of these specimens and an amphi-Atlantic distribution of *S. bathymophilus*. The Atlantic species *S. nobilis* and the Indo-Pacific *S. mundus* showed very low divergence in *16S* (0.23%), but the anatomy of the male reproductive system is different, supporting that they are different species.

The Incongruence Length Difference (ILD) test (Farris *et al.*, 1995) was performed on the concatenated data set, and indicated no incongruence

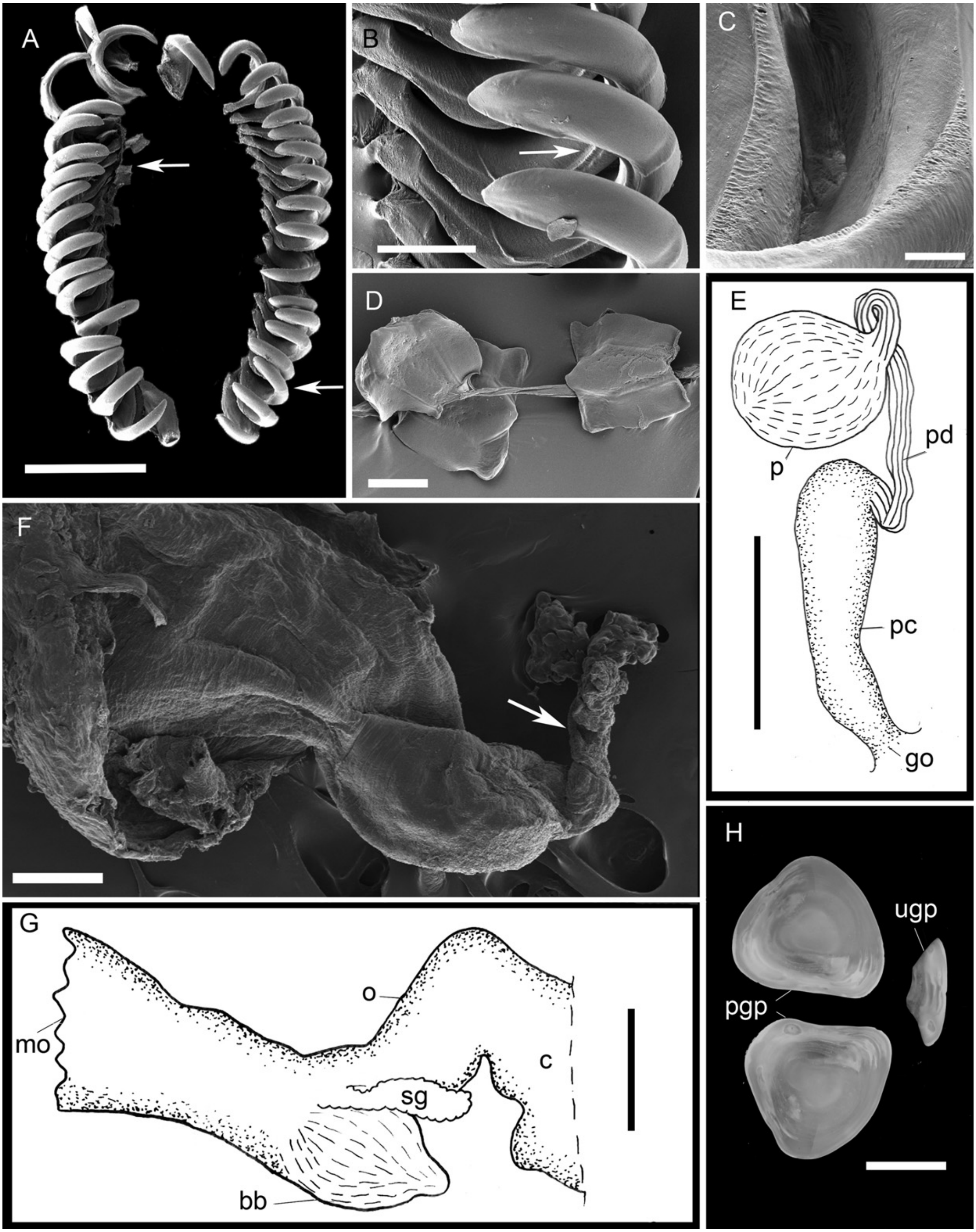

Figure 11. Anatomical details of *Scaphander watsoni*: A, radula, arrows pointing to location of rachidian teeth and details of lateral teeth; B, details of lateral teeth, arrow pointing to edge of lateral teeth; C, edge of lateral teeth with no denticulation; D, rachidian teeth; E, male reproductive system; F, penial papilla, arrow pointing to flagellum; G, anterior part of digestive tract; H, gizzard plates; bb, buccal bulb; c, crop; go, genital opening; m, muscle; mo, mouth; o, oesophagus; p, prostate; pc, penial chamber; pd, penial duct; pgp, paired gizzard plates; sg, salivary gland; upg, unpaired gizzard plate. Scale bars: A, 800 μm; B, 100 μm; C, 50 μm; D, 20 μm; E, F, G, 5 mm; H, 50 μm.

