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Bringing light into deep-sea biodiversity: a systematic revision and molecular phylogeny of the genus *Scaphander* Montfort, 1810 (Gastropoda: Cephalaspidea), with a focus on the Indo-Pacific

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ABSTRACT

Scaphander is a genus of mostly deep-sea, soft-bottom gastropods distributed nearly worldwide. Its taxonomic history is complex, with 32 species currently accepted, most based on shells only. In this work, we revise the diversity and systematics of *Scaphander*, with a focus on the Indo-Pacific region, using a detailed morphological study and molecular phylogenetics. Conchological and anatomical characters, such as digestive and male reproductive systems were compared, and original descriptions and type material were investigated. Additionally, molecular species delimitation methods were used, such as Assemble Species by Automatic Partitioning (ASAP) based on the gene cytochrome *c* oxidase subunit I, and the multispecies coalescent method Species Tree And Classification Estimation, Yarely (STACEY) based on a dataset of five gene markers. Thirty-three *Scaphander* species were recognized worldwide, 10 still based only on shells. Five species are here described as new to science, namely *Scaphander amygdalus* sp. nov., *Scaphander cornus* sp. nov., *Scaphander obnubilus* sp. nov., *Scaphander semicallus* sp. nov. and *Scaphander solomonensis* sp. nov. The most diverse region is the Western Pacific (17 species), followed by the Atlantic (12 species) and the Indian Ocean (7 species).

Keywords: biogeography; Heterobranchia; integrative taxonomy; Mollusca; species delimitation

INTRODUCTION

Scaphander Montfort, 1810 is a near worldwide genus of Heterobranchia gastropods, known between latitudes 72°N and 45°S and comprised, up to now, 32 accepted extant species (MolluscaBase 2022a). Most *Scaphander* species inhabit deep-sea soft bottoms down to a recorded 5427 m (present study), with only five species occurring in shallower waters: *Scaphander darius* Marcus & Marcus, 1967 ranges between 16 and 97 m, *Scaphander lignarius* (Linnaeus, 1758) between 40 and 707 m, *Scaphander watsoni* Dall, 1881 between 70 and 630 m, *Scaphander illecebrosus* Iredale, 1925 recorded at 119 m depth, and *Scaphander teramachii* (Habe, 1954) between 100 and 1533 m, while all other recorded *Scaphander* species are restricted to deeper waters, below 200 m (Dall 1881, Marcus & Marcus 1967, Valdés 2008, Eilertsen and Malaquias 2013a, Chaban *et al.* 2019a, Siegwald *et al.* 2022; present study).

Scaphander snails include the largest representatives of the order Cephalaspidea (bubble snails). They have a strong external shell and burrow in soft sediment, where they feed mostly on foraminifera, but also on many clades of smaller invertebrates (polychaetes, echinoderms and other molluscs), whose hard tests and shells they are able to grind thanks to the three strong calcareous gizzard plates characteristic of the Scaphandridae Sars, 1878 (Sars 1878, Eilertsen and Malaquias 2013b). Very little is known about their reproduction and development, but the study of the protoconch of *Scaphander punctostriatus* Mighels & Adams, 1842 suggests that they might have a short planktotrophic larval stage (Mighels & Adams 1842, Colman 1987).

A detailed account of the taxonomic history of the genus name is given by Eilertsen and Malaquias (2013a). In brief, the first species described, namely *S. lignarius*, was placed in the genus *Bulla* by Linnaeus (1758). Later, Martini (1769)

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introduced the name *Charta* for the species *Charta convoluta*, a synonym of *S. lignarius* (see Eilertsen and Malaquias 2013a), and Montfort (1810) introduced the name *Scaphander* for *S. lignarius*. The genus name *Scaphander* became popular among authors, whereas *Charta* was hardly used and never after 1899. Consequently, Eilertsen and Malaquias (2013a) suggested reversal of precedence and made *Scaphander* the valid genus name for these snails (ICZN opinion 287, 1954; ICZN article 23.9, 1999a; Eilertsen and Malaquias 2013a).

Dall (1890a) split *Scaphander* into the subgenera *Scaphander*, with a pyriform shell shape such as the one of *S. lignarius*, and *Bucconia* Dall, 1890, with a more globose shell shape and an outer lip extending posteriorly, such as in *Scaphander* (*Bucconia*) *nobilis* Verrill, 1884. *Bucconia* continued to be used as a subgenus (Bullis 1956, Okutani 1966) or as a genus (Habe 1954, 1955, Okutani 1987), but later taxonomic works found no evidence for the validity of *Bucconia* and synonymized it to *Scaphander* (Bouchet 1975, Valdés 2008, Eilertsen and Malaquias 2013a).

Two other, closely related genera that have a history of being associated and confused with *Scaphander* are *Sabatia* Bellardi, 1876 and *Nipponoscaphander* Kuroda and Habe, 1971. *Sabatia* was based on the Pliocene fossil species *Sabatia isseli* Bellardi, 1876, with a conspicuously strong parietal callus (Bellardi 1876). Dall (1908) considered *Sabatia* a subgenus of *Scaphander* and introduced the name *Sabatina* Dall, 1908 as another subgenus to contain the extant portion of the genus *Scaphander*. However, the name was only ever used to refer to a single species, namely *Scaphander* (*Sabatina*) *planeticus* Dall 1908. Kuroda and Habe (in Kuroda *et al.* 1971) introduced the genus *Nipponoscaphander* for *Scaphander japonicus* Adams, 1862, based on its smaller, pyriform shell. Later morphological work synonymized *Nipponoscaphander* with *Scaphander* (Valdés 2008) but kept *Sabatia* separate, and the first phylogenetic study of *Scaphander* synonymized both *Sabatia* and *Nipponoscaphander* with *Scaphander* (Eilertsen and Malaquias 2013a). However, more recent systematics work on the family Scaphandridae included a more extensive taxon sampling and showed the validity of the three distinct genera, *Nipponoscaphander*, *Sabatia*, and *Scaphander* (Siegwald *et al.* 2022). Identification of the first two is eased by the presence of robust shell synapomorphies (a rounder egg-shaped shell and a raised, thick and tuberculate callus for *Sabatia*; and a smaller, pyriform shape, with an umbilicate spire for *Nipponoscaphander*), but the shells of *Scaphander* are more variable, making taxonomy of the genus and species recognition difficult (Valdés 2008, Eilertsen and Malaquias 2013a, Siegwald *et al.* 2022).

The systematics of the Atlantic species of *Scaphander* was revised recently (Eilertsen and Malaquias 2013a), with eight species being cited in this realm. Two additional species were subsequently added to the Atlantic diversity of these snails, namely *Scaphander imperceptus* (Bouchet, 1975) (Chaban *et al.* 2019a) and *Scaphander meridionalis* Siegwald, Pastorino, Oskars & Malaquias, 2020. However, no analogous work exists for the Indo-Pacific species, which were studied only occasionally for their anatomy and always with a regional focus. Most species remain known only from their shells, and a broad comparative study of species across the entire region is lacking.

In this work, we produced extended specimen and barcoding datasets based on museum and newly collected material, in addition to using already published sequence data (Siegwald *et al.* 2022), to revise the systematics of the genus *Scaphander* with a focus on the Indo-Pacific diversity, based on an integrative approach combining detailed morpho-anatomical study of the species and molecular species delimitation methods.

MATERIALS AND METHODS

Taxon sampling

Studied material was obtained by loans from natural history collections and specimens donated by colleagues (see Acknowledgements section). A bibliography database was assembled for all nominal names of *Scaphander*, including original descriptions and more recent works. Type specimens or images of type specimens for nearly all nominal species were studied.

Geographical distributions were assembled from the study of museum material, newly collected specimens, and reliable literature records, and were plotted using R (R Core Team 2021). When geographical coordinates were not available, they were estimated from locality descriptions. Bathymetric distributions were established using a conservative approach: for species where both empty shells and live specimens were known, information was collected only from the latter.

Abbreviations used

Institutional abbreviations

AM, Australian Museum, Sydney, NSW, Australia; DBUA, Department of Biology of the University of the Azores, Ponta Delgada, Azores, Portugal; LACM, Natural History Museum of Los Angeles County, CA, USA; MACN, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina; MCZ, Museum of Comparative Zoology, Harvard University, Boston, MA, USA; MIMB, Museum of the National Scientific Center of Marine Biology, Vladivostok, Russia; MNHN, Muséum national d'Histoire naturelle, Paris, France; MNZ, Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; MZUSP, Museu de Zoologia da Universidade de São Paulo, Brazil; NHMUK, The Natural History Museum, London, UK; NIWA, National Institute of Water and Atmospheric Research, Auckland, New Zealand; NSMT, National Museum of Nature and Science, Tokyo, Japan; NZSI, National Zoological Collection of the Zoological Survey of India, Kolkata, West Bengal, India; RMNH, National Museum of Natural History (Naturalis Biodiversity Center), Leiden, The Netherlands; SCBUCN, Sala de Colecciones Biológicas de la Universidad Católica del Norte, Coquimbo, Chile; USNM, National Museum of Natural History [United States National Museum], Smithsonian Institution, Washington, DC, USA; ZISP, Zoological Institute, St. Petersburg, Russia; ZMBN, Department of Natural History, University Museum of Bergen, Norway; ZSM, Zoologische Staatssammlung München, Munich, Germany.

Other abbreviations

ASAP, Assemble Species by Automatic Partitioning; bb, buccal bulb; BI, Bayesian inference; c, crop; *COI*, cytochrome *c* oxidase subunit I; cs, cephalic shield; ep, everted penial structure; go, genital opening; H, shell height; m, mouth; N/A, not assessed; o, oesophagus; p, prostate; pc, penial chamber; pd, prostatic duct; pgp, paired gizzard plates; PP, posterior probability; SEM,

Table 1. List of specimens for sequence analyses, with sampling localities, voucher numbers, and GenBank and BOLD accession numbers (numbers marked in bold are novel sequences generated for the present study).

Species	Voucher	Code	Locality	*COI*	12S	16S	18S	28S
Eoscaphander fragilis Habe, 1952	ZMBN 131874	SJ149	Off Hachinohe, Aomori, Honshu Island, Japan	MZ473267	MZ478726	MZ478672	MZ479109	MZ479064
Nipponoscaphander japonicus (Adams, 1862)	ZMBN 127895	YK4376	Off Misaki Marine Biological Station, Kanagawa, Japan	MZ473268	MZ478728	MZ478673	MZ479111	MZ479065
Sabatia bathymophila (Dall, 1881)	MNHN-IM-2013-67211	SJ184	South Plain, Walters Shoals, Indian Ocean	MZ473274	MZ478733	MZ478679	MZ479119	MZ479069
Scaphander amygdalus	NIWA 30258	st31	New Zealand	MZ473299	MZ478758	MZ478704	MZ479145	
Scaphander amygdalus	NIWA 30374 A	SJ42	Off Western New Zealand	MZ473300	MZ478759	MZ478705	MZ479146	
Scaphander amygdalus	AM C.563070	SJ77	Hunter Commonwealth Marine Reserve, New South Wales, Australia	**OR552922**		**OR557483**	**OR559122**	**OR555862**
Scaphander amygdalus	AM C.519351	SJ78	Central Eastern Commonwealth Marine Reserve, New South Wales, Australia	**OR552923**		**OR557484**	**OR559123**	**OR555863**
Scaphander amygdalus	NIWA 30512	SJ200	New Zealand	**OR552924**	**OR557468**			
Scaphander amygdalus	NIWA 30469	SJ203	New Zealand	**OR552925**	**OR557469**			
Scaphander amygdalus	NIWA 30235	SJ216	New Zealand	**OR552926**				
Scaphander amygdalus	NIWA 30291	SJ217	New Zealand	**OR552927**				
Scaphander amygdalus	NIWA 48567	SJ218	New Zealand	**OR552928**				
Scaphander cancellatus Martens, 1902	MNHN-IM-2007-35413	NP7	Off Balicasag Island, Bohol Sea, Philippines	BOLD PHILI001-10				
Scaphander cancellatus Martens, 1902	MNHN-IM-2009-4339	SC33	Bohol Sea, Philippines	KC351574	MZ478768	KC351539	MZ479155	KC351556
Scaphander cancellatus Martens, 1902	MNHN-IM-2013-52478	SJ18	New Georgia, Solomon Islands	**OR552929**				
Scaphander cancellatus Martens, 1902	MNHN-IM-2009-6678	SJ20	East of San Cristobal, Solomon Islands	**OR552930**		**OR557485**		
Scaphander cancellatus Martens, 1902	MNHN-IM-2013-52472	SJ29	Solomon Islands	**OR552931**		**OR557486**		
Scaphander cancellatus Martens, 1902	MNHN-IM-2007-35412	SJ35	Bohol Sea, Philippines	MZ473309	MZ478769	MZ478714	MZ479156	MZ479103
Scaphander cancellatus Martens, 1902	MNHN-IM-2019-7925	SJ198	Tanimbar Islands, Indonesia	**OR552932**				
Scaphander cornus	AM C.563069	SJ15	Tasmania/Victoria, Australia	MZ473302	MZ478762	MZ478707	MZ479148	MZ479097
Scaphander cornus	AM C.519368	SJ38	East of Cape St George, New South Wales, Australia	MZ473303	MZ478763	MZ478708	MZ479149	MZ479098
Scaphander cornus	AM C.590959	SJ205	Bass Strait, Tasmania/Victoria, Australia	**OR552933**	**OR557470**			
Scaphander cornus	AM C.590968	SJ221	Off Cape Howe, Victoria, Australia	**OR552934**				

Table 1. Continued

Species	Voucher	Code	Locality	*COI*	12S	16S	18S	28S
Scaphander darius Marcus & Marcus, 1967	MZSP 29016	SC21	Brazil	KC351560		KC351521		
Scaphander gracilis Watson, 1883	DBUA 1630	SJ104	Azores	MZ457932	MZ478742	MZ478691	MZ479130	MZ479081
Scaphander grandis (Minichev, 1967)	MIMB 36540	CH207	Kuril-Kamchatka Abyssal Plain	MK952767		MK952768		MK952769
Scaphander grandis (Minichev, 1967)	ZSM Mol 20150062	st2	Kuril-Kamchatka Abyssal Plain	MZ473286	MZ478743	MZ478692	MZ479131	MZ479082
Scaphander grandis (Minichev, 1967)	ZSM Mol 20210096	st3	Kuril-Kamchatka Abyssal Plain	MZ473287	MZ478744	MZ478693	MZ479132	MZ479083
Scaphander grandis (Minichev, 1967)	ZSM Mol 20210053	SJ68	Kuril-Kamchatka Abyssal Plain	**OR552935**	**OR557471**	**OR557488**		**OR555864**
Scaphander interruptus Dall, 1890b	NIWA 30427 A	SJ199	Off Western New Zealand	MZ473297	MZ478756	MZ478702	MZ479143	MZ479092
Scaphander interruptus Dall, 1890b	AM C.563068	SJ201	Off Cape Howe, Victoria, Australia	MZ473298	MZ478757	MZ478703	MZ479144	MZ479093
Scaphander interruptus Dall, 1890b	AM C.590961	SJ219	Bass Strait, Tasmania/Victoria, Australia	**OR552936**				
Scaphander interruptus Dall, 1890b	SCBUCN-2837	SJ236	South of Concepción, Chile	**OR552937**	**OR557472**	**OR557489**	**OR559124**	**OR555865**
Scaphander cf. *lignarius* 1	ZMBN 88000	SC37	Bergen, Norway	KC351563	MZ478745	KC351526	MH933326	KC351545
Scaphander cf. *lignarius* 1	ZMBN 127893	SJ49	Cadiz, Spain	MZ473288	MZ478746	MZ478694	MZ479133	MZ479084
Scaphander cf. *lignarius* 2	ZMBN 127869	SJ5	Vigo, Spain	MZ473289	MZ478747	MZ478695	MZ479134	MZ479085
Scaphander cf. *lignarius* 2	ZMBN 127870	SJ50	Cadiz, Spain	MZ473290	MZ478748	MZ478696	MZ479135	MZ479086
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	ZMBN 127881	st11	Off Mar del Plata, Argentina	MN433681	MZ478749	MN450225	MZ479136	MN450265
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	ZMBN 127882	st17	Off Mar del Plata, Argentina	MN433676		MN450226	**OR559125**	
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	AM C.590963	SJ14	Freycinet Commonwealth Marine Reserve, Tasmania, Australia	**OR552938**	**OR557473**	**OR557490**	**OR559126**	**OR555866**
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	ZMBN 127882	SJ36	Off Mar del Plata, Argentina	MN433682		MN450221		MN450263
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	AM C.482252	SJ39	Hunter Commonwealth Marine Reserve, New South Wales, Australia	**OR552939**	**OR557474**	**OR557491**	**OR559127**	**OR555867**
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	AM C.519366	SJ74	Freycinet Commonwealth Marine Reserve, Tasmania, Australia	MZ473291	MZ478750	MZ478697	MZ479137	MZ479087
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	AM C.590966	SJ75	Jervis Commonwealth Marine Reserve, New South Wales, Australia	**OR552940**		**OR557492**	**OR559128**	**OR555868**
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	MACN-In 42431	SJ101	Off Mar del Plata, Argentina	MN433680		MN450223		
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	MACN-In 42432	SJ102	Off Mar del Plata, Argentina	**OR552941**				
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	AM C.590967	SJ220	East Gippsland Commonwealth Marine Reserve, Victoria, Australia	**OR552942**				
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	AM C.594398	SJ225	Bass Strait, Tasmania/Victoria, Australia	**OR552943**				