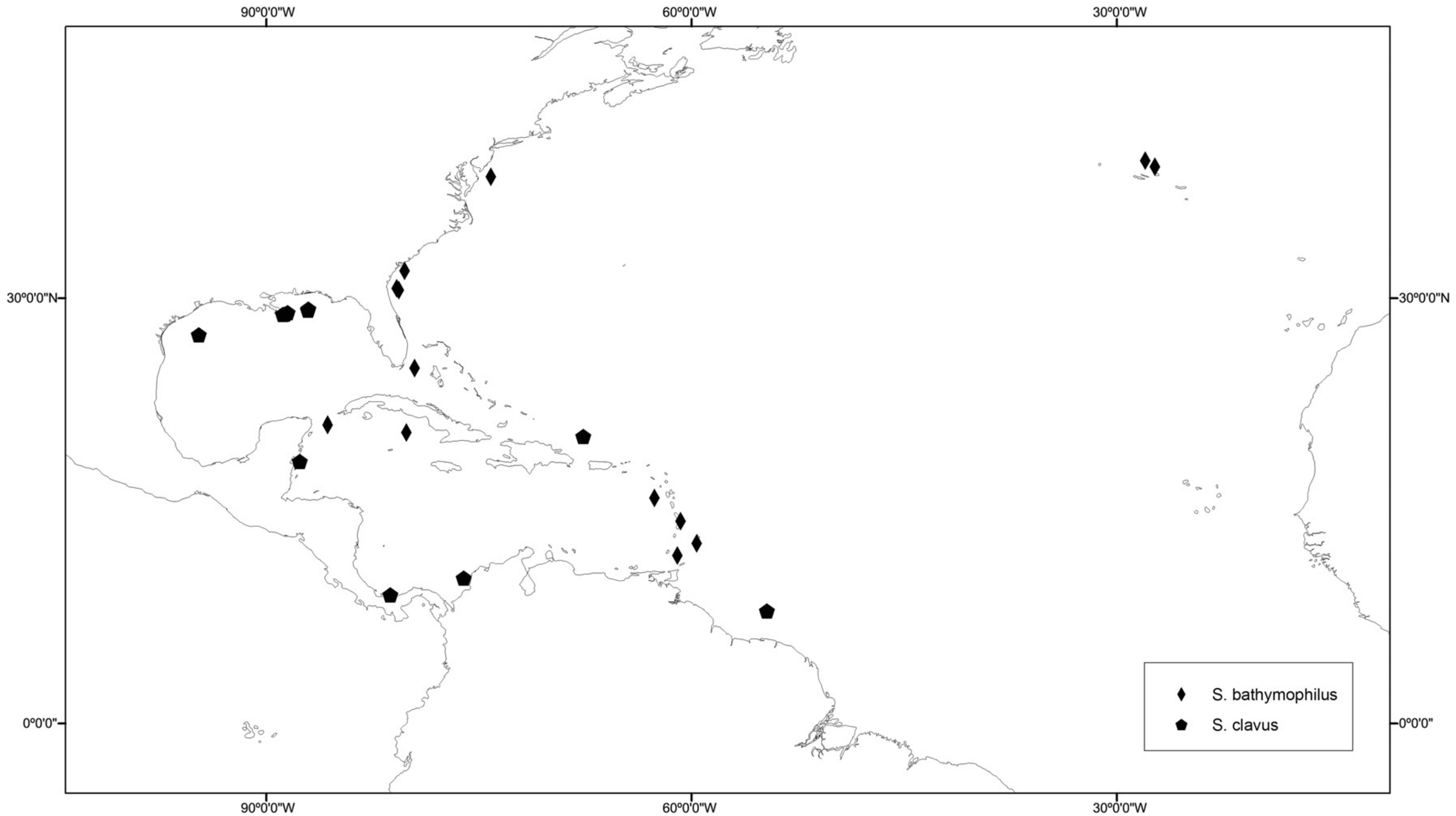

Figure 12. Distributions of *Scaphander bathymophilus* and *Scaphander clavus*. Distributions are based on studied material and reliable literature records. Only records of live specimens are included.

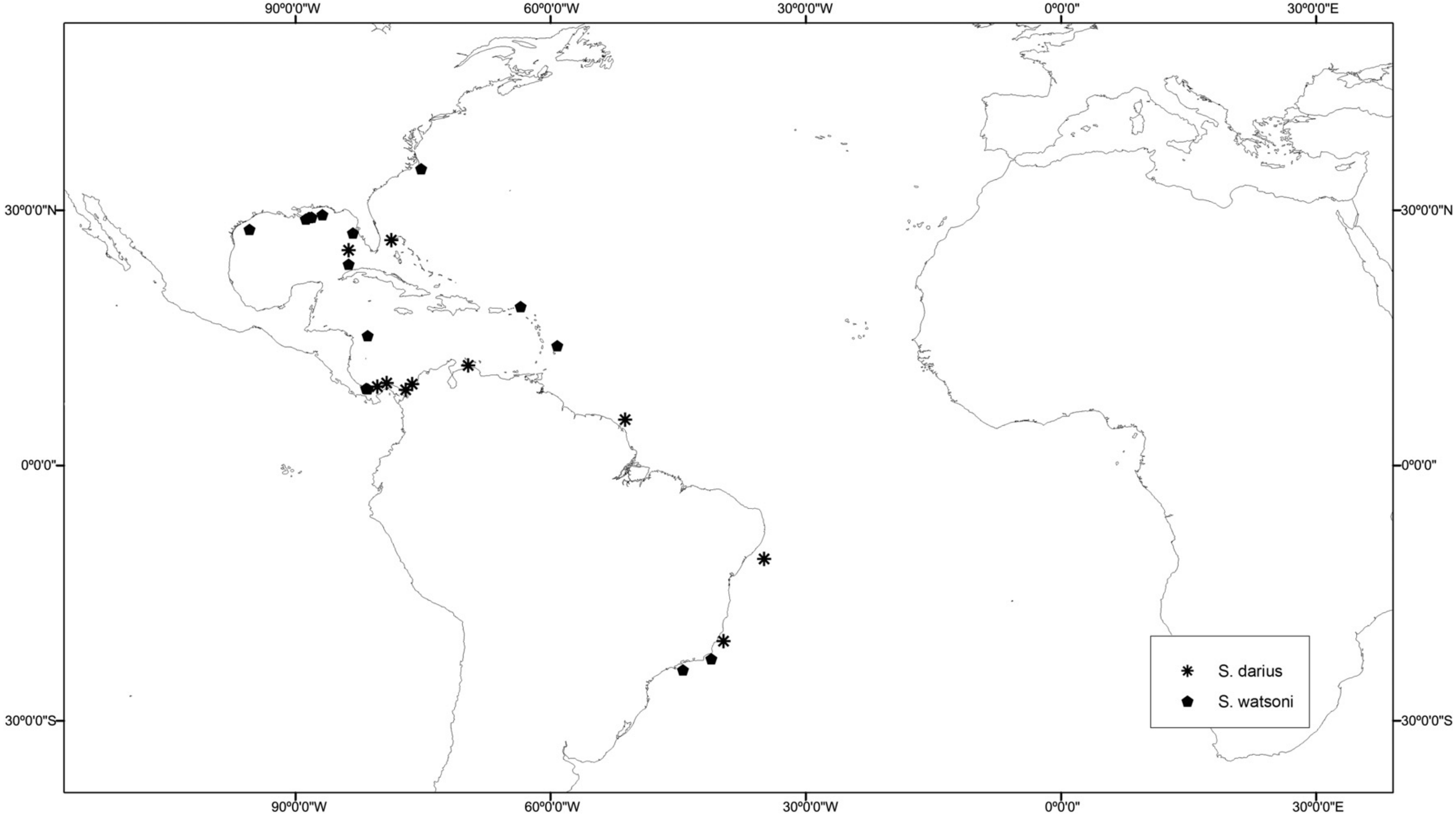

Figure 13. Distributions of *Scaphander darius* and *Scaphander watsoni*. Distributions are based on studied material and reliable literature records. Only records of live specimens are included.

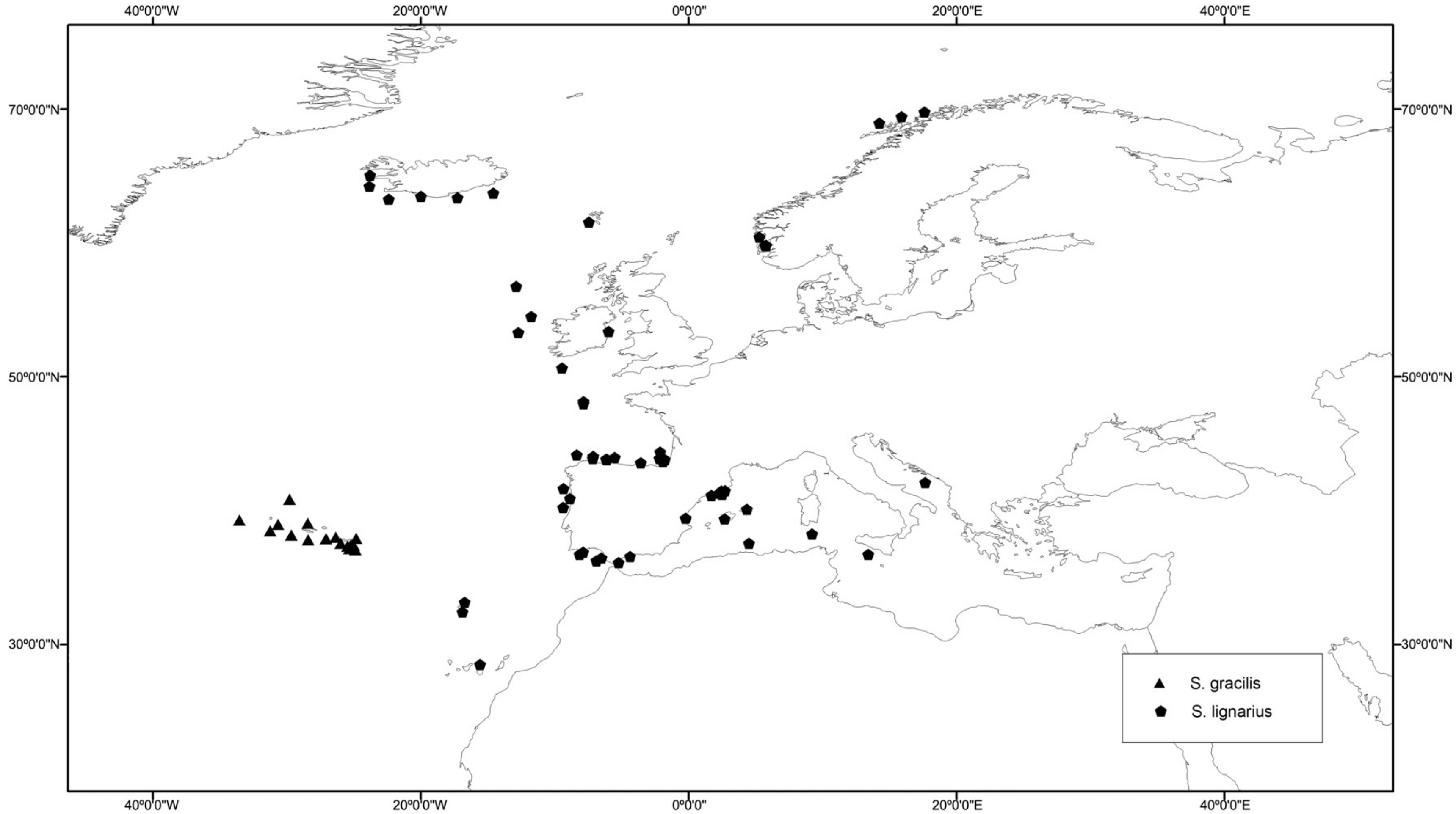

Figure 14. Distributions of *Scaphander gracilis* and *Scaphander lignarius*. Distributions are based on studied material and reliable literature records. For *S. lignarius*, only records of live specimens are included. Live specimens of *S. gracilis* are not known, and the distribution is based on shells.