Table 1. Continued

Species	Voucher	Code	Locality	*COI*	12S	16S	18S	28S
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020	AM C.594399	SJ226	Bass Strait, Tasmania/Victoria, Australia	**OR552944**				
Scaphander mundus Watson, 1883	MNHN-IM-2013-61614	NP1	Southwest of DongSha, South China Sea	**OR552945**				
Scaphander mundus Watson, 1883	MNHN-IM-2013-61612	NP2	Southwest of DongSha, South China Sea	**OR552946**				
Scaphander mundus Watson, 1883	MNHN-IM-2013-50091	NP3	Southwest of Taiwan, South China Sea	**OR552947**				
Scaphander mundus Watson, 1883	MNHN-IM-2013-50090	NP4	Southwest of Taiwan, South China Sea	**OR552948**				
Scaphander mundus Watson, 1883	MNHN-IM-2013-50089	NP5	Southwest of Taiwan, South China Sea	**OR552949**				
Scaphander mundus Watson, 1883	MNHN-IM-2013-50039	NP6	Southwest of Taiwan, South China Sea	**OR552950**				
Scaphander mundus Watson, 1883	MNHN-IM-2009-4319	SC29	Philippines	KC351565	**OR557475**	KC351529	**OR559129**	KC351547
Scaphander mundus Watson, 1883	MNHN-IM-2009-4318	SC31	Philippines	KC731429	MZ478751	KC351528	MZ479138	KC351546
Scaphander mundus Watson, 1883	MNHN-IM-2013-44305	st15	Off Taiping Island, South China Sea	**OR552951**	**OR557476**			
Scaphander mundus Watson, 1883	MNHN-IM-2013-44310	st28	Off Taiping Island, South China Sea	**OR552952**	**OR557477**		**OR559130**	**OR555869**
Scaphander mundus Watson, 1883	AM C.519372	SJ12	East of Bundaberg, Queensland, Australia	MZ473292	MZ478752	MZ478698	MZ479139	MZ479088
Scaphander nobilis Verrill, 1884	ZMBN 127875	SJ67	Azores	MN433679		MN450222		
Scaphander nobilis Verrill, 1884	MNHN-IM-2013-67215	SJ183	South Plain, Walters Shoals, Indian Ocean	MZ473294	MZ478753	MZ478699	MZ479140	MZ479089
Scaphander obnubilus	AM C.519273	SJ40	East of Cape St George, New South Wales, Australia	MZ473305	MZ478765	MZ478710	MZ479151	MZ479100
Scaphander obnubilus	AM C.482192	SJ76	Northwest of Flinders Island, Tasmania, Australia	MZ473306	MZ478766	MZ478711	MZ479152	MZ479101
Scaphander obnubilus	AM C.590969	SJ223	Bass Strait, Tasmania/Victoria, Australia	**OR552953**				
Scaphander otagoensis Dell, 1956	MNZ 301800/1.1	st6	New Zealand	MZ473295	MZ478754	MZ478700	MZ479141	MZ479090
Scaphander otagoensis Dell, 1956	NIWA 63032 A	SJ79	South of the North Island, New Zealand	MZ473296	MZ478755	MZ478701	MZ479142	MZ479091
Scaphander otagoensis Dell, 1956	MNZ M.301800/1.2	SJ109	New Zealand	**OR552954**				
Scaphander otagoensis Dell, 1956	NIWA 30182	SJ202	New Zealand	**OR552955**	**OR557478**			
Scaphander otagoensis Dell, 1956	NIWA 63804 A	SJ204	New Zealand	**OR552956**	**OR557479**			
Scaphander otagoensis Dell, 1956	MNZ M.301817/1.1	SJ227	New Zealand	**OR552957**				
Scaphander otagoensis Dell, 1956	MNZ M.301817/1.2	SJ228	New Zealand	**OR552958**				
Scaphander punctostriatus (Mighels & Adams, 1842)	ZMBN 88006	SC34	Norway	KC351571	MZ478760	KC351536	MH933325	KC351553
Scaphander punctostriatus (Mighels & Adams, 1842)	DBUA 1629	SJ105	Azores	MZ473301	MZ478761	MZ478706	MZ479147	MZ479096
Scaphander punctostriatus (Mighels & Adams, 1842)	ZMBN 127899	SJ207	Gulf of St. Lawrence, Québec, Canada	**OR552959**	**OR557480**	**OR557493**	**OR559131**	**OR555870**

Table 1. Continued

Species	Voucher	Code	Locality	*COI*	12S	16S	18S	28S
Scaphander semicallus	MNHN-IM-2013-52464	st16	Inhambane, Mozambique	MZ473304	MZ478764	MZ478709	MZ479150	MZ479099
Scaphander sibogae Schepman, 1913	MNHN-IM-2013-18549	st14	East of Kotakot, Papua New Guinea	MZ473284	MZ478740	MZ478689	MZ479128	MZ479079
Scaphander sibogae Schepman, 1913	MNHN-IM-2019-7922	SJ17	New Georgia, Solomon Islands	**OR552960**				
Scaphander sibogae Schepman, 1913	MNHN-IM-2013-52471	SJ45	Northwest of Isabel, Solomon Islands	MZ473285	MZ478741	MZ478690	MZ479129	MZ479080
Scaphander sibogae Schepman, 1913	MNHN-IM-2019-7918	SJ168	Big Bay, Santa, Vanuatu	**OR552961**				
Scaphander sibogae Schepman, 1913	MNHN-IM-2013-52477	SJ188	New Georgia, Solomon Islands	**OR552962**				
Scaphander sibogae Schepman, 1913	MNHN-IM-2013-58331	SJ189	New Ireland, Papua New Guinea	**OR552963**				
Scaphander solomonensis	MNHN-IM-2013-52480	st21	Northwest of Choiseul, Solomon Islands	MZ473307		MZ478712	MZ479153	
Scaphander solomonensis	MNHN-IM-2019-7923	SJ163	Northwest of Isabel, Solomon Islands	**OR552964**				
Scaphander solomonensis	MNHN-IM-2013-52483	SJ166	Northwest of Choiseul, Solomon Islands	MZ473308	MZ478767	MZ478713	MZ479154	MZ479102
Scaphander teramachii (Habe, 1954)	ZMBN 131888	SJ150	West of Takara Island, East China Sea, Japan	MZ473310	**OR557481**	MZ478715	**OR559132**	**OR555871**
Scaphander teramachii (Habe, 1954)	ZMBN 131891	SJ151	Tosa Bay, Kochi, Shikoku Island, Japan	MZ473311	MZ478770	MZ478716	MZ479157	MZ479104
Scaphander teramachii (Habe, 1954)	ZMBN 131888	SJ229	West of Takara Island, East China Sea, Japan	**OR552966**				
Scaphander teramachii (Habe, 1954)	ZMBN 131888	SJ230	West of Takara Island, East China Sea, Japan	**OR552967**				
Scaphander teramachii (Habe, 1954)	ZMBN 131891	SJ231	Tosa Bay, Kochi, Shikoku Island, Japan	**OR552968**				
Scaphander teramachii (Habe, 1954)	ZMBN 131891	SJ232	Tosa Bay, Kochi, Shikoku Island, Japan	**OR552969**				
Scaphander watsoni Dall, 1881	MNHN-IM-2013-56523	SJ19	French Guyana	MZ473312	MZ478771	MZ478717	MZ479158	MZ479105
Scaphander watsoni Dall, 1881	MNHN-IM-2013-60242	SJ58	North of Grande-Terre, Guadeloupe	MZ473313	MZ478772	MZ478718	MZ479159	MZ479106

scanning electron microscopy; sg, salivary gland; sh., shell; spc., specimen; STACEY, Species Tree And Classification Estimation, Yarely; ugp, unpaired gizzard plate.

Morpho-anatomical work

Specimens were gently separated from their shell using forceps. Shells were photographed using a DSLR camera equipped with a macro lens. The soft parts were dissected by dorsal incision, and the male reproductive and digestive systems were isolated and drawn using a stereo microscope fitted with a *camera lucida*. The buccal bulb was dissolved in a proteinase K solution composed of 20 μL proteinase K and 180 μL buffer ATL obtained from the Qiagen DNeasy Blood and Tissue kit, and incubated at 56°C overnight (protocol modified from Holznagel 1998, Vogler 2013) in order to clean the radula. The gizzard and stomach were dissected. Gizzard plates were extracted and gut content was examined. Gizzard plates were photographed using a Leica M205C stereo microscope fitted with a Leica DMC5400 camera, and images were stacked using Zerene Stacker v.1.04 software (http://zerenesystems.com/cms/home). The male reproductive system was dissected, and sections of the penial chamber were opened longitudinally and critical-point dried for SEM analysis. Radulae and sections of the penial chamber were coated with gold–palladium and examined with a ZEISS SUPRA 55VP SEM at the Electron Microscopy Laboratory (Department of Earth Science, University of Bergen).

Phylogenetic analyses and sequence-based species delimitation

DNA was extracted from foot tissue using the Qiagen DNeasy Blood and Tissue Kit, following the manufacturer's instructions. The mitochondrial markers cytochrome *c* oxidase subunit I (*COI*), 12S rRNA, and 16S rRNA and the nuclear markers 18S rRNA and 28S rRNA were amplified, purified, and sequenced following the methods described by Siegwald *et al.* (2022). The software programme Geneious (Biomatters Ltd; Prime v.2021.1.1) was used to inspect, edit, and assemble chromatograms. Sequences were blasted to check for potential contamination (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Ninety-one new sequences were generated, and an additional 202 were pulled from GenBank, resulting in a dataset of 293 sequences comprising 20 putative species of *Scaphander* and three outgroup species: the Scaphandridae *Nipponoscaphander japonicus* and *Sabatia bathymophila* (Dall, 1881), and the Eoscaphandridae *Eoscaphander fragilis* Habe, 1952 (Table 1). Sequences were aligned using MUSCLE (Edgar 2004) implemented in Geneious. For the protein-coding *COI* sequences, the quality of the alignment was assessed by translating it to amino acids and checking for stop codons. Hypervariable regions in the ribosomal alignments (12S, 16S, 18S, and 28S) were excluded with Gblocks 0.91b (Talavera and Castresana 2007), using relaxed and stringent settings (Supporting Information, Figs S1–S13).

The best-fitting substitution model was selected for each single-gene alignment using the Akaike information criterion (Akaike 1974) as implemented in jModeltest v.2.1.6 (Darriba *et al.* 2012; Supporting Information, Table S1). Bayesian inference analyses were performed in MrBayes v.3.2.7 (Huelsenbeck and Ronquist 2001), with three parallel runs of 1×10^7 generations for the single-gene alignments and 5×10^7 generations for the concatenated dataset, with sampling every 100th generation.

The ribosomal alignments selected for the concatenated dataset were the ones that yielded the best-resolved trees with higher support values in single-gene analyses. The concatenated dataset was partitioned by gene, and each partition was run with the best-fitting substitution model (Supporting Information, Table S1). Convergence was checked in Tracer v.1.7.1 (Rambaut *et al.* 2018), with a burn-in set to 10%. Trees were visualized and annotated in FigTree v.1.4.3 (Morariu *et al.* 2009), and adjustments were made in Adobe Illustrator CS6.

Species delimitation was evaluated under the multispecies coalescent, and analyses were run using the template for STACEY v.1.2.5 (Jones 2014, 2017) as implemented in BEAST v.2.6.6 (Bouckaert *et al.* 2019). Site and clock models were unlinked for all partitions, to allow each partition their own substitution model and clock rate. Tree models were linked for all mitochondrial partitions and unlinked for the nuclear partitions. All specimens were assigned to their own taxon, leaving species assignment to the analysis. The selected best-fitting model was specified for each partition. The clock model used for all partitions was the uncorrelated relaxed lognormal clock, with clock rate estimated, and its prior set as a lognormal distribution with a mean (M) of zero and a standard deviation (S) of one. The ploidy level was set to one for the mitochondrial markers and to two for the nuclear markers. The species growth rate was given a lognormal distribution prior, with $M = 4.6$ and $S = 2$, and the relative death rate was fixed to .5. The popPriorScale prior was given a lognormal distribution, with $M = -7$ and $S = 2$. The genus *Scaphander* was set up by including all *Scaphander* specimens in a clade and defining it as monophyletic. The remaining priors were left to default. Three independent runs of 1×10^9 generations, sampled every 1×10^7 generations, were run in BEAST2. Convergence was assessed by examining the resulting log files in Tracer (effective sample size ≥ 200 for all parameters of the combined analyses). LogCombiner (from the BEAST v.2.6.6 package; Bouckaert *et al.* 2019) was used to discard the first 25% of each run as burn-in and combine the rest of the trees, and maximum clade credibility trees were generated from the combined trees with TreeAnnotator (from the BEAST v.2.6.6 package; Bouckaert *et al.* 2019), setting the node heights as mean heights. A similarity matrix of the PP that pairs of specimens belong to the same multispecies coalescent cluster was produced from the combined trees using the SpeciesDelimitationAnalyser tool provided in DISSECT (Jones 2015) and default settings. Results were visualized by generating a heatmap in R, using a modified version of the script provided in the supplementary information for DISSECT.

The molecular species delimitation method Assemble Species by Automatic Partitioning (ASAP; Puillandre *et al.* 2021) was also used, based on the *COI* alignment. The Web version of the program (https://bioinfo.mnhn.fr/abi/public/asap) was run for the three available models (Jukes Cantor, Kimura, and simple distance) using default settings.

RESULTS

TAXONOMIC SECTION

Scaphander Montfort, 1810

Charta Martini, 1769: 283, 284, pl. 21, figs 194, 195; Eilertsen and Malaquias 2013a: 394–395. Type by monotypy *Charta convoluta* [= *Scaphander lignarius* (Linnaeus, 1758)]. Declared *nomen oblitum* by Eilertsen and Malaquias (2013a: 394–395).

Gioeni Gioeni, 1783: 5–36, pl. 1, figs 1–13 Gioeni (1783); Eilertsen and Malaquias 2013a: 394–395. Type by subsequent designation *Tricla gioeni* Philipsson, 1788 (Philipsson 1788) [= *Scaphander lignarius* (Linnaeus, 1758)]. Declared *nomen oblitum* by Eilertsen and Malaquias (2013a: 394–395).

Tricla Philipsson, 1788: 8; Winckworth 1932: 232; Eilertsen and Malaquias 2013a: 394–395. Type by monotypy *Tricla gioeni* Philipsson, 1788 [= *Scaphander lignarius* (Linnaeus, 1758)]. Suppressed by ICZN (1954: opinion 287).

Gioenia Bruguière, 1792: 12, 502–504; Eilertsen and Malaquias 2013a: 394–395. Type by monotypy *Gioenia sicula*. Suppressed by ICZN (1954: opinion 287).

Scaphander de Montfort, 1810: 334–336, pl. 84; Eilertsen and Malaquias 2013a: 394–395. Type by monotypy *Bulla lignaria* Linnaeus, 1758 [= *Scaphander lignarius* (Linnaeus, 1758)]. Declared *nomen protectum* by Eilertsen and Malaquias (2013a: 394–395).

Assula Schumacher, 1817: 258 (Schumacher 1817); Eilertsen and Malaquias 2013a: 394–395. Type by monotypy *Assula convoluta* [= *Scaphander lignarius* (Linnaeus, 1758)].

Bulla (*Scaphander*) Adams, 1855: 574; Weinkauff 1862: 336; Eilertsen and Malaquias 2013a: 394–395.

Bucconia Dall, 1890a: 16, 17, pl. 10, fig. 9; Habe 1954: 307, pl. 38, figs 1, 2; 1955: 70; Bullis 1956: 2, 3, pl. 2, figs A, B, D, E; Habe 1964: 140, pl. 43, fig. 20; Eilertsen and Malaquias 2013a: 394–395. Type by original designation *Scaphander nobilis* Verrill 1884: 209, 210, pl. 32, figs 18, 18a–d.

Scaphander (*Sabatina*) Dall, 1908: 240, 241; Eilertsen and Malaquias 2013a: 394–395. Type by original designation *Scaphander* (*Sabatina*) *planeticus* Dall, 1908.

Meloscaphander Schepman, 1913: 464, pl. 31, figs 5–9; Minichev 1967: 130–134, figs 25–29; 1969: 43; Bouchet 1975: 341–343, pl. 3g, h, figs 9, 10. Type by original designation *Meloscaphander sibogae* Schepman, 1913 [= *Scaphander tortuosus* Siegwald & Malaquias nom. nov.].

Sabatia (*Sabatina*) Dall, 1927: 25; Eilertsen and Malaquias 2013a: 394–395.

Bulla (*Bullocardia*) Nordsieck, 1972: 29, pl. 7, fig. 25; Eilertsen and Malaquias 2013a: 394–395. Type by original designation *Bulla millepunctata* Locard, 1897 [= *Scaphander nobilis* Verrill, 1884].

Taxonomic history

The taxonomic history of the genus *Scaphander* was comprehensively revised by Eilertsen and Malaquias (2013a), but the recent molecular phylogeny of the family Scaphandridae by Siegwald *et al.* (2022) showed that genera previously considered junior synonyms of *Scaphander* represent valid taxa. This is the case for *Sabatia* Bellardi, 1876 (type by monotypy *Sabatia isseli*), *Eoscaphander* Habe, 1952 (type by monotypy *Eoscaphander fragilis* Habe, 1952; Habe 1952), and *Nipponoscaphander* Kuroda & Habe, 1971 (type by original designation *Scaphander japonicus* Adams, 1862).

Meloscaphander Schepman, 1913 was erected for the species *M. sibogae* Schepman, 1913 based on its partly visible spire. Subsequent studies noted the anatomical resemblance between *Meloscaphander* and *Scaphander* (Minichev 1967, Bouchet 1975, Rudman 1978), and the inclusion of *Meloscaphander grandis* Minichev, 1967 in molecular studies showed that *Meloscaphander* is a junior synonym for *Scaphander* (Chaban *et al.* 2019a, Siegwald *et al.* 2022).

Revised diagnosis (updated from Siegwald et al. 2022)

Shell external, solid, ovoid, pyriform, or sub-rectangular, covered by thin white to yellow or brown periostracum. Parietal callus white and smooth, thickened or thin. Spire concealed, flat, partly raised, or involute. Only one body whorl visible. Shell sculpture composed of punctuated striations or spiral grooves. Aperture as long or nearly as long as shell, narrowing towards apex. Outer lip posteriorly wing-like and raised beyond apex, even with apex, or forming a shoulder immediately below apex. Operculum absent. Animal can withdraw only in part into shell. Large head shield lacking posterior lobes. Parapodial lobes present, short. Eyes spots absent. Radular formula N × 1.1.1. Lateral teeth hamate, with fine or weak denticulation on inner edge. Rachidian teeth vestigial, fragile, quadrate or H-shaped. Gizzard large, highly muscularized. Gizzard plates calcified; paired plates quadrate, sub-triangular to kidney-shaped; unpaired gizzard plate thinner and elongate. Penial chamber cylindrical, separated from prostate by thinner prostatic duct. Muscular penial papilla or eversible penial chamber wall. Prostate bulbous and cylindrical. Distribution: worldwide, between latitudes 72°N and 47°S. Depth range: 16–5427 m.

Scaphander mundus Watson, 1883

(Figs 1–3; Table 2)

Scaphander mundus Watson, 1883: 342–343; 1886: 643–644, pl. 48, fig. 2; Pilsbry 1893: 251–252, pl. 31, figs 13, 14; Kobelt 1896: 6–7, pl. 2; Smith 1906: 247; Valdés 2008: 674–677, figs 40C, D, 43 (in part).

Scaphander alatus Dall, 1895: 676, pl. 27, fig. 2; Valdés 2008: 674, 676.

Scaphander vicinus Smith, 1906: 248; Annandale and Stewart 1909: pl. 19, figs 5, 6.

Taxonomic history: Scaphander mundus was first introduced by Watson (1883) from shell material collected at 1460 m west of New Guinea island by the *Challenger* expedition. Watson (1883) described the shells as thin and white, covered with spiral punctuated sculpture and with an outer lip extending in a small posterior projection. Watson (1886) illustrated the species and compared it with *S. nobilis*, referring to differences in the upper part of the outer lip and general shape of the shell. Dall (1895) described the species *S. alatus* from a specimen found at 545 m in Hawaii and named it after the wing-like projection of the outer lip of the shell. Dall (1895) again compared this species with *S. nobilis*, but differentiated *S. alatus* by having a thicker, less inflated shell. He also referred to *S. mundus*, but declared the two species impossible to confuse, without adding any further comment. Valdés synonymized the name *S. alatus* with *S. mundus*, yet his description and illustrations include specimens of *S. mundus* (Valdés 2008: figs 40C, D) and of a distinct lineage (Valdés 2008: figs 40A, B) here described as a distinct species, namely *S. cornus*. The latter strongly resembles *S. nobilis*, with a more inflated posterior half of the shell, and does not match the main features mentioned by Dall (1895) for *S. alatus* (see below for a detailed description).

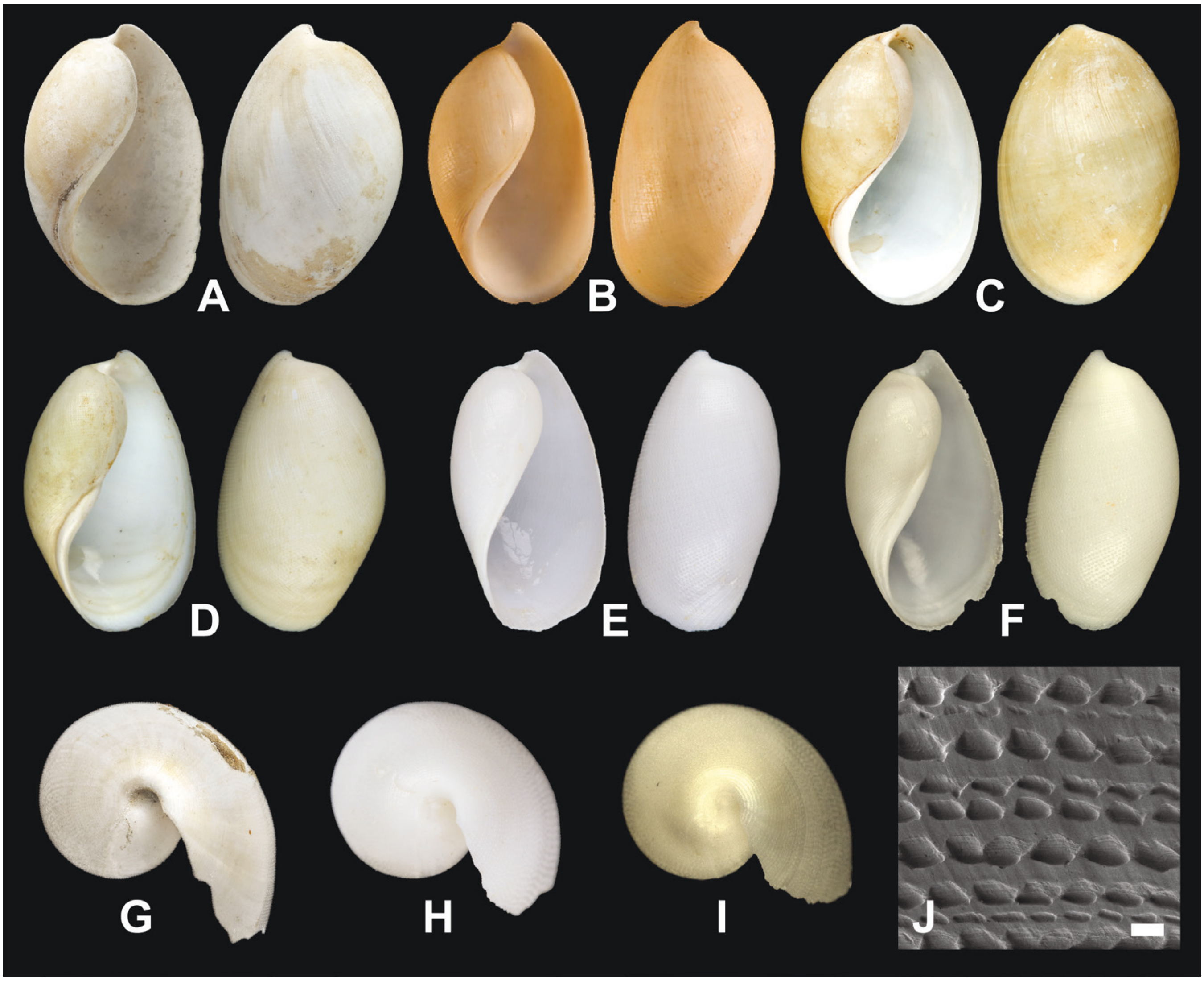

Figure 1. Shells and SEM image of the shell sculpture of *Scaphander mundus*. A, Indonesia, west of Papua, off Aore Islands (syntype, NHMUK 1887.2.9.2181, H = 29 mm, images courtesy of the NHMUK). B, Hawaii (holotype, *Scaphander alatus*, *USNM 107161*, H = 35 mm, images courtesy of the USNM). C, Sri Lanka (paratype, *Scaphander vicinus*, NHMUK 1906.7.21.4.9, H = 31 mm, images courtesy of the NHMUK). D, South China Sea, off Taiping Island (MNHN-IM-2013-44305, H = 30 mm). E, Philippines, east of Luzon (MNHN-IM-2009-4319, H = 22 mm). F, Australia, Queensland, Coral Sea Commonwealth Marine Reserve (AM C.519372, H = 22 mm). G, Indonesia, west of Papua, off Aore Islands (syntype, NHMUK 1887.2.9.2181, H = 26 mm, image courtesy of the NHMUK). H, Philippines, east of Luzon (MNHN-IM-2009-4319, H = 22 mm). I, J, Australia, Queensland, Coral Sea Commonwealth Marine Reserve (AM C.519372, H = 22 mm). Scale bar: J = 200 μm.

Smith (1906) described *S. vicinus* from shells collected by the *Investigator* west of Sri Lanka (as Ceylon). He commented on the similarities with *S. mundus* and *S. alatus* but considered differences in the sculpture of the shell (punctation) and shape of the posterior outer lip to support *S. vicinus* as a distinct species. Our observations revealed substantial variation in the spiral sculpture of *S. mundus*, and in the shape of the posterior part of the outer lip, overlapping with the description of these features in *S. vicinus*. Therefore, we here consider *S. vicinus* a junior synonym of *S. mundus*.

Type material: Scaphander mundus Watson, 1883—**Indonesia**: west of Papua, off Aore (= Aru) Islands, *Challenger* Expedition, station 191, 5°41'00"S, 134°04'00"E, 1463 m, two syntypes, NHMUK 1887.2.9.2181, H = 24.5, 28 mm, images seen (Fig. 1A, G). *Scaphander alatus* Dall, 1895—**Hawaii**: *Albatross* Expedition, station 3476, 21°09'00"N, 157°53'00"W, 545 m, holotype, *USNM 107161*, H = 35 mm, images seen (Fig. 1B). *Scaphander vicinus* Smith, 1906—**Sri Lanka**: west of Sri Lanka, *Investigator* Expedition, station 318, 7°28'00"N, 79°19'30"E, 1984 m, six paratypes, NHMUK 1906.7.21.4–9, H = 26–36 mm, images seen (Fig. 1C).

Other material examined: **Philippines**: east of Luzon, one spc., dissected and sequenced, MNHN-IM-2009-4318, H = 29 mm; one spc., sequenced, MNHN-IM-2009-4319, H = 22 mm. **China Sea**: southwest of Taiwan, one spc., sequenced, MNHN-IM-2013-50091, H = 18 mm; one spc.,

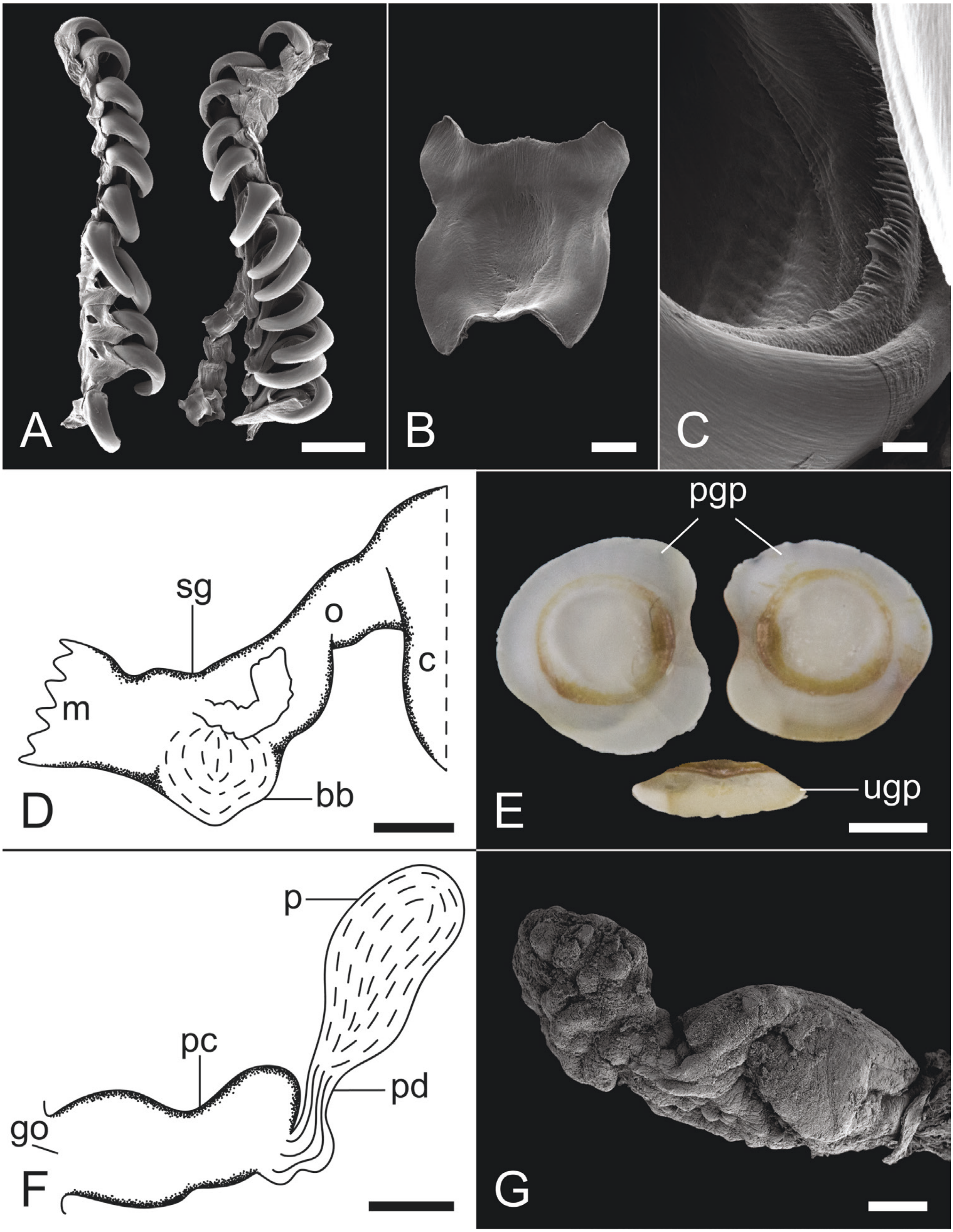

Figure 2. Anatomical details of *Scaphander mundus*. A, radula, Australia, Queensland, Coral Sea Commonwealth Marine Reserve (AM C.519372, H = 22 mm). B, rachidian teeth (AM C.519372, H = 22 mm). C, detail of lateral teeth (AM C.519372, H = 22 mm). D, anterior part of digestive tract, South China Sea, off Taiping Island (MNHN-IM-2013-44305, H = 30 mm). E, gizzard plates (AM C.519372, H = 22 mm). F, male reproductive system (AM C.519372, H = 22 mm). G, penial papilla, South China Sea, off Taiping Island (MNHN-IM-2013-44310, H = 26 mm). Scale bars: A, G = 200 μm; B, C = 20 μm; D, F = 1 mm; E = 2 mm.

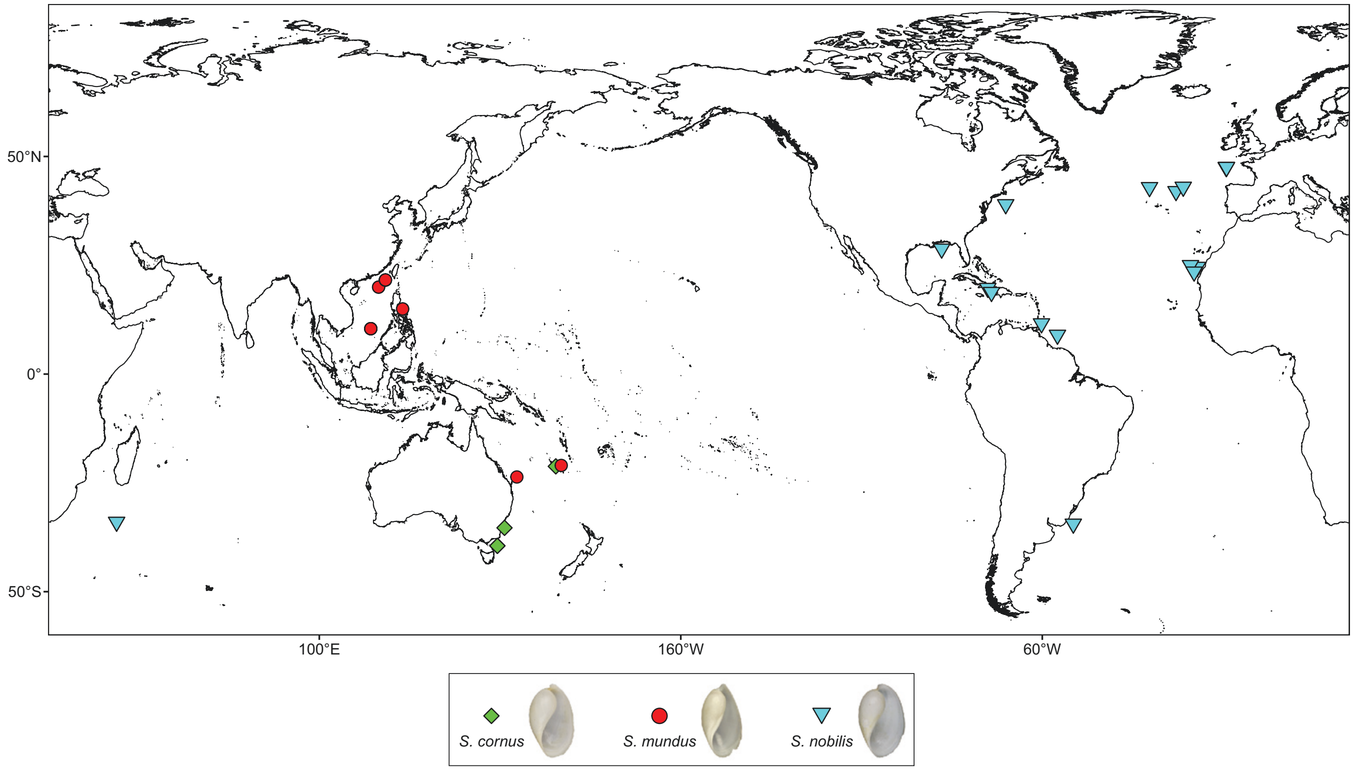

Figure 3. Geographical distribution of ***Scaphander cornus***, *Scaphander mundus*, and *Scaphander nobilis*. Geographical records are based on studied material and reliable literature records.

sequenced, MNHN-IM-2013-50090, H = 24 mm; one spc., sequenced, MNHN-IM-2013-50039, H = 21 mm; one sh., MNHN-IM-2016-5761, H = 30 mm; one spc., sequenced, MNHN-IM-2013-50089, H = 37 mm; southwest of DongSha, one spc., sequenced, MNHN-IM-2013-61614, H = 29 mm; one spc., sequenced, MNHN-IM-2013-61612, H = 32 mm; South China Sea, off Taiping Island, one spc., dissected and sequenced, MNHN-IM-2013-44305, H = 30 mm; one spc., dissected and sequenced, MNHN-IM-2013-44310, H = 26 mm; one spc., MNHN-IM-2013-44306, H = 22 mm; one spc., MNHN-IM-2013-44308, H = 27 mm; one spc., MNHN-IM-2013-44313, H = 32 mm. **Australia**: Queensland, Coral Sea Commonwealth Marine Reserve, one spc., dissected and sequenced, AM C.519372, H = 22 mm. **New Caledonia**: Loyalty Basin, five sh., MNHN-IM-2010-2075, H = 15–22 mm.

Diagnosis: Shell elongated oval, white. Outer lip protruding in a straight wing above the apex. Spiral sculpture composed of separate or interconnected punctuated striations. Rachidian teeth H-shaped. Prostate cylindrical, separated from penial chamber by thin, short prostatic duct. Penial papilla elongate.

Shell (Fig. 1): Maximum H observed = 37 mm. Shell oval to oval elongate, widest around centre, only one whorl visible. Aperture as long as shell, narrowing posteriorly. Spire concealed. Posterior edge of outer lip rising in small straight wing above apex. Parietal wall covered with thick, smooth white callus. Spiral sculpture composed of punctuated striations. Punctations oblong, round, elongated, or squarish. Thin, translucent to pale yellow periostracum. Shell white.

Radula (Fig. 2A–C): Radular formula 17 × 1.1.1 (H = 29 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth H-shaped, central area convex on one side, and slightly concave on the other side; developed pointed-triangular cusps present.

Digestive tract (Fig. 2D, E): Salivary glands medium long, surface uneven. Paired gizzard plates kidney-shaped to sub-triangular.

Male reproductive system (Fig. 2F, G): Penial chamber cylindrical, bulged towards prostatic duct, lined with soft longitudinal ridges. Muscular penial papilla elongate, covered in warts. Penial chamber separated from prostate by short prostatic duct. Prostate cylindrical, rounded at end.

Ecology: Found between 900 and 1800 m depth. Feeds on foraminifera, tubicolous polychaetes, and small molluscs (present study).

Distribution (Fig. 3): Western Pacific Ocean to Eastern Indian Ocean, from Hawaii (Dall 1895), New Caledonia (Valdés 2008), Australia (present study), China Sea, the Philippines (Valdés 2008), Banda Sea, Indonesia (Watson 1883), and Sri Lanka (Smith 1906).

Remarks: Scaphander mundus has often been confused with the new species here described as *S. cornus* (Indo-West Pacific) (e.g. Valdés 2008) and with *S. nobilis* (Atlantic, Western Indian Ocean), which explains several misidentifications and reports of *S. mundus* in the Atlantic (Locard 1897, Marcus and Marcus

Table 2. Summary of the most useful characters for diagnosis of the Indo-Pacific species of *Scaphander*.