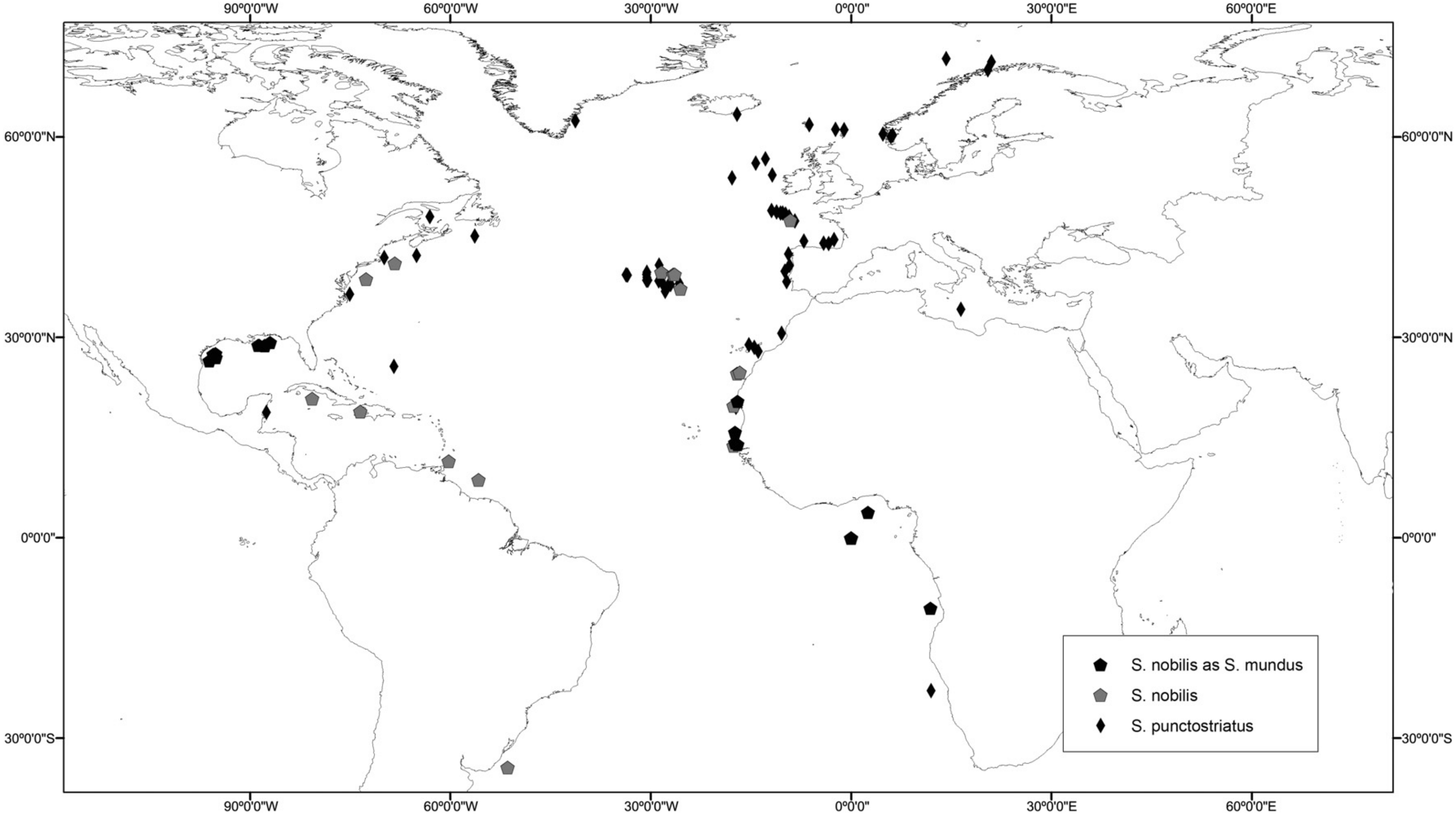

Figure 15. Distributions of *Scaphander nobilis* and *Scaphander punctostriatus*. Distributions are based on studied material and reliable literature records. Only records of live specimens are included.

Table 4. *COI* uncorrected *p*-distance matrix

	2	3	GB2	GB1	51	37	19	35	34	36	38	4	13	21	17	15	29	33	30
Scaphander lignarius Norway 2																			
Scaphander punctostriatus Norway 3	0.1523																		
Scaphander lignarius GenBank 2	0.0117	0.1577																	
Scaphander lignarius GenBank 1	0.0079	0.1499	0.0000																
Scaphander lignarius Norway 51	0.0044	0.1508	0.0132	0.0079															
Scaphander lignarius Norway 37	0.0060	0.1578	0.0090	0.0080	0.0045														
Scaphander lignarius Spain 19	0.0983	0.1646	0.1000	0.0965	0.0970	0.1028													
Scaphander punctostriatus Norway 35	0.1536	0.0045	0.1544	0.1508	0.1522	0.1561	0.1703												
Scaphander punctostriatus Norway 34	0.1507	0.0060	0.1499	0.1456	0.1493	0.1536	0.1701	0.0045											
Scaphander punctostriatus Norway 36	0.1592	0.0075	0.1585	0.1565	0.1579	0.1624	0.1743	0.0090	0.0106										
Scaphander punctostriatus Norway 38	0.1518	0.0088	0.1495	0.1472	0.1504	0.1548	0.1695	0.0059	0.0015	0.0119									
Scaphander punctostriatus Newfoundland 4	0.1523	0.0015	0.1529	0.1494	0.1509	0.1562	0.1672	0.0030	0.0045	0.0060	0.0074								
Scaphander bathymophilus Azores 13	0.1650	0.1385	0.1650	0.1626	0.1637	0.1695	0.1549	0.1389	0.1406	0.1474	0.1416	0.1408							
Scaphander darius Brazil 21	0.1733	0.1618	0.1706	0.1644	0.1707	0.1739	0.1592	0.1633	0.1601	0.1713	0.1622	0.1646	0.1457						
Scaphander watsoni Gulf of Mexico 17	0.1676	0.1514	0.1667	0.1623	0.1647	0.1677	0.1378	0.1527	0.1531	0.1559	0.1543	0.1528	0.1466	0.1221					
Scaphander watsoni Gulf of Mexico 15	0.1641	0.1532	0.1631	0.1576	0.1626	0.1654	0.1353	0.1528	0.1526	0.1598	0.1551	0.1528	0.1473	0.1232	0.0120				
Scaphander mundus Philippines 29	0.1564	0.1124	0.1614	0.1619	0.1550	0.1591	0.1684	0.1152	0.1156	0.1206	0.1169	0.1139	0.1451	0.1511	0.1438	0.1422			
Scaphander subglobosus Philippines 33	0.1615	0.1310	0.1608	0.1534	0.1617	0.1637	0.1529	0.1316	0.1330	0.1371	0.1326	0.1302	0.1489	0.1488	0.1245	0.1209	0.0901		
Scaphander sp. A New Caledonia 30	0.1924	0.1861	0.1938	0.1968	0.1893	0.1952	0.1788	0.1879	0.1897	0.1952	0.1876	0.1882	0.1729	0.1668	0.1856	0.1846	0.1882	0.1863	
Scaphander sp. B New Caledonia 32	0.1739	0.1515	0.1741	0.1723	0.1724	0.1754	0.1620	0.1531	0.1534	0.1561	0.1559	0.1531	0.1632	0.1848	0.1593	0.1591	0.1576	0.1622	0.1594