		S. cornus	*S. nobilis*	*S. mundus*	*S. otagoensis*	*S. interruptus*	*S. amygdalus*
Shell	Shape	Oval	Ovoid	Elongated oval	Elongate	Pyramidal/elongate	Elongate/oval
	Spiral sculpture	Sub-rectangular punctations	Round/sub-rectangular punctations	Oblong/round/elongated/square	Rectangular punctuations	Ovoid punctuations/interconnected	Ovoid punctations
	Colour	White	White	White	Pale orange/brown	White/pale yellow/brown	White/cream
	Callus on parietal wall	Thin	Slight	Thick	Thick	Thick	Thick
	Parietal wall	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth
	Outer lip, posterior edge	Curved wing	Curved wing	Small straight wing	Rising slightly above apex	Rounded/Rising slightly above apex	Rising slightly above apex
	Spire	Concealed	Concealed	Concealed	Concealed	Concealed	Concealed
Male reproductive system	Prostate	Ovoid	Round/Club-shaped	Cylindrical	Cylindrical	Club-shaped, short	Cylindrical, short
	Prostatic duct	Short	Medium	Short	Short	Medium	Thin
	Penial papilla	Absent	Present	Present	Absent	Absent	Absent
	Ornamentation of papilla/chamber	Warts	Warts/wrinkles	Warts	Warts/Wrinkles	Ridges	Warts
Digestive tract	Rachidian teeth	Sub-rectangular, rounded corners	Sub-quadrate	H-shaped, raised corners	Sub-rectangular, pointed corners	Sub-rectangular	Sub-rectangular, acute corners
	Salivary glands	Medium long	Medium long	Medium long	Long, thin	Short, thin	Medium
	Paired gizzard plates	Kidney-shaped	Kidney-shaped/sub-triangular	Kidney-shaped/Sub-triangular	Kidney-shaped/Sub-rectangular	Kidney-shaped/Sub-triangular	Kidney-shaped/sub-triangular
Depth range (m)		2338–2760	1493–4255	900–1800	964–1793	497–2760	531–1257
Distribution		Eastern Australasia	Atlantic, Southwestern Indian Ocean	Southwestern and central Pacific, Eastern Indian Ocean	New Zealand	Southern Pacific	Southern Australasia

Table 2. Continued

		S. meridionalis	*S. obnubilus*	*S. grandis*	*S. planeticus*	*S. tortuosus*	*S. semicallus*
Shell	Shape	Ovoid/ sub-rectangular	Ovoid	Ovoid/ elongate	Ovoid	Ovoid	Elongate
	Spiral sculpture	Large, sub-rectangular punctuations	Sub-rectangular/ovoid punctuations	Sub-rectangular punctations, irregular	Punctuations	Ovoid punctuations	Ovoid punctuations
	Colour	White	White	White	White	Brown	White
	Callus on parietal wall	Thick	Thick	Thick	Thick	Thick	Thick
	Parietal wall	Spire groove	Spire groove	Spire groove	Spire groove	Smooth	Smooth
	Outer lip, posterior edge	Rounded shoulder	Rounded shoulder	Acute shoulder	Soft shoulder	Soft shoulder	Small wing
	Spire	Small, flat or partly raised	Flat	Small, flat or partly raised	Raised	Raised	Concealed
Male reproductive system	Prostate	Cylindrical	Cylindrical	Cylindrical/oval	N/A	N/A	Cylindrical
	Prostatic duct	Thin	Thin	Long, thin	N/A	N/A	Medium
	Penial papilla	Present	Present	Present	N/A	N/A	Absent
	Ornamentation of papilla/chamber	Warts/wrinkles	Warts/Wrinkles	Wrinkles	N/A	N/A	Ridges
Digestive tract	Rachidian teeth	Sub-quadrate, pointed corners	Sub-quadrate, sharp outward corners	Rectangular, inward corners	N/A	N/A	X-shaped, squarish corners
	Salivary glands	Long	Long, thin	Medium long	N/A	N/A	Short, small
	Paired gizzard plates	Sub-rectangular	Sub-triangular/ Kidney-shaped	Ovoid to sub-quadrate, irregular	N/A	N/A	Kidney-shaped
Depth range (m)		2338–2952	2636–2760	3585–5427	4504	2798	1092–1195
Distribution		Southwestern Atlantic, Southern Australia	Southeastern Australia	Northern Pacific	Southern Australasia	Indonesia	Mozambique

Table 2. Continued

		S. sibogae	*S. andamanicus*	*S. solomonensis*	*S. teramachii*	*S. cancellatus*	*S. illecebrosus*
Shell	Shape	Ovate	Ovate	Ovoid/attenuate	Ovoid/sub-rectangular	Ovoid/sub-rectangular	Ovoid
	Spiral sculpture	Ovoid punctuations/interconnected	Ovoid/sub-rectangular punctuations/interconnected	Ovoid punctuations/Interconnected	Ovoid punctuations	Ovoid/sub-rectangular punctuations/grooves	Ovoid punctations
	Colour	Dirty white/orange/brown	Orange/dark reddish brown	White	White	Dirty white/orange	Pale yellow
	Callus on parietal wall	Thicker in anterior half	Thick	Thicker, slighter in posterior half	Thicker, slighter in posterior half	Thicker in anterior half	Thick
	Parietal wall	Smooth	Smooth	Smooth	Smooth	Smooth	Smooth
	Outer lip, posterior edge	Curved wing	Curved wing	Rounded wing	Rounded wing	Rounded wing	Rounded, protruding slightly beyond apex
	Spire	Concealed	Concealed	Slightly umbilicate	Concealed, slightly umbilicate in juveniles	Concealed	Concealed
Male reproductive system	Prostate	Cylindrical	N/A	Cylindrical, narrowed at end	Oval, rounded at end	Cylindrical	N/A
	Prostatic duct	Thin	N/A	Thin	Short	Short	N/A
	Penial papilla	Present	N/A	Absent	Absent	Absent	N/A
	Ornamentation of papilla/chamber	Warts/Wrinkles	N/A	Ridges	Ridges	Warts	N/A
Digestive tract	Rachidian teeth	Tetragonal, long inward upper corners	N/A	Sub-rectangular/H-shaped, curved corners	H-shaped	Elongate, curved upper cusps	N/A
	Salivary glands	Short/medium	N/A	Medium long	Thin	Medium long	N/A
	Paired gizzard plates	Sub-triangular, rounded	N/A	Sub-triangular/kidney-shaped/crescent-shaped	Sub-triangular/kidney-shaped	Kidney-shaped, rounded	N/A
Depth range (m)		650–977	338–1714	718–1100	100–1533	440–869	119
Distribution		Western Pacific	Northeastern Indian Ocean	Solomon Islands	Japan	Western Pacific, Eastern Indian Ocean	Southern Australasia

1966, Pequegnat 1983). However, as Eilertsen and Malaquias (2013a) first showed, *S. mundus* and *S. nobilis* are distinct both genetically and morphologically, and records of *S. mundus* in the Atlantic should be considered as misidentifications of *S. nobilis*. Our study revealed a second species first identified as *S. mundus* by us, which is here described as a new taxon, *S. cornus*. These two species are not only molecularly divergent (*COI* uncorrected *p*-distance of 5.47%–6.46% between *S. mundus* and *S. nobilis* and 4.56%–5.74% between *S. mundus* and *S. cornus*), but also show several morphological and conchological differences; the shell of *S. mundus* is less inflated than in *S. cornus* and *S. nobilis*, and the posterior outer lip protrudes above the apex in a shorter and less curved wing-like shape.

The species *Bulla insperata* Fischer, 1883 (in Locard 1897) was described from shells sampled off the coast of Western Sahara. Locard (1897) commented on its resemblance to *Bulla millepunctata* Locard, 1987 (a synonym of *Scaphander nobilis*; see *S. nobilis* section) and to *S. punctostriatus*. Bouchet (1975) synonymized *B. insperata* with *S. mundus* in the Atlantic. However, the shell of the type material for *B. insperata* is more evenly rounded and generally more globose, rather than oval or elongated as in *S. mundus*. The syntype housed in the Paris Museum (MNHN-IM-2000-27695) resembles some larger and roundish forms of *S. punctostriatus*, a species that has been referred along the cost of West Africa southwards down to South Africa (Bouchet 1975, Steyn and Lussi 2005, Herbert *et al.* 2018). Thus, until further specimens from the Western Sahara matching the morphotype of *B. insperata* are discovered and studied, we suggest this species to be considered a synonym of *S. punctostriatus*.

Scaphander nobilis Verrill, 1884

(**Figs 3–5**; **Table 2**)

Scaphander nobilis Verrill, 1884: 209, 210, pl. 32, fig. 18a–d; Dall 1889a: 86; 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, fig. 7A–C, pl. 3, figs a–c, map 5; Eilertsen and Malaquias 2013a: 406, 408, 410, figs 2, 8, 15.

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

Bulla millepunctata Locard, 1897: 52–54, pl. 2, figs 3–6; Pallary 1912: 21.

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

Bulla (*Bullocardia*) *millepunctata*—Nordsieck 1972: 29, pl. P7, fig. 25.

Scaphander stigmatica Dall, 1927: 26.

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

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

Taxonomic history: Scaphander nobilis was described by Verrill (1884) based on shells from the *Albatross* expedition collected in Delaware Bay (Atlantic, USA). Locard (1897) described a similar species, *Bulla millepunctata*, from specimens sampled during the *Talisman* expedition off the Azores and coast of Sahara, which was reassigned by Martens and Thiele (1903) to the genus *Atys*. Dall (1927) described *S. stigmatica* based on Caribbean shells he had previously identified as *S. nobilis* (Dall 1889a, 1889b). Bouchet (1975) synonymized *B. millepunctata* and *S. stigmatica* with *S. nobilis*, which Eilertsen and Malaquias (2013a) confirmed in their study of the genus in the Atlantic.

Type material: Scaphander nobilis Verrill, 1884—**Northwestern Atlantic**: Delaware Bay, *Albatross* Expedition, station 2102, 38°44'00"N, 72°38'00"W, 2211 m, holotype, *USNM 35641*, H = 34.2 mm, images seen (Fig. 2A). *Bulla millepunctata* Locard, 1897—**Northeastern Atlantic**: north of the Azores, *Talisman* Expedition, station DR135, 43°15'00"N, 19°19'00"W, 4163 m, syntype MNHN-IM-2000-38367, H = 41 mm, images seen (Fig. 2C); west of the Sahara, *Talisman* Expedition, station DR76, 25°01'00"N, 16°55'00"W, 2638 m, syntype, MNHN-IM-2000-38276, H = 43 mm, images seen. *Scaphander stigmatica* Dall, 1927—**Caribbean**: south of Cuba, *Albatross* Expedition, station 2127, 19°45'00"N, 75°04'00"W, 2997 m, holotype, *USNM 95196*, H = 35.4 mm, images seen (Fig. 2B).

Other material examined: **Atlantic**: Azores, one spc., sequenced, ZMBN 127875, H = 24 mm; Bay of Biscay, one spc., dissected, MNHN-IM-2019-11702, H = 27 mm; one spc., MNHN-IM-2019-11720, H = 27 mm; one spc., dissected, MNHN-IM-2009-29696, H = 39 mm; one spc., dissected, MNHN-IM-2016-5767, H = 40 mm. **Indian Ocean**: Walters Shoals, South Plain, one spc., dissected and sequenced, MNHN-IM-2013-67215, H = 23 mm; one sh., MNHN-IM-2013-67214, H = 15 mm.

Diagnosis: Shell ovoid, white. Spiral sculpture composed of round to sub-rectangular punctuations. Apex rounded. Posterior edge of outer lip rising above apex in sharp curved wing. Rachidian teeth sub-quadrate. Prostate round to club-shaped. Penial papilla narrow, covered with warts.

Shell (Fig. 4): Maximum H observed = 40 mm. Shell ovoid to elongated oval, only one whorl visible. Aperture wide, as long as shell, narrowing posteriorly. Spire concealed. Posterior edge of outer lip rising in sharp curved wing protruding well beyond apex. Parietal wall covered with slight, smooth white callus. Spiral sculpture composed of punctuated striations. Punctations round to sub-rectangular. Thin, translucent to pale yellow periostracum. Shell white.

Radula (Fig. 5A–C): Radular formula 20 × 1.1.1 (H = 40 mm). Lateral teeth curved, with fine denticulation on inner edge. Rachidian teeth sub-quadrate.

Digestive tract (Fig. 5D, E): Salivary glands medium long, surface uneven. Paired gizzard plates kidney-shaped to sub-triangular.

Male reproductive system (Fig. 5F, G): Penial chamber cylindrical, lined with soft longitudinal ridges near genital opening, with soft warts near prostatic duct entrance. Penial papilla long, narrow, covered with warts and wrinkles. Penial chamber separated from prostate by medium prostatic duct, narrowing towards prostate. Prostate round to club-shaped.

Ecology: Found between 1493 and 4255 m depth. Feeds on foraminifera, tubicolous polychaetes, and small gastropods (Eilertsen and Malaquias 2013a; present study).

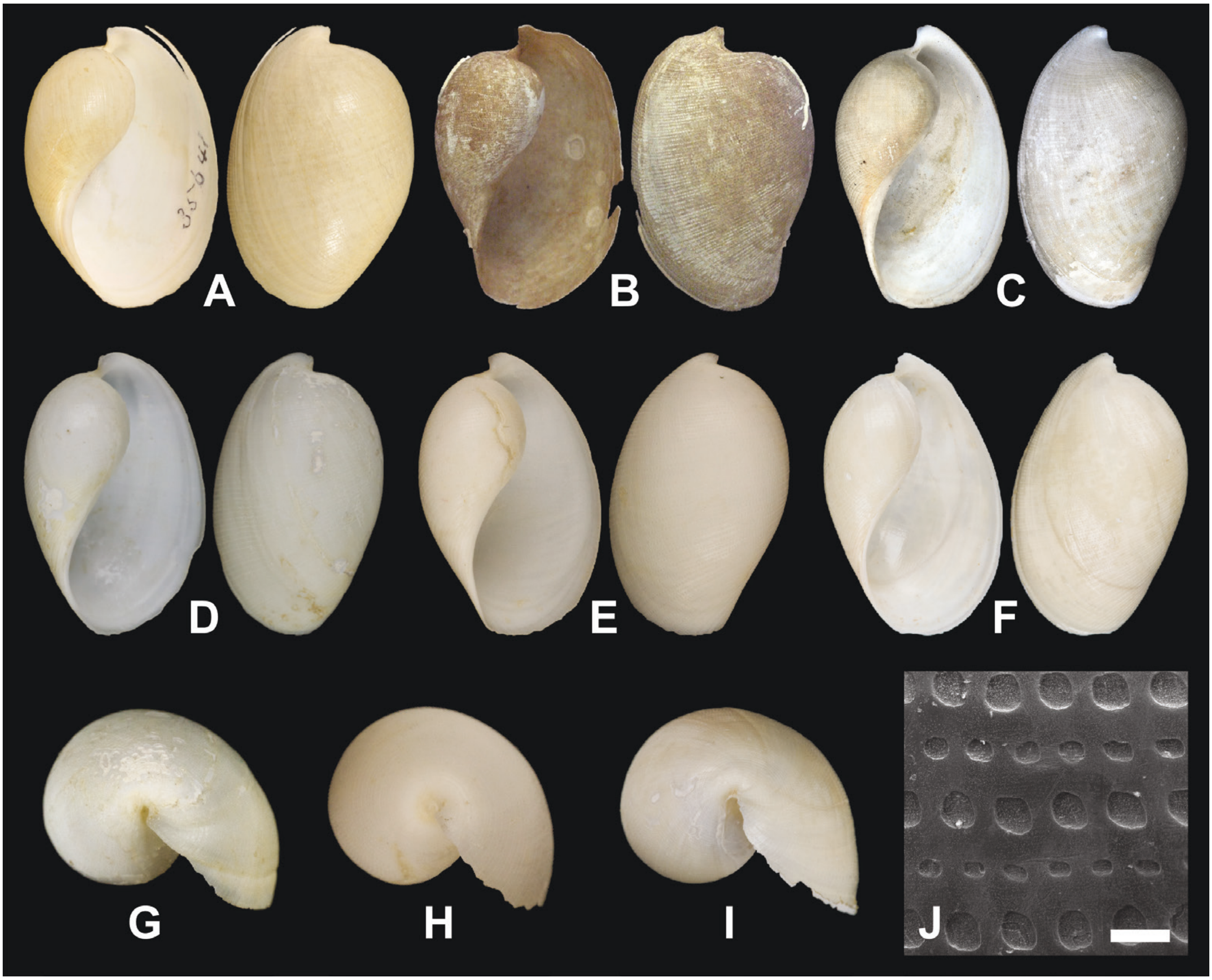

Figure 4. Shells and SEM image of the shell sculpture of *Scaphander nobilis*. A, Northwestern Atlantic, Delaware Bay (holotype, *USNM 35641*, H = 34.2 mm, images courtesy of the USNM). B, Caribbean Sea, south of Cuba (holotype, *Scaphander stigmatica*, *USNM 95196*, H = 35.4 mm, images courtesy of the USNM). C, Northeastern Atlantic (syntype, *Bulla millepunctata*, MNHN-IM-2000-38367, H = 41 mm, images courtesy of the MNHN). D, Southwestern Indian Ocean, Walters Shoals (MNHN-IM-2013-67215, H = 23 mm). E, Southwestern Indian Ocean, Walters Shoals (MNHN-IM-2013-67214, H = 15 mm). F, Northeastern Atlantic, Bay of Biscay (MNHN-IM-2019-11702, H = 27 mm). G, Southwestern Indian Ocean, Walters Shoals (MNHN-IM-2013-67215, H = 23 mm). H, Southwestern Indian Ocean, Walters Shoals (MNHN-IM-2013-67214, H = 15 mm). I, Northeastern Atlantic, Bay of Biscay (MNHN-IM-2019-11702, H = 27 mm). J, Southwestern Indian Ocean, Walters Shoals (MNHN-IM-2013-67214, H = 15 mm). Scale bar: J = 200 μm.

Distribution (Fig. 3): Western Atlantic from Martha's Vineyard, USA (Dall 1927), Gulf of Mexico (Bullis 1956), and from the Caribbean Sea to South Brazil (Marcus 1974). Eastern Atlantic from the Bay of Biscay, the Azores (Bouchet 1975), and the northwestern coast of Africa from the Canaries to Senegal (Locard 1897, Marcus 1974). Southwestern Indian Ocean, Walters Shoals (present study).

Remarks: Three specimens are labelled as syntypes for *B. millepunctata* at the Natural History Museum in Paris. However, examination of images of these specimens revealed that one of them (MNHN-IM-2000-27696) did not fit Locard (1897)'s description and illustration. The shell of this specimen instead has the apparent flat spire and inflated shape characteristic of *S. imperceptus* and expands the range of this species from Mauritania to north of the Azores (see Fig. 14).

As highlighted by Eilertsen and Malaquias (2013a) and discussed above, reports of Western Pacific species *S. mundus* in the Atlantic (Locard 1897, Pallary 1912, Marcus and Marcus 1966, Pequegnat 1983) should be considered misidentifications of *S. nobilis*. Another Western Pacific species, *S. cornus*, is remarkably similar to *S. nobilis* and has commonly been confused with *S. mundus* (Valdés 2008), which might explain those misidentifications. However, *S. nobilis* has a more elongated shell and a muscular penial papilla, whereas *S. cornus* has a rounder shell and lacks a penial papilla.

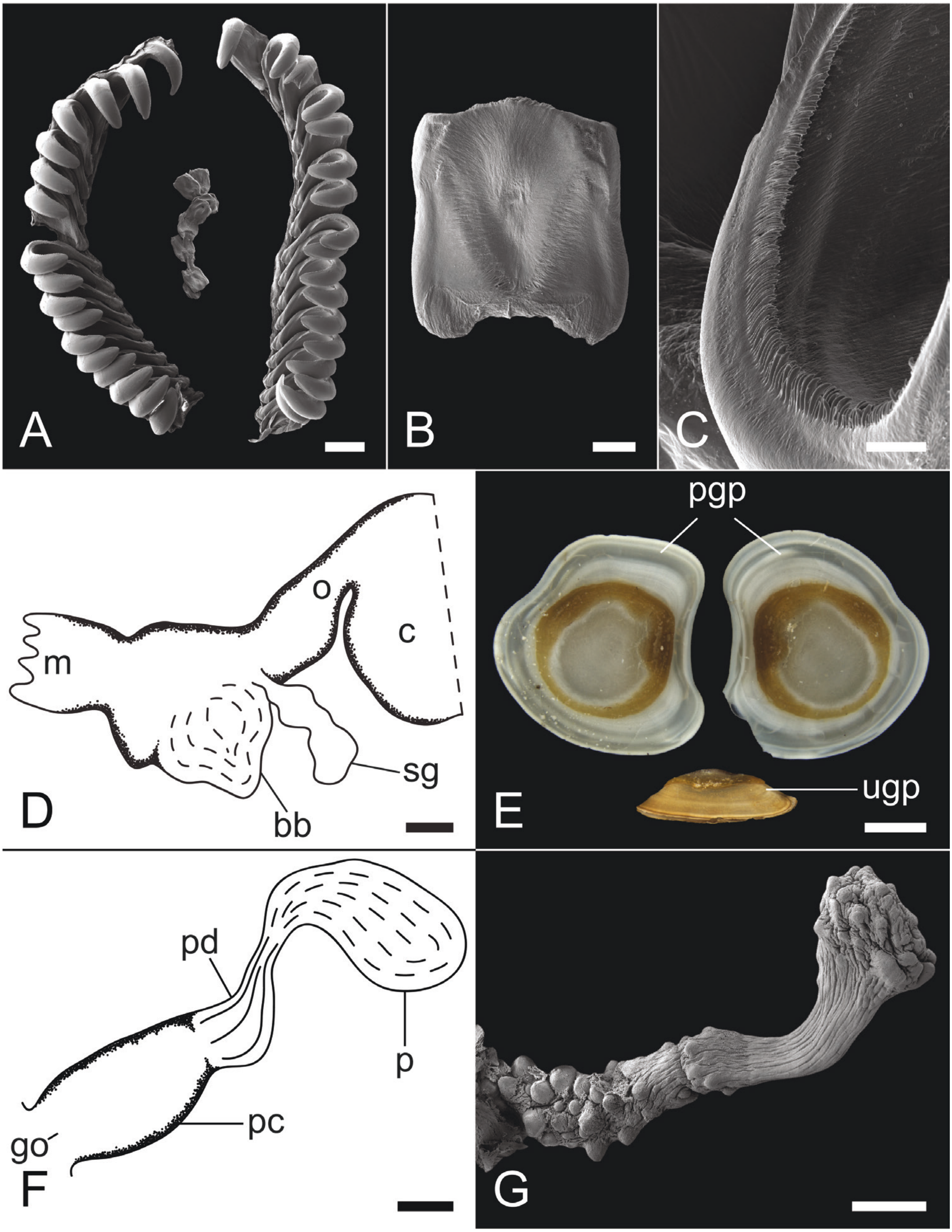

Figure 5. Anatomical details of *Scaphander nobilis*. A, radula, Northeastern Atlantic, Bay of Biscay (MNHN-IM-2019-11702, H = 27 mm). B, rachidian teeth (MNHN-IM-2019-11702, H = 27 mm). C, detail of lateral teeth (MNHN-IM-2019-11702, H = 27 mm). D, anterior part of digestive tract (MNHN-IM-2019-11702, H = 27 mm). E, gizzard plates, Southwestern Indian Ocean, Walters Shoals (MNHN-IM-2013-67215, H = 23 mm). F, male reproductive system (MNHN-IM-2019-11702, H = 27 mm). G, penial papilla (MNHN-IM-2019-11702, H = 27 mm). Scale bars: A, G = 200 μm; B, C = 20 μm; D, F = 1 mm; E = 2 mm.

Scaphander interruptus Dall, 1890b

(Figs 6–8; Table 2)

Scaphander interruptus Dall, 1890b: 297, pl. 12, fig. 12; Pilsbry 1893: 250–251, pl. 31, fig. 26; Kobelt 1896: 9–10, pl. 7, fig. 12; Dall 1908: 239; Finet 1991: 273; Gosliner 1991: 302; Finet *et al.* 2011: 119; Valdés and McLean 2015 (in part): 119–120, figs 1, 6–8; Valdés 2019: 276–277, fig. 18A, B.

Scaphander cf. *otagoensis* 2—Siegwald *et al.* 2022.

Taxonomic history: Dall (1890b, 1908) described *S. interruptus* based on shells collected offshore of Chile and the Galapagos during the *Albatross* expedition and remarked on their resemblance to the European species *S. lignarius*. Valdés and McLean (2015) redescribed the species based on samples available at the LACM from the Northeastern Pacific (between Oregon and Chile), including anatomical data. However, examination of the material used in that paper revealed that the specimens used were a mix of species and that the specimens dissected present a visible spire and rounder shells and belong to the species *S. grandis*, also occurring in the Northeastern Pacific (see *S. grandis* section). The anatomy of *S. interruptus* presented here is therefore based on novel material.

Type material: Scaphander interruptus Dall, 1890b—**Chile**: west coast of Chile, *Albatross* Expedition, station 2788, 45°35'00"S, 75°55'00"W, 1920 m, three syntypes, USNM 97075, H = 33 mm, images seen (Fig. 6A).

Other material examined: **Chile**: Laguna San Rafael National Park, one sh., SCBUCN-2206, H = 14.3 mm; west of Chiloé Island, one spc., dissected, ZMBN 127896,

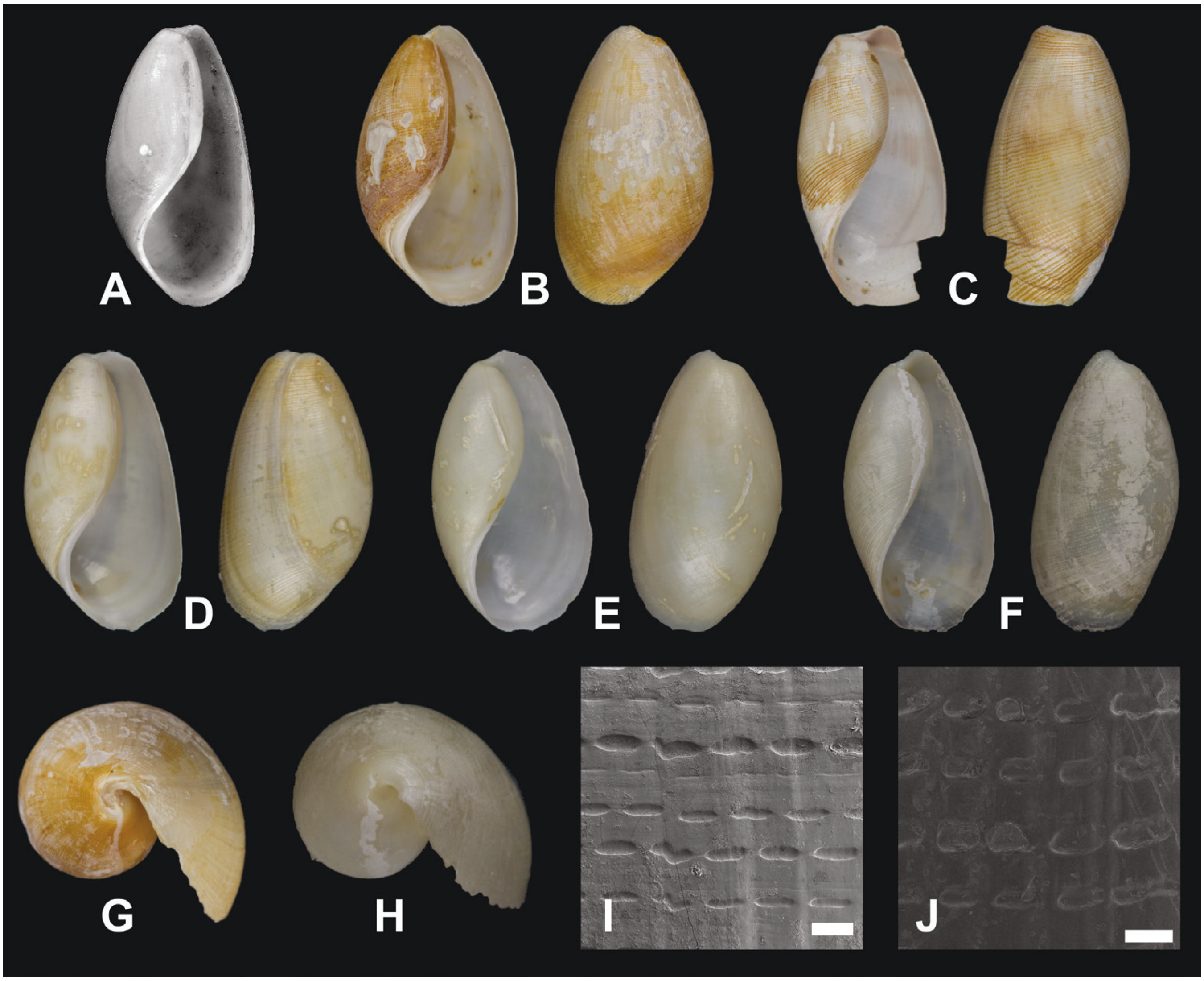

Figure 6. Shells and SEM images of the shell sculpture of *Scaphander interruptus*. A, Chile, west coast (syntype, UNSM 97075, H = 33 mm; image adapted from Valdés and McLean 2015). B, Chile, south of Concepción (SCBUCN-2837, H = 41.7 mm). C, Costa Rica (Pacific side), southwest of Punta Guiones (LACM 1973-109.5, H = 22 mm). D, Chile, west of Chiloé Island (ZMBN 127896, H = 22.7 mm). E, Australia, Bass Strait (AM C.590961, H = 23 mm). F, Australia, Victoria, East Gippsland Commonwealth Marine Reserve (AM C.563068, H = 20 mm). G, Chile, south of Concepción (SCBUCN-2837, H = 41.7 mm). H, I, Australia, Victoria, East Gippsland Commonwealth Marine Reserve (AM C.563068, H = 20 mm). J, Costa Rica (Pacific side), southwest of Punta Guiones (LACM 1973-109.5, H = 22 mm). Scale bars: I, J = 200 µm.

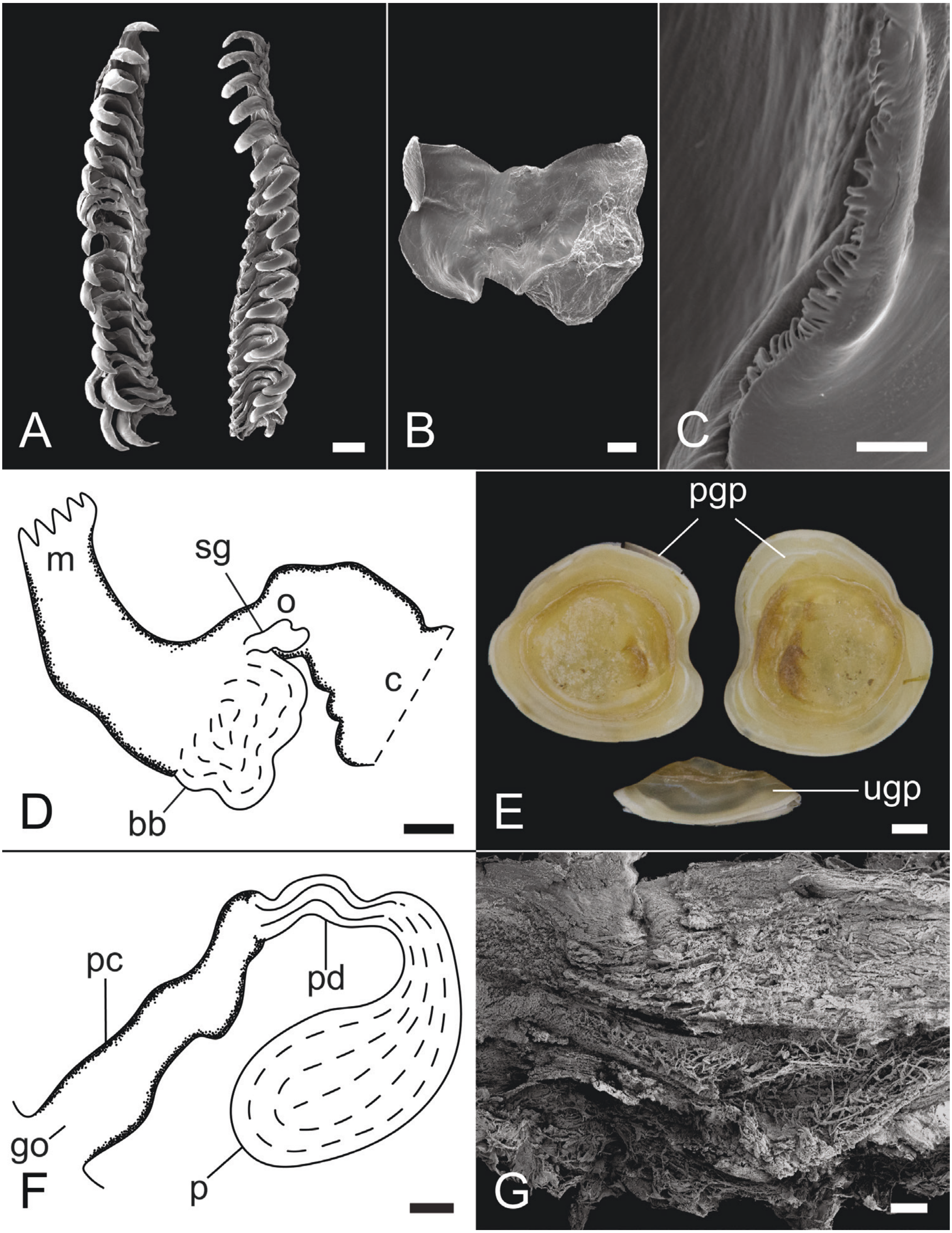

Figure 7. Anatomical details of *Scaphander interruptus*, Chile, south of Concepción (SCBUCN-2837, H = 41.7 mm). A, radula. B, rachidian teeth. C, detail of lateral teeth. D, anterior part of digestive tract. E, gizzard plates. F, male reproductive system. G, lining of penial chamber. Scale bars: A, G = 200 μm; B, C = 20 μm; D, F = 1 mm; E = 2 mm.

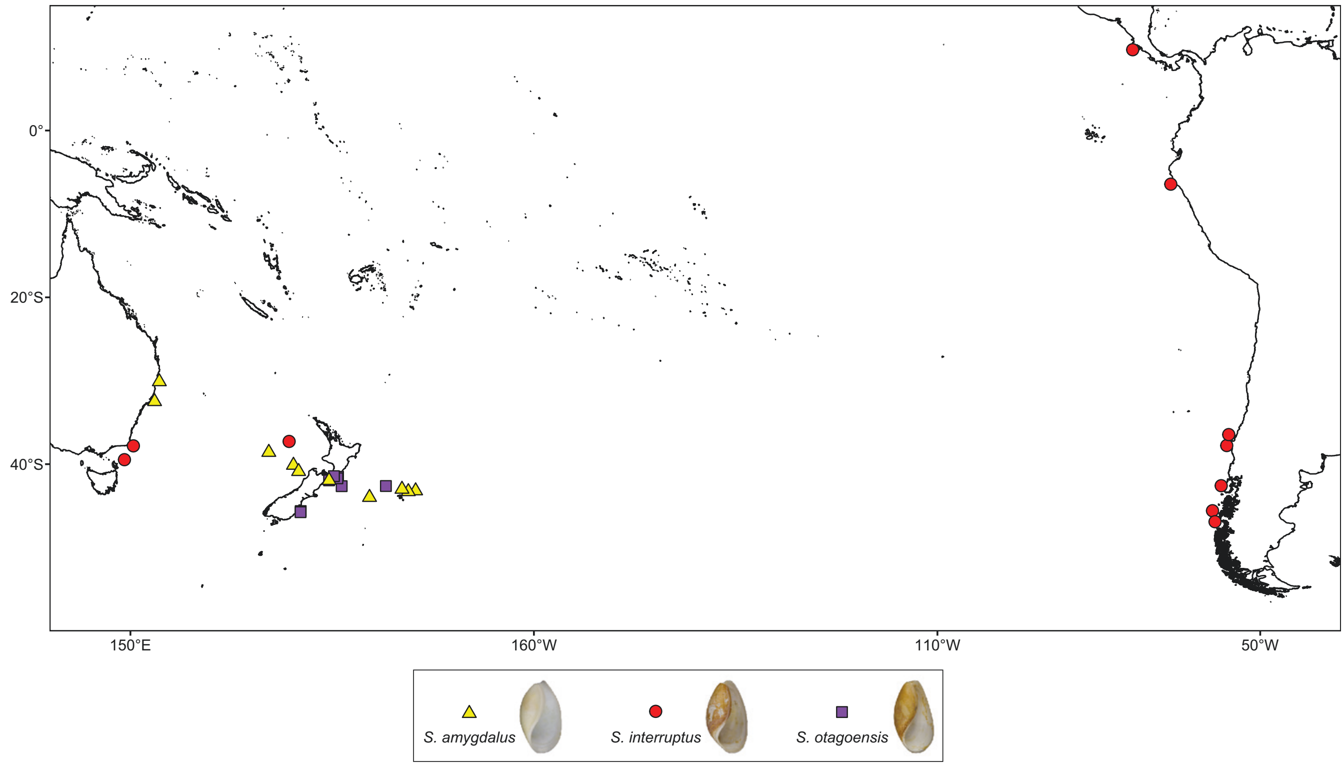

Figure 8. Geographical distribution of ***Scaphander amygdalus***, *Scaphander interruptus*, and *Scaphander otagoensis*. Geographical records are based on studied material and reliable literature records.

H = 22.7 mm; three sh., ZMBN 127897, H = 14.5–16.3 mm; south of Concepción, one spc., dissected and sequenced, SCBUCN-2837, H = 41.7 mm; west of Concepción, one spc., ZMBN 127898, H = 17.1 mm. **Peru**: west of Isla Lobos de Tierra, one sh., LACM 1974-18.4, H = 14 mm. **Panama**: off Azuero Peninsula, west of Punta Mala, one sh., MCZ 27921, H = 11 mm, images seen. **Costa Rica**: southwest of Punta Guiones, one sh., LACM 1973-109.5, H = 22 mm. **Australia**: Bass Strait, one spc., dissected and sequenced, AM C.590961, H = 23 mm; Victoria, East Gippsland Commonwealth Marine Reserve, one spc., dissected and sequenced, AM C.563068, H = 20 mm. **New Zealand**: Tasman Sea, 400 km west of the North Island, two sh. and 13 spcs, one sequenced, NIWA 30427, H = 10–18 mm.

Diagnosis: Shell pyramidal to elongate, covered by thick brown to thin dirty white periostracum. Spiral sculpture composed of ovoid punctations, mostly distinct but can be interconnected. Spire concealed. Posterior edge of outer lip rising slightly above apex. Rachidian teeth sub-rectangular. Prostate short, club-shaped. Penial papilla absent. Penial chamber lined with soft longitudinal ridges.

Shell (Fig. 6): Maximum H observed = 41.7 mm. Shell pyramidal to elongate, only one whorl visible. Aperture as long as shell, narrowing posteriorly. Spire concealed. Posterior edge of outer lip rounded, rising slightly above apex. Parietal wall covered with thick, smooth white callus, thinner in juvenile forms. Spiral sculpture composed of punctuated striations, alternating wider and narrower rows. Punctations ovoid or rectangular, distinct or interconnected. Periostracum transparent to pale yellow or light brown. Shell dirty white.

Radula (Fig. 7A–C): Radular formula 21 × 1.1.1 (H = 41.7 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth sub-rectangular, cusps slightly curved inward.

Digestive tract (Fig. 7D, E): Salivary glands short, thin, surface uneven. Gizzard plates kidney-shaped to sub-triangular.

Male reproductive system (Fig. 7F, G): Penial chamber cylindrical, lined with soft longitudinal ridges. Muscular papilla absent. Penial chamber separated from prostate by prostatic duct. Prostate short, club-shaped.

Ecology: Found between 497 and 2760 m depth (Dall 1890b, 1908; present study). Feeds on foraminifera (present study).

Distribution (Fig. 8): Southern Pacific, from Chile to Costa Rica (Dall 1890b, Valdés and McLean 2015; present study), Southern Australia to Northwestern New Zealand (present study).

Remarks: Scaphander interruptus is, with *S. grandis* and *Scaphander willetti* Dall, 1919, one of the only three known *Scaphander* species in the Eastern Pacific. However, the distribution ranges of the two species do not seem to overlap, with *S. willetti* known only from Southern Alaska, *S. grandis* known to occupy the Northern Pacific downwards to California, and *S. interruptus* present in southern latitudes between Chile and Costa Rica. Furthermore, the presence of a visible spire in *S. grandis* makes it unmistakable with *S. interruptus*.