between the gene markers ($P > 0.05$). Substitution saturation analysis for the *COI* gene showed signs of saturation in the third codon position, and therefore a data set was created including only first and second codon positions for comparison. This data set was run in MrBayes with the same settings as the one including the third codon position, but the resulting consensus tree and node support (posterior probability, PP) was the same as for the complete data set (data not shown).

PHYLOGENETIC HYPOTHESIS

Scaphander was shown to be monophyletic, with maximum branch support (see Fig. 16). All individual gene trees were congruent, recognizing the monophyly of the species that have been analysed in common. The only exception is the pair *S. darius*/*S. watsoni* in the *16S* gene tree analysis, where reciprocal monophyly was not achieved. The concatenated data set was analysed twice. The first analysis (data not shown) rendered *S. watsoni* paraphyletic, very likely influenced by the fact that the two specimens from Brazil only had data from the *16S* gene, which already rendered paraphyly of this species in its own individual analysis. The two specimens from Brazil were removed, and the data set was analysed again, retrieving monophyly of *S. watsoni* and maximum support for a sister relationship between *S. watsoni* and *S. darius* (see Fig. 16). Specimens from the two best-sampled morphospecies, *S. lignarius* and *S. punctostriatus*, rendered monophyletic groups with maximum node support (Fig. 16), and the monophyly of *S. punctostriatus*, including specimens from both sides of the Atlantic, is confirmed. The two specimens of *S. bathymophilus* form a monophyletic clade with maximum node support. The sister relationship between *S. nobilis* and *S. mundus* is not supported in the phylogeny (PP = 0.58), but morpho-anatomical similarities between these two species suggest a potential close relationship (see remarks for *S. nobilis*).

DISCUSSION

MONOPHYLY OF *SCAPHANDER* AND GENERIC CLASSIFICATION

Previous molecular phylogenies have included sequences of *Scaphander*, but not more than a single species (Tholleson, 1999; Dayrat *et al.*, 2001; Klussmann-Kolb *et al.*, 2008; Malaquias *et al.*, 2009a; Jörger *et al.*, 2010); therefore, the monophyly of the genus has never been tested in a molecular phylogenetic framework, and is here confirmed for the first time (Fig. 16).

Several authors have advocated the separation of *Scaphander* in several genera/subgenera based on

Table 5. 16S rRNA uncorrected *p*-distance matrix

	9	4	38	34	35	3	13	36	15	8	5	21
S. nobilis Bay of Biscay 9												
S. punctostriatus Nowfoundland 4	0.0047											
S. punctostriats Norway 38	0.0069	0.0023										
S. punctostriatus Norway 34	0.0049	0.0000	0.0000									
S. punctostriatus Norway 35	0.0072	0.0024	0.0024	0.0000								
S. punctostriatus Norway 3	0.0071	0.0023	0.0024	0.0000	0.0047							
S. bathymophilus Azores 13	0.0232	0.0285	0.0301	0.0288	0.0310	0.0311						
S. punctostriatus Skagerrak 36	0.0068	0.0023	0.0000	0.0000	0.0024	0.0023	0.0302					
S. watsoni Gulf of Mexico 15	0.0231	0.0234	0.0208	0.0214	0.0237	0.0237	0.0302	0.0208				
S. watsoni Brazil 8	0.0247	0.0207	0.0183	0.0189	0.0212	0.0207	0.0324	0.0180	0.0069			
S. watsoni Brazil 5	0.0209	0.0163	0.0166	0.0166	0.0166	0.0161	0.0289	0.0162	0.0047	0.0024		
S. darius Brazil 21	0.0270	0.0225	0.0195	0.0201	0.0225	0.0226	0.0370	0.0196	0.0147	0.0121	0.0099	
S. bathymophilus Brazil 52	0.0246	0.0302	0.0275	0.0286	0.0308	0.0301	0.0023	0.0270	0.0276	0.0291	0.0280	0.0345
S. lignarius Spain 19	0.0344	0.0301	0.0306	0.0308	0.0330	0.0321	0.0498	0.0298	0.0424	0.0391	0.0369	0.0379
S. lignarius Celtic Sea 12	0.0347	0.0302	0.0284	0.0285	0.0285	0.0301	0.0479	0.0300	0.0403	0.0393	0.0370	0.0357
S. lignarius Spain 1	0.0320	0.0277	0.0303	0.0284	0.0306	0.0298	0.0473	0.0296	0.0422	0.0389	0.0347	0.0377
S. lignarius GenBank 1	0.0340	0.0302	0.0278	0.0285	0.0308	0.0300	0.0488	0.0272	0.0394	0.0362	0.0349	0.0347
S. lignarius Norway 51	0.0259	0.0258	0.0259	0.0238	0.0261	0.0236	0.0451	0.0259	0.0378	0.0400	0.0355	0.0403
S. lignarius Norway 37	0.0238	0.0238	0.0237	0.0239	0.0239	0.0239	0.0431	0.0238	0.0357	0.0380	0.0358	0.0381
S. lignarius Norway 2	0.0232	0.0233	0.0236	0.0238	0.0261	0.0257	0.0427	0.0232	0.0353	0.0371	0.0351	0.0378
S. mundus Philippines 31	0.0023	0.0071	0.0071	0.0072	0.0072	0.0072	0.0264	0.0071	0.0238	0.0261	0.0238	0.0277
S. mundus Philippines 29	0.0023	0.0071	0.0071	0.0071	0.0072	0.0071	0.0263	0.0071	0.0237	0.0260	0.0237	0.0276
S. subglobosus Philippines 33	0.0166	0.0166	0.0165	0.0167	0.0166	0.0166	0.0359	0.0165	0.0284	0.0307	0.0284	0.0327
Scaphander sp. A New Caledonia 30	0.0374	0.0376	0.0378	0.0381	0.0403	0.0399	0.0473	0.0374	0.0471	0.0491	0.0472	0.0501
Scaphander sp. B New Caledonia 32	0.0426	0.0476	0.0475	0.0477	0.0478	0.0477	0.0429	0.0476	0.0453	0.0476	0.0453	0.0529