Our study revealed the presence of *S. interruptus* in the Tasman Sea, between Southeastern Australia and New Zealand. *Scaphander interruptus* can be differentiated from congenerics *S. otagoensis* and *Scaphander amygdalus* that also inhabit Trans-Tasman waters by its narrower, more elongate shell shape, a translucent periostracum rather than cream or yellow-brown in colour, in addition to a parietal callus significantly less marked than in the other two species. The rachidian teeth in *S. interruptus* have straighter edges that do not bend outwards at the upper cusps as in *S. otagoensis* and lack the acute corners and wider shape of the rachidian in *S. amygdalus*. The male reproductive system in *S. interruptus* is also distinct, because no warts line the deeper part of the penial chamber (see *S. otagoensis* and *S. amygdalus* sections). Furthermore, the three species are genetically distinct, with high uncorrected *p*-distances for *COI* between them: 10.14%–11.76% between *S. interruptus* and *S. amygdalus*, 9.01%–10.03% between *S. interruptus* and *S. otagoensis*, and 11.91%–13.39% between *S. otagoensis* and *S. amygdalus* (Supporting Information, Table S2).

Scaphander andamanicus Smith, 1894

(Figs 9, 10; Table 2)

Scaphander andamanicus Smith, 1894: 167, pl. 4, fig. 15; Pilsbry 1895: 235, frontispiece, fig. 18; Kobelt 1896: 9, pl. 5, fig. 10; Smith 1904: 5; 1906: 247; Annandale and Stewart 1909: pl. 19, figs 7, 8.

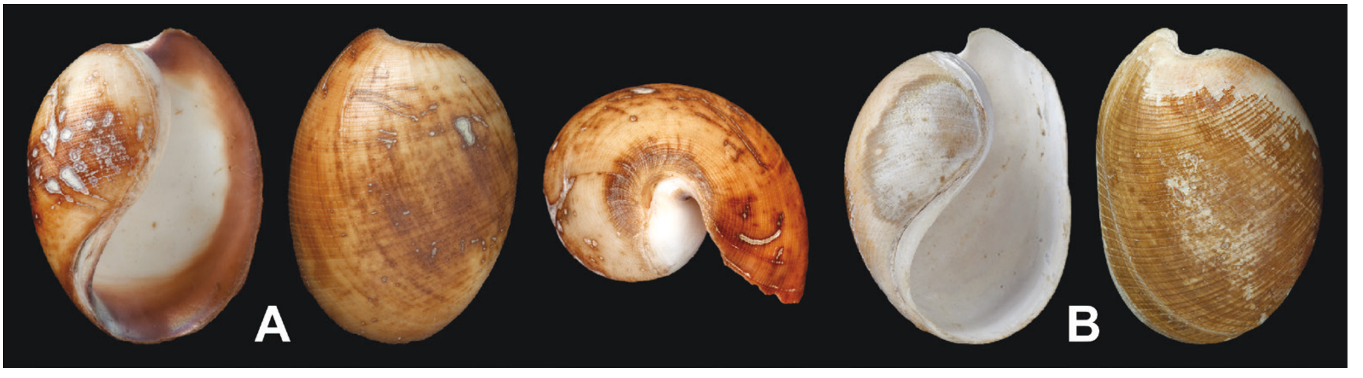

Figure 9. Shells of *Scaphander andamanicus*. A, Andaman Sea (paratype, NHMUK 1894.9.11.31, H = 24 mm, images courtesy of the NHMUK). B, south of Sri Lanka (NHMUK 1906.10.12.69-70, H = 24 mm, images courtesy of the NHMUK).

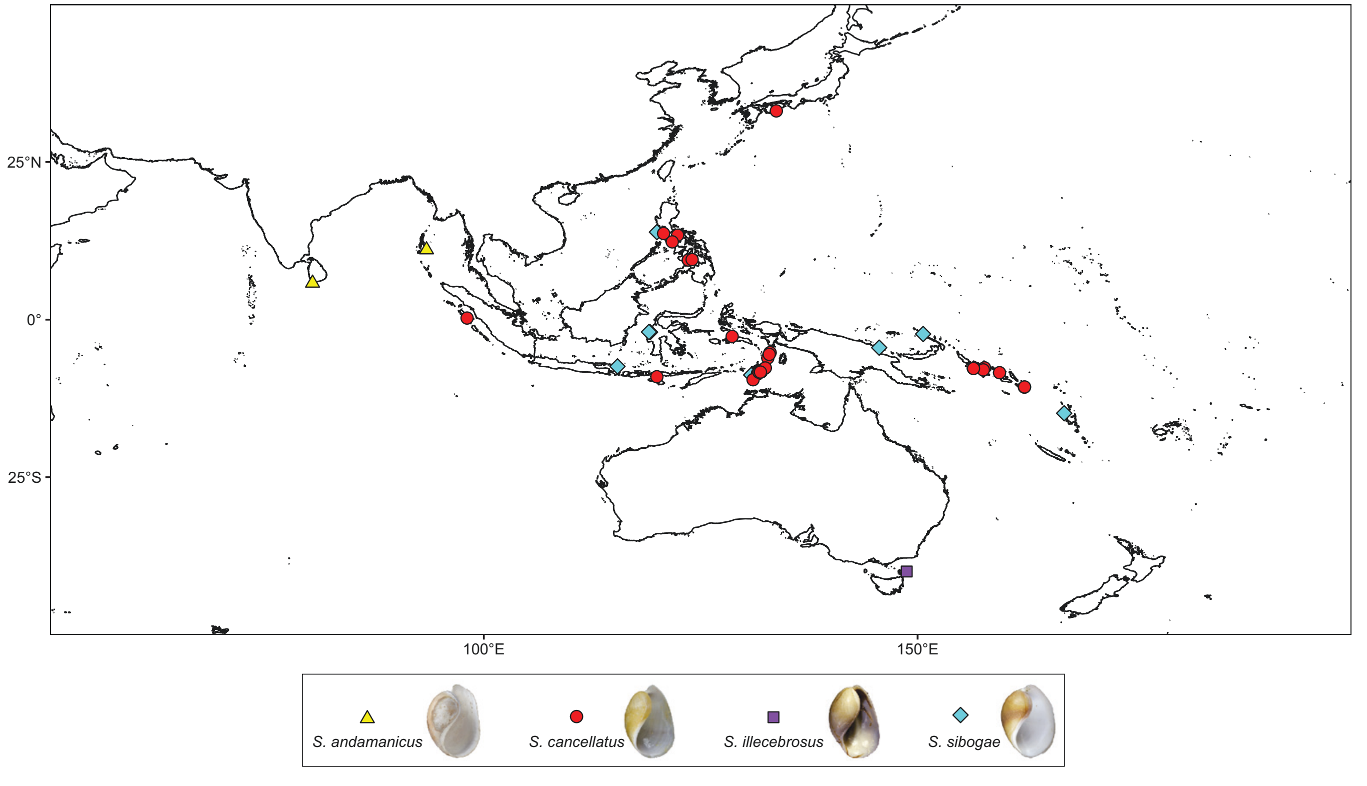

Figure 10. Geographical distribution of *Scaphander andamanicus*, *Scaphander cancellatus, Scaphander illecebrosus*, and *Scaphander sibogae*. Geographical records are based on studied material and reliable literature records.

Taxonomic history: Scaphander andamanicus was described from a shell collected by the *Investigator* in the Andaman Sea (Smith 1894). Several additional shells were later recorded from the Bay of Bengal and the Andaman Sea from material collected during the same expedition (Smith 1904, 1906).

Type material: Scaphander andamanicus Smith, 1894—**India**: Andaman Sea, 457 m, holotype, *NZSI M.5271*, H = 18 mm; one paratype, NHMUK 1894.9.11.31, H = 24 mm, images seen (Fig. 9A).

Other material examined: **Sri Lanka**: south of Ceylon, 1207 m, four sh., NHMUK 1906.10.12.69-70, H = 18–25 mm, images seen (Fig. 9B).

Diagnosis: Shell external, ovate, orange to dark reddish brown. Spiral sculpture composed of punctations, distinct or interconnected. Apex rounded, with posterior edge of outer lip rising above it in a wing.

Shell (Fig. 9): Maximum H observed = 24 mm. Shell ovoid to rounded, only one whorl visible. Aperture wide, as long as shell, narrowing posteriorly. Apex rounded, spire concealed. Posterior edge of outer lip protruding beyond apex in a small wing. Parietal wall covered with thick, smooth white callus. Spiral sculpture composed of punctuated striations. Punctations ovoid to subrectangular pits, close together, sometimes interconnected. Periostracum orange to dark reddish-brown. Shell white.

Radula: Unknown.

Digestive tract: Unknown.

Male reproductive system: Unknown.

Ecology: Found between 338 and 1714 m depth. Feeding habits unknown.

Distribution (Fig. 10): Andaman Sea (Smith 1894) and Bay of Bengal (Smith 1904, 1906).

Remarks: This species is known from a few shells only and bears a strong resemblance to *Scaphander sibogae* Schepman, 1913; however, the type and original description of *S. andamanicus* present a wing-like posterior lip, but less sharp than the one of *S. sibogae*. Furthermore, given that distinct species of *Scaphander* can have remarkably similar shells (see *S. otagoensis*, *S. interruptus*, and *S. amygdalus* sections) and that there are no records of *S. sibogae* westwards of Indonesia, both species are kept as valid. Future sampling in the Bay of Bengal might revise this hypothesis, in which case *S. andamanicus* would become the senior synonym of *S. sibogae*.

Scaphander cancellatus Martens, 1902

(Figs 10–13; Table 2)

Scaphander cancellatus Martens, 1902: 244; 1903: 131–133, pl. 5, fig. 19; Smith 1906: 247–248.

Scaphander subglobosa Schepman, 1913: 466; Valdés 2008: 678, figs 43, 44C–G, 45D–F.

Scaphander subglobosus Schepman, 1913: pl. 32, fig. 1; Poppe 2010: pl. 760, fig. 3.

Scaphander attenuatus Schepman, 1913: 465, pl. 31, fig. 11.

Bucconia attenuata—Habe 1955: 69.

Nipponoscaphander teramachii Kuroda & Habe, 1971 (in Kuroda *et al.* 1971): 293, pl. 64, fig. 27.

Taxonomic history: The species *S. cancellatus* was described by Martens (1902) from shells collected in Indonesia during the *Valdivia* expedition. Later, Schepman (1913) described *S. subglobosa*, *S. attenuatus*, and *S. sibogae*, also based on empty shells collected in Indonesia during the *Siboga* expedition. Valdés (2008) redescribed *S. subglobosa* and included details about the digestive system, but did not refer to the reproductive system. In addition, Valdés (2008) redescribed *S. sibogae* and considered *S. attenuatus* a synonym. Chaban *et al.* (2019a) subsequently used the name *S. attenuatus* to designate *S. sibogae*. However, the examination of the type material and original descriptions for these three species (present work) showed that *S. subglobosa* and *S. attenuatus* are both junior synonyms of *S. cancellatus* (Fig. 11), and a distinct species from *S. sibogae* (see *S. sibogae* section). *Scaphander cancellatus* was reported from Japan as *B. attenuata* by Habe (1955), but was later depicted as *N. teramachii* by Kuroda and Habe (in Kuroda *et al.* 1971).

Type material: Scaphander cancellatus Martens, 1902—**Indonesia**: west of Sumatra, Pulau Nias, *Valdivia* expedition, station 199, 0°15'00"N, 98°04'00"E, 470 m, one type, ZMB Moll 60055, H = 24.6 mm, images seen (Fig. 11A). *Scaphander attenuatus* Schepman, 1913—**Indonesia**: Nusa Tenggara Timur, Laut Sawu, *Siboga* expedition, station 52, 9°3'24"S, 119°56'42"E, 959 m, four syntypes, ZMA.MOLL.138504, H = 23 mm, images seen (Fig. 11C). *Scaphander subglobosus* Schepman, 1913—**Indonesia**: Maluku, Laut Seram, *Siboga* expedition, station 178, 2°40'00"S, 128°37'30"E, 835 m, one syntype, ZMA.MOLL.137604, H = 28 mm, images seen (Fig. 11B).

Other material examined: **Indonesia**: Tanimbar Islands, one sh., MNHN-IM-2010-2086, H = 28 mm; one spc., dissected and sequenced, MNHN-IM-2019-7925, H = 27 mm; one spc., dissected, MNHN-IM-2019-7931, H = 28 mm; one spc., MNHN-IM-2019-7928, H = 26 mm; one spc., MNHN-IM-2019-7929, H = 27 mm; one spc., MNHN-IM-2019-7927, H = 21 mm; one spc., dissected, MNHN-IM-2019-7930 H = 26.5 mm. **Papua New Guinea**: Kimbe Bay, one sh., MNHN-IM-2016-5759, H = 30 mm. **Philippines**: east of Marinduque, two sh., MNHN-IM-2010-2090, H = 21, 22 mm; Bohol Sea, off Balicasag Island, one spc., sequenced, MNHN-IM-2007-35413, H = 26 mm; Bohol Sea, one sh. plus DNA aliquot, sequenced, MNHN-IM-2007-35412, H = 17 mm; one spc., sequenced, MNHN-IM-2009-4339, H = 24 mm; one spc., MNHN-IM-2013-52485, H = 25 mm. **Solomon Islands**: west of Vella Lavella, one spc., dissected and sequenced, MNHN-IM-2013-52474, H = 32 mm; one spc., MNHN-IM-2013-52470, H = 31.4 mm; one spc., MNHN-IM-2019-11709, shell greatly damaged; one spc., MNHN-IM-2019-11710, H = 27.7 mm; one spc., MNHN-IM-2019-11711, H = 32.1 mm; one spc., MNHN-IM-2019-11712, H = 30 mm; one spc., MNHN-IM-2013-52473, H = 34.5 mm; east of San Cristobal, one spc., dissected and sequenced, MNHN-IM-2009-6678,

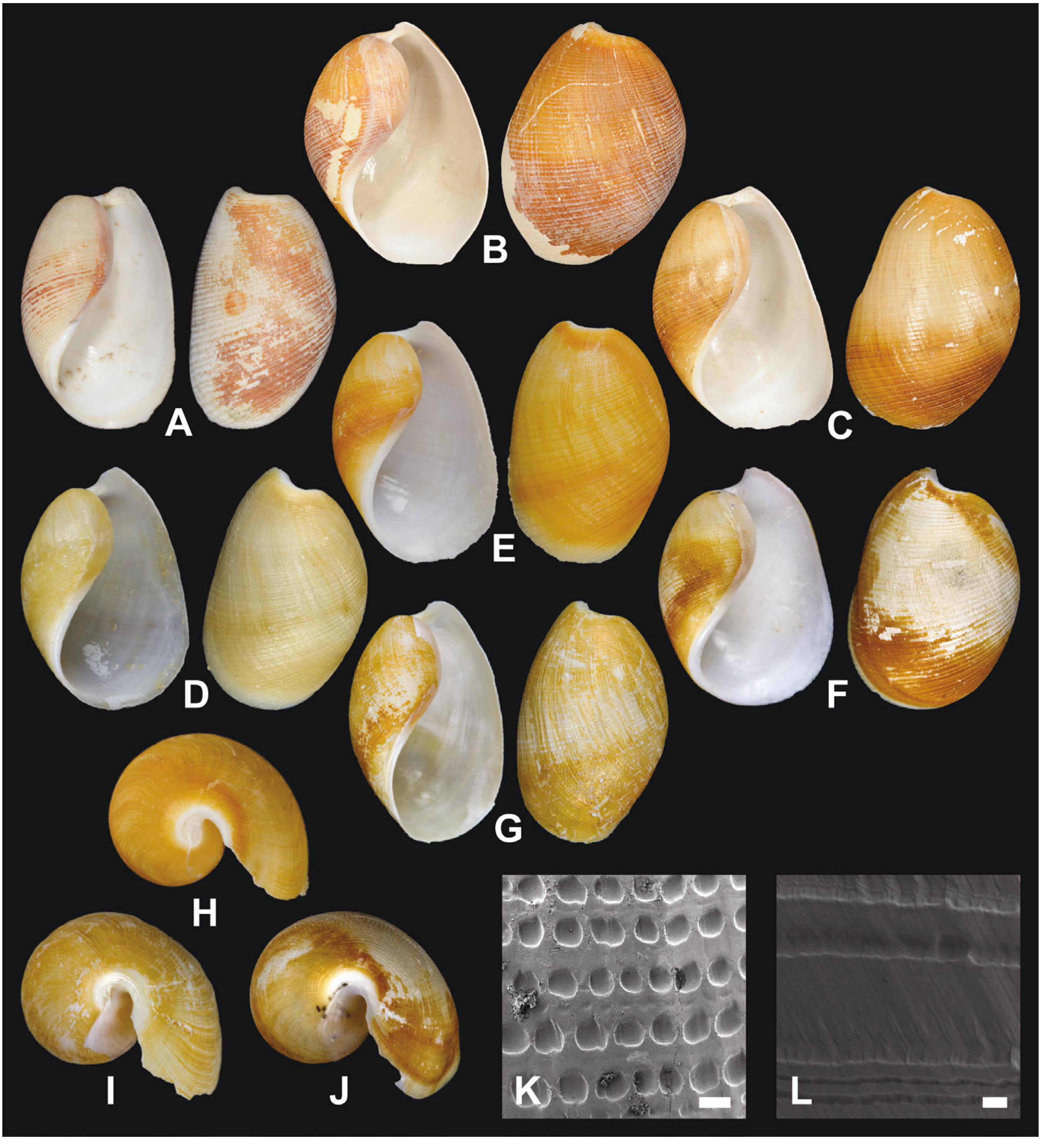

Figure 11. Shells and SEM images of the shell sculpture of *Scaphander cancellatus*. A, Indonesia, west of Sumatra, Pulau Nias (type, ZMB Moll 60055, H = 24.6 mm). B, Indonesia, Maluku, Laut Seram (syntype, *Scaphander subglobosus*, ZMA.MOLL.137604, H = 28 mm; images taken by K. Hasegawa and courtesy of Naturalis Biodiversity Center). C, Indonesia, Nusa Tenggara Timur, Laut Sawu (syntype, *Scaphander attenuatus*, ZMA.MOLL.138504, H = 23 mm; images taken by K. Hasegawa and courtesy of Naturalis Biodiversity Center). D, Solomon Islands, west of Vella Lavella (MNHN-IM-2013-52474, H = 32 mm). E, Solomon Islands, southwest of Santa Isabel (MNHN-IM-2013-52472, H = 30 mm). F, Philippines, Bohol Sea, off Balicasag Island (MNHN-IM-2007-35413, H = 26 mm). G, Japan, Tosa Bay (NSMT Mo-90588, H = 26 mm). H, Solomon Islands, southwest of Santa Isabel (MNHN-IM-2013-52472, H = 30 mm). I, Japan, Tosa Bay (NSMT Mo-90588, H = 26 mm). J, Philippines, Bohol Sea, off Balicasag Island (MNHN-IM-2007-35413, H = 26 mm). K, Solomon Islands, east of San Cristobal (MNHN-IM-2009-6686, H = 12 mm). L, Solomon Islands, southwest of Santa Isabel (MNHN-IM-2013-52472, H = 30 mm). Scale bars: K, L = 200 μm.