	52	19	12	1	GB1	51	37	2	31	29	33	30
S. nobilis Bay of Biscay 9												
S. punctostriatus Nowfoundland 4												
S. punctostriats Norway 38												
S. punctostriatus Norway 34												
S. punctostriatus Norway 35												
S. punctostriatus Norway 3												
S. bathymophilus Azores 13												
S. punctostriatus Skagerrak 36												
S. watsoni Gulf of Mexico 15												
S. watsoni Brazil 8												
S. watsoni Brazil 5												
S. darius Brazil 21												
S. bathymophilus Brazil 52												
S. lignarius Spain 19	0.0484											
S. lignarius Celtic Sea 12	0.0488	0.0046										
S. lignarius Spain 1	0.0483	0.0069	0.0069									
S. lignarius GenBank 1	0.0454	0.0069	0.0069	0.0023								
S. lignarius Norway 51	0.0450	0.0189	0.0165	0.0118	0.0118							
S. lignarius Norway 37	0.0430	0.0167	0.0143	0.0095	0.0095	0.0000						
S. lignarius Norway 2	0.0420	0.0164	0.0163	0.0093	0.0093	0.0024	0.0000					
S. mundus Philippines 31	0.0263	0.0381	0.0357	0.0357	0.0357	0.0262	0.0263	0.0263				
S. mundus Philippines 29	0.0262	0.0380	0.0356	0.0355	0.0356	0.0262	0.0263	0.0262	0.0000			
S. subglobosus Philippines 33	0.0357	0.0379	0.0356	0.0355	0.0356	0.0262	0.0263	0.0261	0.0143	0.0143		
Scaphander sp. A New Caledonia 30	0.0469	0.0516	0.0519	0.0539	0.0541	0.0471	0.0454	0.0447	0.0406	0.0405	0.0451	
Scaphander sp. B New Caledonia 32	0.0429	0.0524	0.0501	0.0500	0.0499	0.0452	0.0454	0.0453	0.0454	0.0453	0.0548	0.0428

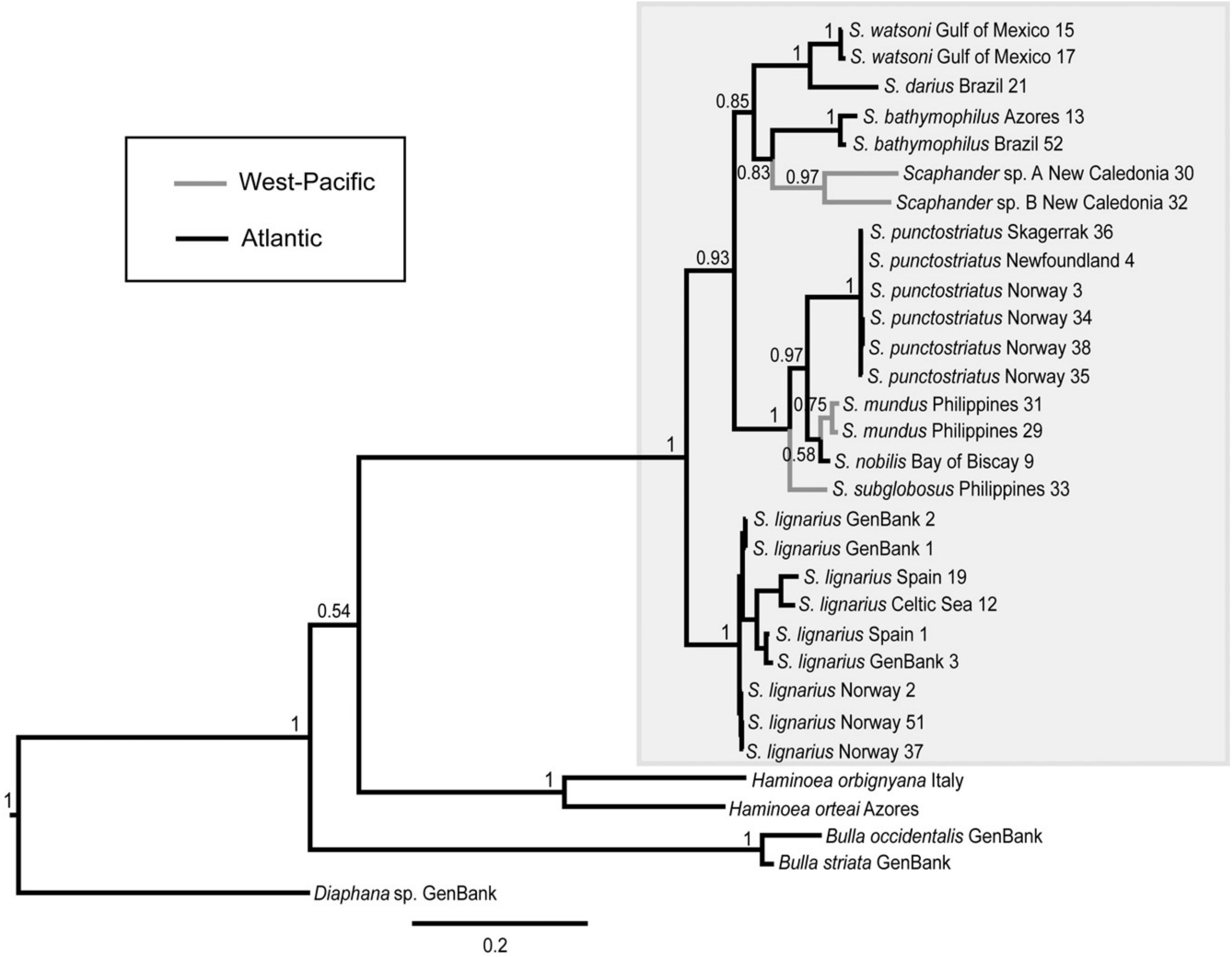

Figure 16. Phylogram generated by Bayesian inference analysis of the concatenated data set (*COI* + *16S* + *28S*) in MrBayes. Lables on branches represent node support as posterior probabilities (PPs). *Scaphander* species are delimited by the grey box. A representative of the genus *Diaphana* was used as the out-group. Grey branches refer to western Pacific species.

shell characters (see the taxonomic history of *Scaphander*). In our phylogeny we included representatives of three of these genera/subgenera, namely *Bucconia* [*S. nobilis*, type species, and *S. mundus* (e.g. Bullis, 1956)], *Sabatina* [*S. bathymophilus*; also ascribed to the genus *Sabatia* (e.g. Dall, 1927; Bullis, 1956)], and *Scaphander* (*S. lignarius*, type species). Recognition of *Bucconia* and *Sabatina*/*Sabatia* as natural groups would imply the paraphyly of *Scaphander* proper (Fig. 16). Moreover, our anatomical studies did not find any correlation between differences in shell morphology and anatomy (see systematic descriptions). Eventually a revision and phylogeny of the worldwide species of *Scaphander* may produce evidence for the division of Scaphandridae in several genera, but present results suggest the inclusion of all species in the genus *Scaphander*.

SPECIES RECOGNITION

After revising the genus *Scaphander* in the Atlantic Ocean, eight species are recognized as valid, one of which is only known from shells (*S. gracilis*). Most species can be identified based on shells only, even though shell characters can be variable within species. The dichotomous key presented here (Table 6) is mainly based on shell characters, as these can be studied easily and non-destructively with a stereomicroscope. Additional diagnostic characters for species delimitation are included in Table 7. Only two species (that are reciprocally monophyletic; see Fig. 16) could not be separated based on shells alone, namely *S. darius* and *S. watsoni*, but these can be differentiated by examining the male copulatory apparatus.

Table 6. Identification key to the Atlantic species of *Scaphander*, based on shells and anatomical characters

Entry	Description	Species
1	Outline of shell subrectangular. Punctuations square, sometimes interconnected forming a continuous line. Medium-thick, white callus on parietal wall usually present.	*Scaphander clavus*
	Outline of shell pyriform.	2
	Outline of shell ovoid.	6
2	Thick, white callus on parietal wall of shell present. Forms tooth-like projection into aperture. Shell with round, separated punctuations.	*Scaphander gracilis*
	If callus present in shell; not forming tooth-like extension.	3
3	Shell striations punctuated with round or elongate punctuations, separated by short spaces. Posterior edge of outer lip curved towards the apex, forming a small cup.	*Scaphander punctostriatus*
	Shell with round punctuations, usually interconnected. Posterior edge of outer lip not curved to form cup.	4
4	Anterior of shell aperture extended, posterior edge of outer lip rounded. Prostate tapering towards penial chamber. Walls of penial chamber covered in soft warts.	*Scaphander lignarius*
	Anterior of shell aperture only very slightly extended, or not at all. Prostate set of from penial chamber by prostatic duct.	5
5	Prostate disc-shaped; prostatic duct long. Penial papilla smooth, flagellate.	*Scaphander watsoni*
	Prostate cylindrical, rounded at distal end. Penial papilla bulbous, covered with soft warts.	*Scaphander darius*
6	Parietal wall of shell covered by a thick, tuberculate callus, sometimes forming a projection into aperture. Punctuations round and interconnected.	*Scaphander bathymophilus*
	Callus, if present, not tuberculate.	7
7	Posterior edge of outer lip extended well beyond apex, pointed. Shell punctuations round, sometimes interconnected.	*Scaphander nobilis*
	Posterior edge of outer lip extending slightly beyond apex, curving towards apex to form a cup. Shell striations punctuated with round or elongate punctuations, separated by short spaces.	*Scaphander punctostriatus*

The male copulatory apparatus provides the most reliable set of characters, and shows a high degree of consistency within species, and consistent variations between species, of *Scaphander*. Penial shape is believed to play a role in mate recognition and function simultaneously, as an isolating mechanism that prevents interspecific mating (Reid, 1996). The penial papilla is frequently not developed in immature specimens, and *S. lignarius* and *S. punctostriatus* do not possess distinct papillae, but in both cases the presence of other structures in the penial chamber (e.g. warts and ridges) can be used to diagnose species in combination with other characters (e.g. shell shape and microstructure).