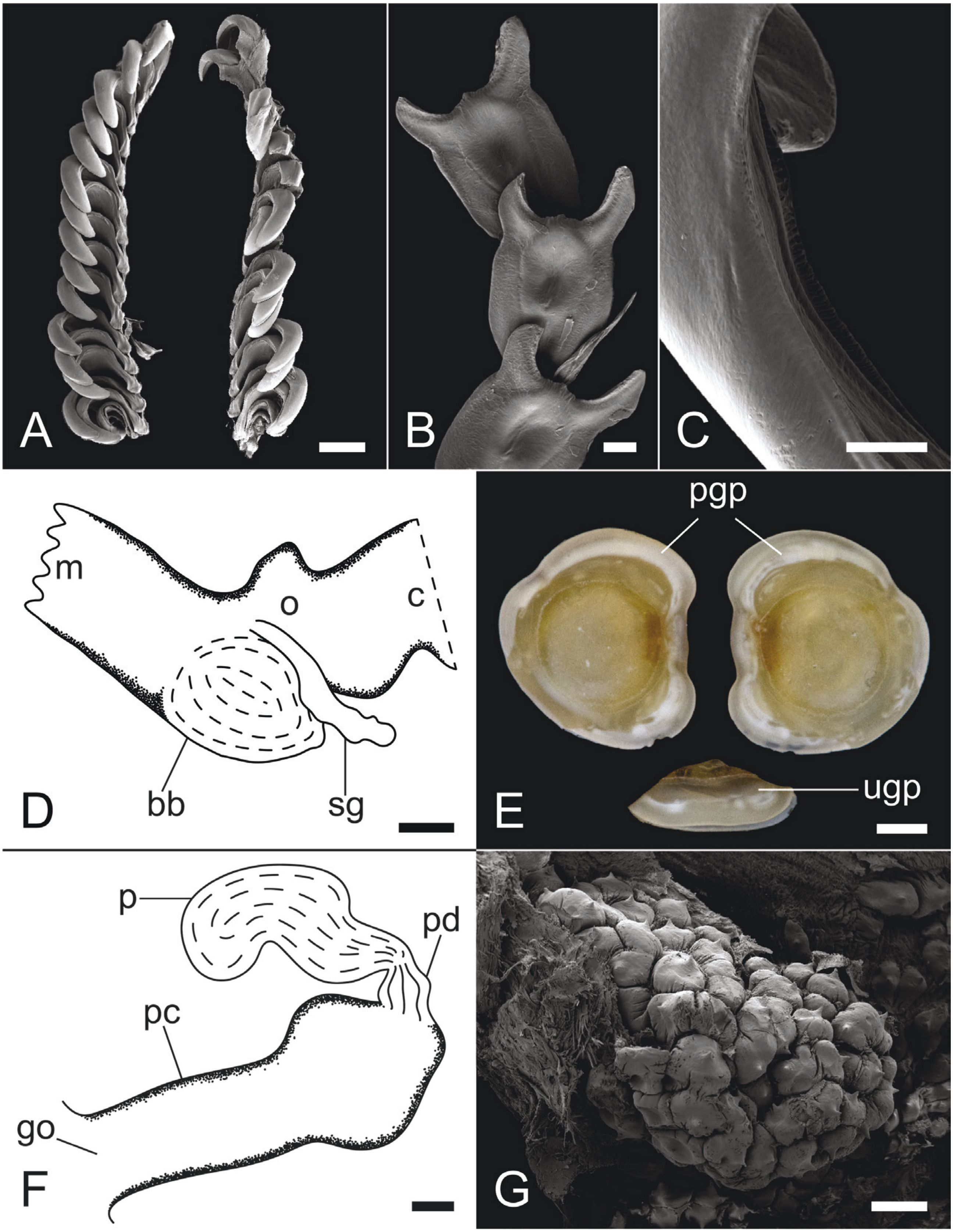

Figure 12. Anatomical details of *Scaphander cancellatus*. A, radula, Solomon Islands, west of Vella Lavella (MNHN-IM-2013-52474, H = 32 mm). B, rachidian teeth, Solomon Islands, east of San Cristobal (MNHN-IM-2009-6678, H = 18 mm). C, detail of lateral teeth, Indonesia, Tanimbar Islands (MNHN-IM-2019-7931, H = 28 mm). D, anterior part of digestive tract, Indonesia, Tanimbar Islands (MNHN-IM-2019-7925, H = 27 mm). E, gizzard plates (MNHN-IM-2019-7925, H = 27 mm). F, male reproductive system (MNHN-IM-2019-7925, H = 27 mm). G, lining of penial chamber, Japan, Tosa Bay (NSMT Mo-90588, H = 31 mm). Scale bars: A = 200 μm; B, C = 20 μm; D = 1 mm; E, F = 2 mm; G = 400 μm.

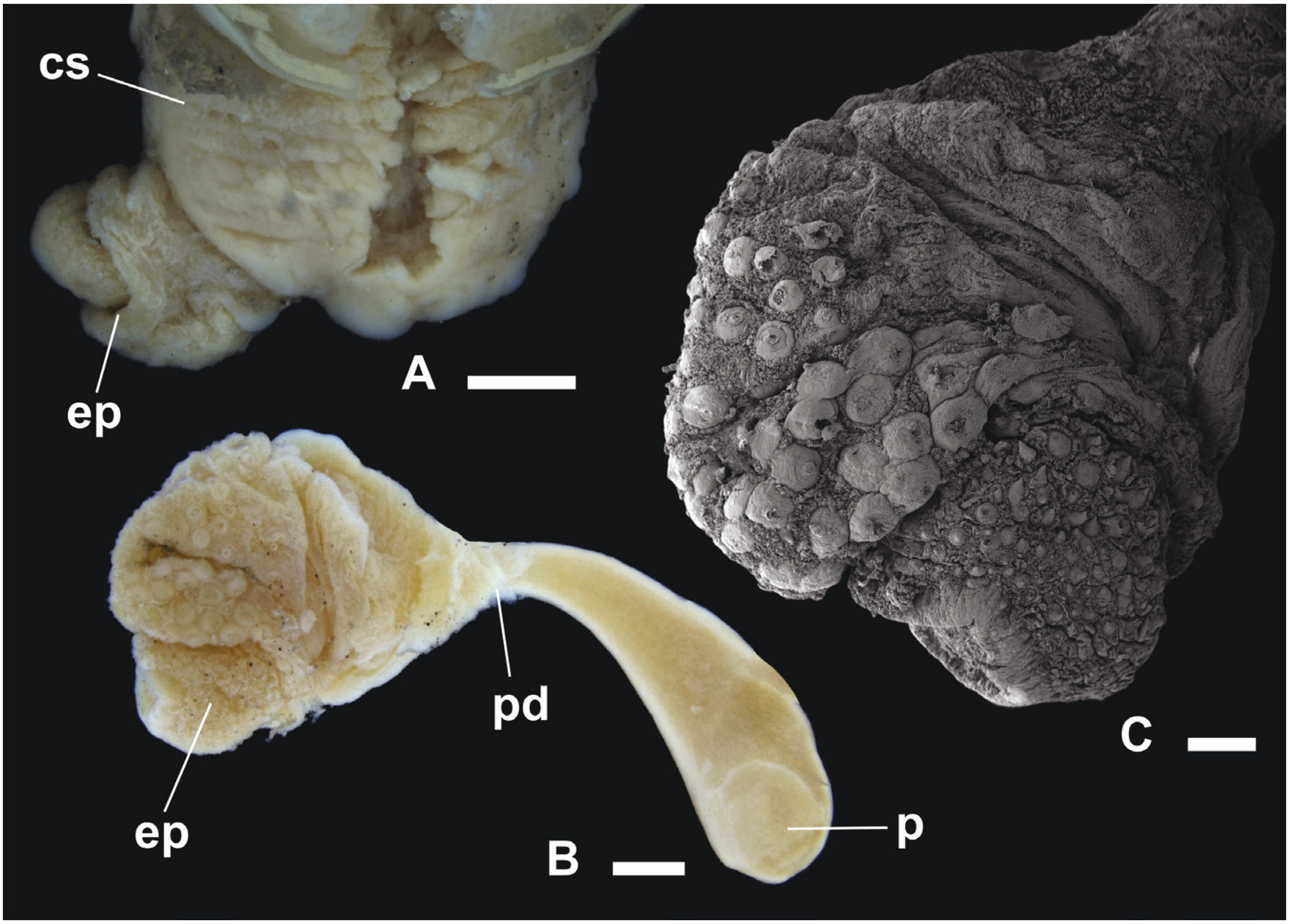

Figure 13. Anatomical details of *Scaphander cancellatus*, Japan, Tosa Bay (NSMT Mo-90588, H = 26 mm). A, dorso-anterior view of the dissected animal, with visible longitudinal incision across the cephalic shield made to access the interior of the body cavity. On the left side, part of the male reproductive system everted through the genital opening can be observed. B, complete male reproductive system. C, SEM detail of the everted warty walls of the penial chamber. Scale bars: A = 2 mm; B = 1 mm; C = 400 μm.

H = 18 mm; one spc., sequenced, MNHN-IM-2009-6686, H = 12 mm; northwest of Santa Isabel, one spc., dissected, MNHN-IM-2013-52475, H = 24 mm; southeast of Choiseul, one spc., MNHN-IM-2013-52476, H = 28 mm; southwest of Santa Isabel, one spc., dissected and sequenced, MNHN-IM-2013-52472, H = 30 mm; southeast of Santa Isabel, one spc., MNHN-IM-2013-52479, H = 29 mm; New Georgia, one spc., sequenced, MNHN-IM-2013-52478, H = 18 mm. **Japan**: Kochi-ken, two sh., NSMT Mo-38721, H = 10.1–10.5 mm; Enshu-nada, four sh., NSMT Mo-55818, H = 15.1–17.9 mm; Tosa Bay, four spcs, NSMT Mo-90577, H = 6–14 mm; 14 spcs, NSMT Mo-90582, H = 6–11.5 mm; seven spcs, two dissected, NSMT Mo-90588, H = 16–31 mm; four spcs, NSMT Mo-90591, H = 27–31 mm.

Diagnosis: Shell ovoid to sub-rectangular, periostracum pale yellow to warm orange. Spiral sculpture composed of ovoid to sub-rectangular punctations, often interconnected and forming punctuated grooves. Apex rounded; posterior edge of outer lip wing-like, rounded or curved, rising above apex. Rachidian teeth elongate, with curved upper cusps. Prostate cylindrical, separated from penial chamber by short prostatic duct. Penial chamber bulged distally near prostatic duct; globose region lined internally with soft warts.

Shell (Fig. 11): Maximum H observed = 34 mm. Shell ovoid to sub-rectangular; only one whorl visible. Aperture wide, as long as shell, narrowing posteriorly. Apex rounded; spire concealed. Posterior edge of outer lip wing-like, rounded, rising beyond apex. Parietal wall covered with callus; thick, smooth, white in anterior half; thin to inconspicuous in posterior half. Spiral sculpture composed of punctuated striations or grooves. Punctations ovoid to sub-rectangular pits, distinct from one another or interconnected, forming spiral grooves of uneven width. Periostracum pale yellow to warm orange. Shell dirty white.

Radula (Fig. 12A–C): Radular formula 21 × 1.1.1 (H = 28 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth elongate, with developed upper cusps curved inwards, with curved, pointed, developed upper cusps.

Digestive tract (Fig. 12D, E): Salivary glands medium long, surface uneven. Paired gizzard plates rounded kidney-shaped.

Male reproductive system (*Figs 12F, G, 13*)*:* Penial chamber cylindrical, bulged towards prostatic duct; globose region lined with warts. Muscular penial papilla absent. Penial chamber separated from prostate by short prostatic duct, widening towards prostate. Prostate cylindrical, rounded at distal end.

Ecology: Found between 440 and 869 m depth. Feeds on foraminifera (calcareous and agglutinating), tubicolous polychaetes, and small gastropods (present study).

Distribution (*Fig. 10*)*:* Western Pacific Ocean, from Indonesia (Schepman 1913; present study), the Philippines (Valdés 2008; present study), Papua New Guinea, Solomon Islands (present study), and Japan (Habe 1955, Kuroda *et al.* 1971; present study).

Remarks: There is remarkable variability in the morphology of this species (Fig. 11); the shell can be elongate, sub-rectangular, or wider and ovate, with the posterior outer lip wing-like and rounded, or significantly longer and acutely curved. This, for example, led to historical taxonomic confusion between *S. cancellatus* and *S. sibogae* (e.g. Valdés 2008, Chaban *et al.* 2019a). However, the shell of *S. sibogae* is rounder and has a thicker parietal callus (see Table 2).

It was not possible to obtain DNA sequences from Japanese specimens, and their occurrence in Japan is therefore confirmed here based only on shell and morphological characters. Around Japan, rounder shells of *S. cancellatus* can be confused with *E. fragilis*, but these two species are easily separated by their anatomy, because *E. fragilis* contains only two oval calcareous plates instead of the three plates that are characteristic of the genus *Scaphander* (Siegwald *et al.* 2022). Their shells can also be distinguished from each other, with adult shells of *E. fragilis* being larger and more inflated, with the posterior end being less rounded.

A dissected specimen from Japan had part of the male reproductive system everted (Fig. 13), exposing the warts lining the interior of the penial chamber. This suggests that this part of the reproductive system is likely to be used functionally as a copulatory organ.

Scaphander planeticus Dall, 1908

(**Figs 14, 15; Table 2**)

Scaphander (*Sabatina*) *planeticus* Dall, 1908: 241.

Taxonomic history: Scaphander planeticus was described by Dall (1908) based on one juvenile specimen collected in the Central Pacific Ocean during the *Albatross* expedition. Dall (1908) designated it as the type for his new subgenus *Sabatina*, which he created to separate extant *Scaphander* species with strong parietal callus from similar fossil species. Only one specimen has ever been recorded.

Type material: Scaphander (*Sabatina*) *planeticus* Dall, 1908—**Central Pacific Ocean**: *Albatross* expedition, station 3684, 0°50′00"N, 137°54′00"W, 4504 m, holotype, *USNM 110748*, H = 8 mm, images seen (Fig. 14A).

Figure 14. Shell of *Scaphander planeticus* (A), *Scaphander tortuosus* (B), and *Scaphander imperceptus* (C, D). A, Northern Pacific Ocean, north of Marquesas Islands (holotype, *Scaphander* (*Sabatina*) *planeticus*, *USNM 110748*, H = 8 mm, images courtesy of the USNM). B, Indonesia, Sulawesi (holotype *Meloscaphander sibogae*, *ZMA.MOLL.136944*, H = 16 mm; images taken by K. Hasegawa and courtesy of Naturalis Biodiversity Center). C, Northeastern Atlantic, northeast of the Azores (syntype, *Bulla millepunctata*, MNHN-IM-2000-27696, H = 14.8 mm, images courtesy of the MNHN). D, Northeastern Atlantic, off Mauritania (holotype, *Meloscaphander imperceptus*, *MNHN-IM-2000-27680*, H = 19.3 mm, images courtesy of the MNHN).

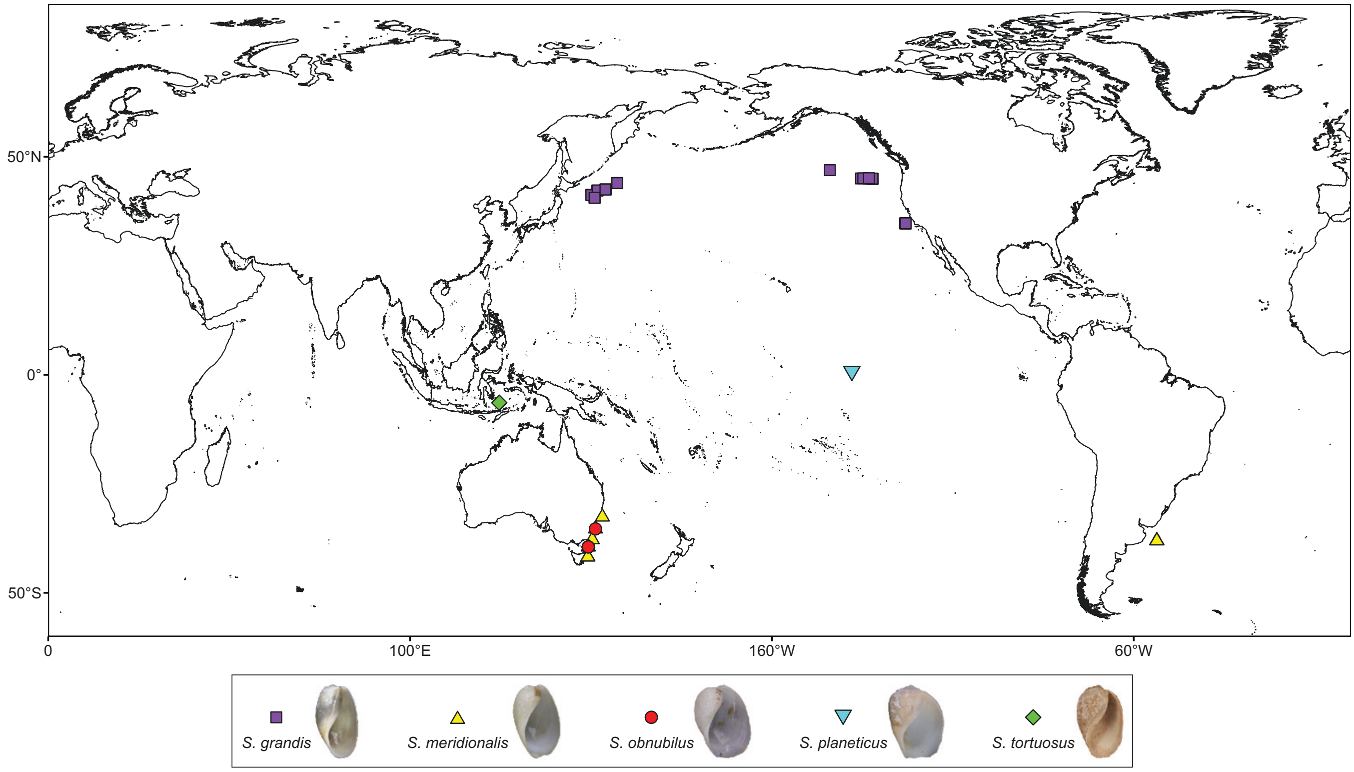

Figure 15. Geographical distribution of *Scaphander grandis*, *Scaphander meridionalis*, ***Scaphander obnubilus***, *Scaphander planeticus*, and *Scaphander tortuosus*. Geographical records are based on studied material and reliable literature records.

Diagnosis: Shell ovoid, white, inflated posteriorly. Small, raised spire. Spiral sculpture composed of punctuated striations.

Shell (Fig. 14): Max H observed = 8 mm. Shell ovoid, wider towards posterior end. Aperture wide, nearly as long as shell, narrowing posteriorly. Small raised spire of three whorls. Shallow suture partly separating spire from body whorl, widening in a narrow groove along uppermost part of parietal wall. Posterior edge of outer lip joining body whorl immediately below spire in rounded shoulder. Parietal wall covered with thick, smooth white callus. Spiral sculpture composed of punctuated striations.

Radula: Unknown.

Digestive tract: Gizzard plates 'of the same type as those of *S. lignarius*' (Dall 1908).

Male reproductive system: Unknown.

Ecology: Found at 4504 m. Feeding habits unknown.

Distribution (Fig. 15): Central Pacific (0°50′N, 137°54′W).

Remarks: To our knowledge, the holotype is the only specimen that has been sampled for this species. The general shape of the shell, and the raised spire in particular, would suggest close relationships with *S. grandis* and *S. tortuosus*, but it is difficult to assess the status of these relationships without additional anatomical or molecular information.

Scaphander sibogae Schepman, 1913

(**Figs 10, 16, 17; Table 2**)

Scaphander sibogae Schepman, 1913: 465, pl. 31, fig. 10; Valdés 2008: 677, figs 43, 44A, B, 45A–C.