The radula is very similar between species, the only differences are in the denticulation of the lateral teeth and shape of the rachidian teeth, and both of these characters can be variable within species. In combination with other characters, however, the radula can provide additional information to help identify specimens.

The definition of a species (the ‘species concept’) is a matter of debate (e.g. Wheeler & Meier, 2000; Coyne & Orr, 2004). We here apply the phylogenetic species concept, where species are recognized as reciprocally monophyletic divergent lineages (Wheeler & Meier, 2000). In sympatry, this overlaps with the biological species concept because reproductive isolation is required to maintain distinct lineages. In allopatry one cannot say if populations might interbreed if given the opportunity, but with sufficient time in isolation reproductive barriers are likely to evolve (Coyne & Orr, 2004). The principle applied here to recognize species in allopatry is that if congruent patterns are observed in two or more independent gene phylogenies (different loci), it is assumed that reproductive barriers have evolved (Avise & Wollenberg, 1997; Reid *et al.*, 2006). Molecular evidence supports the species identification based on morpho-anatomical characters (see Fig. 16), but two species (*S. clavus* and *S. gracilis*) were not sequenced because of a lack of material suitable for DNA extraction, and the species status of both needs to be re-evaluated when suitable material becomes available.

The minimum genetic distance detected between different species was 11% (uncorrected *p*-distance for *COI* gene), but two specimens of *S. lignarius* [seq. 12

Table 7. Summary of the most useful characters for diagnosis of Atlantic species of *Scaphander*

Character	*Scaphander bathymophilus*	*Scaphander clavus*	*Scaphander darius*	*Scaphander gracilis*	*Scaphander lignarius*	*Scaphander nobilis*	*Scaphander punctostriatus*	*Scaphander watsoni*
1. Shell								
– Shape	Ovoid	Subrectangular	Pyriform	Pyriform	Pyriform	Ovoid	Ovoid/pyriform	Pyriform
– Striations	Continuous	Interrupted/ continuous	Continuous	Interrupted	Continuous	Interrupted/ continuous	Interrupted	Continuous
– Colour	White	White	White/yellow/orange	White/yellow	White/orange/brown	White	White/yellow	White/orange/ brown
– Callus on parietal wall	Present, tuberculate	Usually present, smooth	Sometimes present, smooth	Present, smooth	Sometimes present, smooth	Absent	Sometimes present, smooth	Sometimes present, smooth
2. Male reproductive system								
– Prostate	Cylindrical	Cylindrical	Cylindrical	NA	Cylindrical	Round	Cylindrical	Round
– Prostatic duct	Present	Present	Absent	NA	Absent	Absent	Present	Present
– Penial papilla	Present	Present	Present	NA	Absent	Present	Absent	Present
– Ornamentation of papilla/chamber	Smooth	Warts	Warts	NA	Warts	Warts	Ridges	Smooth
3. Digestive tract								
Salivary glands	Long	Short	Short	NA	Short	Short	Short	Short
4. Radula								
– Denticulation of lateral teeth	Weak, on inner edge	Inner edge	Both edges	NA	Outer or both edges	Weak, on inner edge	Present/absent on inner edge	Absent
5. Geographical range	Amphi-Atlantic	West Atlantic	West Atlantic	Azores	North-East Atlantic	Amphi-Atlantic	Amphi-Atlantic	West Atlantic
6. Depth range	805–1609 m	595–1056 m	16–97 m	1299–2995 m	70–630 m	1493–4255 m	264–2730 m	110–476 m

(*16S*) and seq. 19 (*COI* and *16S*) from the Celtic Sea and Barcelona, Spain, respectively] showed high genetic divergence from the conspecific specimens. This variability is here hypothesized to result from stochastic mutations, probably related to intrinsic biological factors. No relation between these divergent specimens and geography was detected, rejecting the hypothesis of occurrence of phylogeographic structure in the species; however, the dimension and geographical coverage of the data set was not ideal to address these questions.

PATTERNS OF DIVERSITY AND BIOGEOGRAPHY

Establishing geographical distributions for *Scaphander* species in the Atlantic Ocean is hampered by sampling bias. The South Atlantic is broadly undersampled (McClain & Hardy, 2010), and even in the North Atlantic sampling has mostly been focused on coastal areas (Ramirez-Llodra *et al*., 2010). Sampling of the open ocean seafloor has been largely restricted to areas around islands, hydrothermal vents and other chemosynthetic habitats, whereas the abyssal plains have received less attention compared with the size of this habitat (Ramirez-Llodra *et al*., 2010). Out of the eight Atlantic species of *Scaphander*, three have amphi-Atlantic distributions, whereas five are restricted to one side of the Atlantic. The highest diversity of *Scaphander* species in the Atlantic is found in the tropical West Atlantic, where the geographic ranges of six of the eight species overlap. None of these are truly sympatric, however, because species have different bathymetric ranges.

The percentage of amphi-Atlantic species in opisthobranch gastropods were originally estimated to be 29% (Marcus & Marcus, 1966), but more recently have been reported to be only 12.5% (Garcìa & Bertsch, 2009). These numbers are, however, based on morphospecies, and recent research using molecular phylogenetic methods have revealed that many amphi-Atlantic ‘species’ are in fact a complex of cryptic species restricted to one of the sides of the Atlantic (Malaquias & Reid, 2008; Reid, Dyal & Williams, 2010; Carmona *et al*., 2011; Claremont *et al*., 2011; Ornelas-Gatdula *et al*., 2012). These works focused on littoral and sublittoral species that are restricted to specific coastal habitats. The present study, however, shows the presence of amphi-Atlantic species in the deep-sea genus *Scaphander* supported by molecular data.

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