Scaphander attenuatus—Valdés 2008: 677; Chaban *et al.* 2019a: 397.

Taxonomic history: Based on empty shells collected in Indonesia during the *Siboga* expedition, Schepman (1913) described the species *S. attenuatus*, *S. sibogae*, *S. subglobosus*, and a fourth species from a complete specimen, which he also named '*sibogae*' but ascribed to the new genus *Meloscaphander* Schepman, 1913 as *Meloscaphander sibogae* Schepman, 1913. Valdés (2008) considered *S. attenuatus* a synonym of *S. sibogae* because of similarities in their original descriptions and type material, but as discussed earlier (see *S. cancellatus* section) we provide evidence that *S. attenuatus* is, in fact, a synonym of *S. cancellatus*. Chaban *et al.* (2019a) suggested *Meloscaphander* to be a junior synonym of *Scaphander*, which was confirmed by Siegwald *et al.* (2022). This led Chaban *et al.* (2019a) to consider *M. sibogae* Schepman, 1913 a secondary homonym of *S. sibogae* Schepman, 1913 and to suggest the name *S. attenuatus* as the valid replacement name for *S. sibogae* Schepman, 1913. However, in our opinion this was a misinterpretation of art. 23.3.5 of the Code (ICZN 1999a,b), because the unavailable name would have been *S. sibogae* (Schepman, 1913), i.e. the name resulting from the synonymizing of *Meloscaphander* and *Scaphander*. Therefore, in accordance with ICZN (1999a: art. 23.3.5.) we consider the species name *S. sibogae* Schepman, 1913 available and the name *S. sibogae* (Schepman, 1913) [= *Meloscaphander sibogae* Schepman, 1913], unavailable. Given that no synonym names are available for the homonym name *S. sibogae* (Schepman, 1913), we introduce the replacement name *Scaphander tortuosus* nom. nov. (ICZN 1999a,b: arts 23.3.5. and 60.3.; see *S. tortuosus* nom. nov. section for further details).

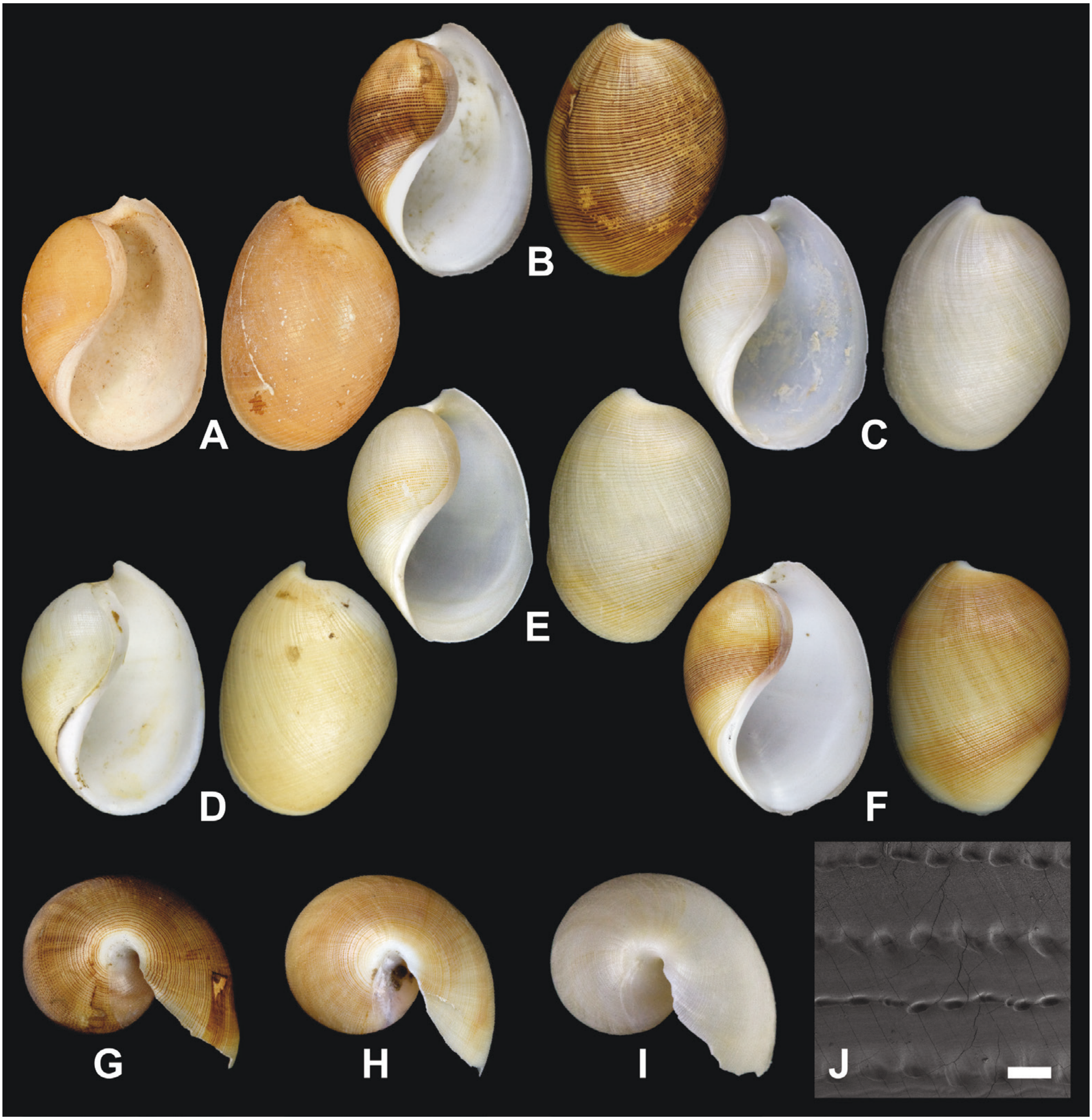

Figure 16. Shells and SEM image of the shell sculpture of *Scaphander sibogae*. A, Indonesia, Bali (syntype, ZMA.MOLL.138503, H = 25 mm; images taken by K. Hasegawa and courtesy of Naturalis Biodiversity Center). B, Indonesia, Sulawesi, Makassar Strait (MNHN-IM-2010-2080, H = 24 mm). C, Solomon Islands, northwest of Isabel (MNHN-IM-2013-52471, H = 25 mm). D, Vanuatu, Santo, Big Bay (MNHN-IM-2019-7918, H = 34 mm). E, Indonesia, Tanimbar Islands (MNHN-IM-2019-7926, H = 30 mm). F, Papua New Guinea, east of Kotakot (MNHN-IM-2013-18549, H = 31 mm). G, Indonesia, Sulawesi, Makassar Strait (MNHN-IM-2010-2080, H = 24 mm). H, Papua New Guinea, east of Kotakot (MNHN-IM-2013-18549, H = 31 mm). I, Solomon Islands, northwest of Isabel (MNHN-IM-2013-52471, H = 25 mm). J, Vanuatu, Santo, Big Bay (MNHN-IM-2019-11719, H = 32 mm). Scale bar: J = 200 µm.

Type material: Scaphander sibogae Schepman, 1913—**Indonesia**: Bali, *Siboga* expedition, station 18, 7°25'12"S, 115°24'36"E, 1018 m, 15 syntypes, ZMA.MOLL.138503, H = 25 mm, images seen (Fig. 16A).

Other material examined: **Indonesia**: Tanimbar Islands, one spc., dissected, MNHN-IM-2019-7926, H = 30 mm; Sulawesi, Makassar Strait, one sh., MNHN-IM-2010-2080, H = 24 mm. **Papua New Guinea**: New Ireland, one spc., sequenced, MNHN-IM-2013-58331, H = 34 mm; east of Kotakot, one spc., dissected and sequenced MNHN-IM-2013-18549, H = 31 mm. **Solomon Islands**: northwest of Isabel Island, one spc., MNHN-IM-2019-7921, H = 27 mm; one spc., MNHN-IM-2019-11713, H = 21 mm; one spc., MNHN-IM-2019-11714, H = 25 mm; one

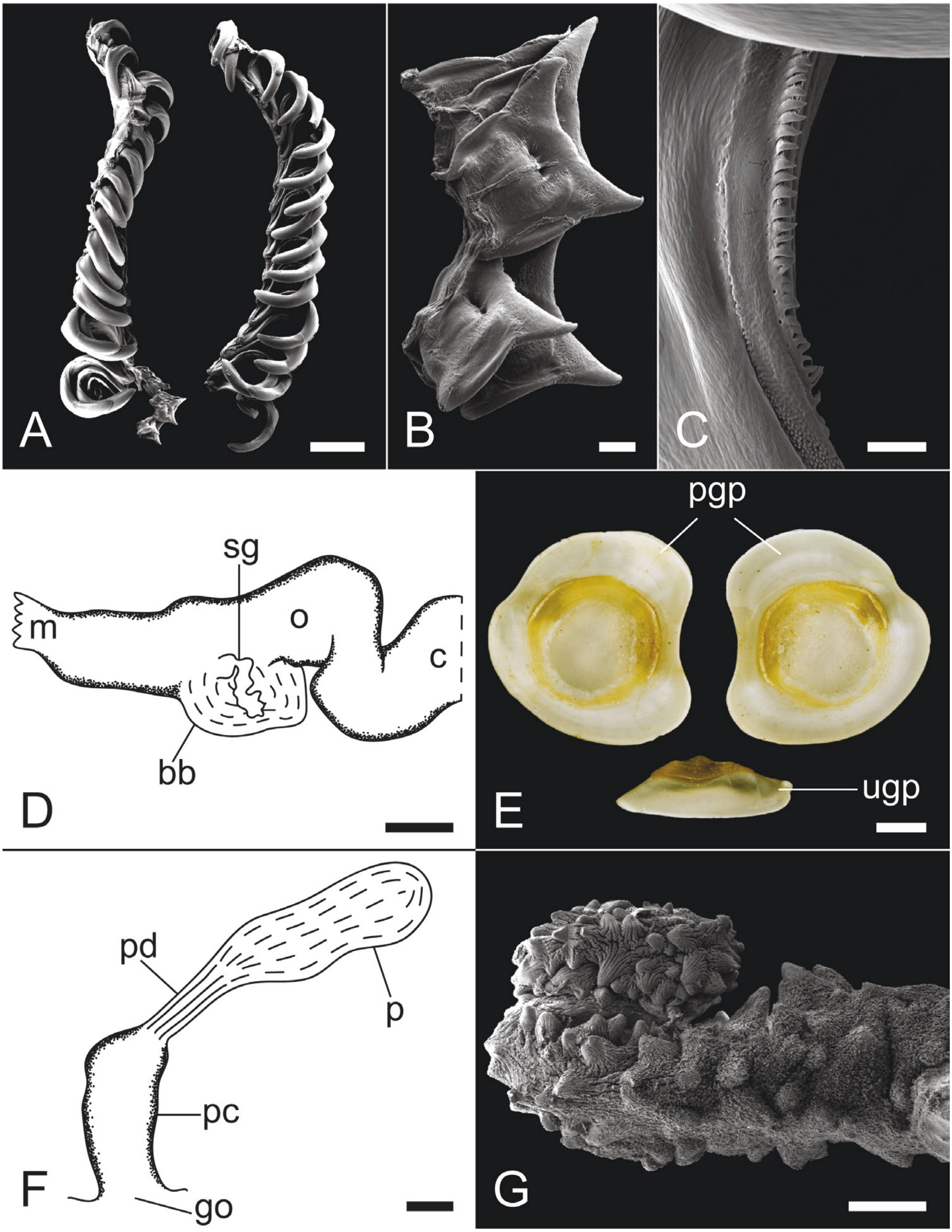

Figure 17. Anatomical details of *Scaphander sibogae*. A, radula, Solomon Islands, New Georgia (MNHN-IM-2013-52477, H = 20 mm). B, rachidian teeth (MNHN-IM-2013-52477, H = 20 mm). C, detail of lateral teeth, Solomon Islands, northwest of Isabel (MNHN-IM-2013-52471, H = 25 mm). D, anterior part of digestive tract (MNHN-IM-2013-52477, H = 20 mm). E, gizzard plates, Papua New Guinea, east of Kotakot (MNHN-IM-2013-18549, H = 31 mm). F, male reproductive system (MNHN-IM-2013-52471, H = 25 mm). G, penial papilla (MNHN-IM-2013-18549, H = 31 mm). Scale bars: A, G = 200 μm; B = 20 μm; C = 10 μm; D, F = 1 mm; E = 2 mm.

spc., MNHN-IM-2019-11715, H = 19 mm; one spc., MNHN-IM-2019-11716, H = 24 mm; one spc., MNHN-IM-2019-11717, H = 23 mm; one spc., MNHN-IM-2019-11718, H = 24.5 mm; one spc., sequenced, MNHN-IM-2013-52471, H = 25 mm; New Georgia, one spc., dissected and sequenced, MNHN-IM-2013-52477, H = 20 mm; one spc., sequenced, MNHN-IM-2019-7922, H = 17 mm. **Vanuatu**: Santo, Big Bay, one spc., sequenced, MNHN-IM-2019-7918, H = 34 mm; one spc., MNHN-IM-2019-11719, H = 32 mm.

Diagnosis: Shell rounded ovate, orange brown to dirty white. Spiral sculpture composed of darker brown ovoid punctations, often slightly interconnected. Apex rounded, with posterior edge of outer lip rising above it in a sharp wing. Rachidian teeth tetragonal. Prostate cylindrical, separated from penial chamber by thin prostatic duct. Thin penial papilla covered in soft warts and wrinkles.

Shell (Fig. 16): Maximum H observed = 38 mm. Shell ovoid to rounded, only one whorl visible. Aperture wide, as long as shell, narrowing posteriorly. Apex rounded; spire concealed. Posterior edge of outer lip rising in a sharp wing protruding beyond apex. Parietal wall covered with thick, smooth white callus; thinner, white to semi-translucent in posterior half. Spiral sculpture composed of punctuated striations. Punctations ovoid, close together, often slightly interconnected. Thin, pale to warm orange brown periostracum, can be darker inside spiral punctation pits. Shell dirty white.

Radula (Fig. 17A–C): Radular formula 20 × 1.1.1 (H = 30 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth tetragonal, with developed upper cusps, slightly curved inwards.

Digestive tract (Fig. 17D, E): Salivary glands short to medium long; surface uneven. Paired gizzard plates sub-triangular, with rounded corners.

Male reproductive system (Fig. 17F, G): Penial chamber cylindrical, lined internally with longitudinal ridges between genital opening and prostatic duct. Eversible penial papilla located at prostatic duct entrance. Thin penial papilla with apical tip rounded, covered in soft warts and wrinkles. Penial chamber separated from prostate by thin prostatic duct, widening towards prostate. Prostate cylindrical, filled with spongy tissue, rounded at end.

Ecology: Found between 650 and 977 m depth. Feeds on foraminifera, tubicolous polychaetes, and smaller molluscs (gastropods, bivalves, and scaphopods) (present study).

Distribution (Fig. 10): Western Pacific Ocean, from Indonesia (Schepman 1913; present study), the Philippines (Valdés 2008), Papua New Guinea, Solomon Islands, and Vanuatu (present study).

Remarks: The taxonomic history of *Scaphander sibogae* is complicated, owing to the fact that it was described by Schepman (1913) together with shells similar in both shape (*S. attenuatus* and *S. subglobosus*) and name (*M. sibogae*, now *S. tortuosus* nom. nov.), which led to subsequent confusion (see *S. cancellatus* and *S. tortuosus* nom. nov. sections). The shell of *S. sibogae* is more ovoid, rather than sub-rectangular as in *S. cancellatus*, and can present dark brown punctations, whereas the punctations in *S. cancellatus* are of the same colour as the shell (see *S. cancellatus* section). The rachidian teeth in *S. sibogae* are more quadrate, with curved upper cusps, but in *S. cancellatus* these teeth are more elongated, H-shaped, with all cusps curved. Differences in the male reproductive system can also be found: *S. sibogae* has a simple cylindrical penial chamber and a muscular penial papilla, whereas *S. cancellatus* has a bulged penial chamber lined with soft warts around the prostatic duct, which is shorter in this species (Figs 12F, 17F).

The shell of *S. sibogae* is very similar to *S. andamanicus*. Their shells are similarly rounded, and the outer lip is raised in a wing-like structure above the apex, although the latter is sharper in *S. sibogae*, more rounded in *S. andamanicus*. However, owing to the lack of records for *S. sibogae* in the Andaman Sea or the Bay of Bengal, together with the scarceness of material for study and the absence of soft body parts for *S. andamanicus* to be compared molecularly and anatomically with *S. sibogae*, the species are both kept as valid for now. Nonetheless, further sampling in the Andaman Sea and Bay of Bengal might require this hypothesis to be revised.

Scaphander illecebrosus Iredale, 1925

(**Figs 10, 18; Table 2**)

Scaphander illecebrosus Iredale, 1925: 269, pl. 42, fig. 14; Beesley *et al.* 1998: 949; Valdés 2008: 681.

Taxonomic history: Scaphander illecebrosus was introduced by Iredale (1925) from a shell collected in the Bass Strait south of Australia during the *Endeavour* expedition. He compared the shell with *S. mundus*, but concluded that differences in the sculpture separated it from the latter species. Iredale (1925) also compared *S. illecebrosus* with the fossil species *Scaphander tatei* Cossmann, 1897 but noted the absence of a widely perforated apex of the spire that characterizes *S. tatei*. Valdés (2008) noted the similarities between the descriptions of *S. subglobosa* (here synonymized with *S. cancellatus*) and *S. illecebrosus* but kept them as separate species.

Type material: Scaphander illecebrosus Iredale, 1925—**Australia**: Tasmania, Bass Strait, 32 km east of Babel Island, 39°57′00"S, 148°45′00"E, 119 m, holotype, *AM C.53766*, H = 12.5 mm, images seen (Fig. 18).

Diagnosis: Shell ovoid, dirty white; periostracum pale yellow. Spiral sculpture composed of rows of ovoid punctuations. Apex rounded; posterior edge of outer lip rising slightly above apex.

Shell (Fig. 18): Maximum H observed = 12.5 mm. Shell ovoid, only one whorl visible. Aperture wide, as long as shell, narrowing posteriorly. Apex rounded; spire concealed. Posterior edge of outer lip rounded, protruding slightly beyond apex. Parietal wall covered with thick, smooth white callus. Spiral sculpture composed of rows of ovoid punctuations. Periostracum pale yellow. Shell dirty white.

Figure 18. Shell of *Scaphander illecebrosus*, Australia, Tasmania (holotype, *AM C.53766*, H = 12.5 mm, images courtesy of the Australian Museum).

Radula: Unknown.

Digestive tract: Unknown.

Male reproductive system: Unknown.

Ecology: Found at 119 m depth. Feeding habits unknown.

Distribution (Fig. 10): Australia; Bass Strait (Iredale 1925).

Remarks: As was remarked by Valdés (2008), *S. illecebrosus* strongly resembles *S. cancellatus*, in addition to *S. teramachii* and the new species here described, *Scaphander solomonensis*. However, given that the three latter species are known only from more northern latitudes and that the holotype for *S. illecebrosus* could be a juvenile, we maintain all these species as valid.

Scaphander teramachii (Habe, 1954)

(Figs 19–21; Table 2)

Bucconia teramachii Habe, 1954: 307, pl. 38, figs 1, 2; 1955: 70; 1964: 140, pl. 43, fig. 20.

Scaphander teramachii—Hori 2017: 1087, pl. 386, fig. 3.

Taxonomic history: The species was described under the name *Bucconia teramachii*, based on shells from Tosa Bay, Japan by Habe (1954), who commented on its similarities with the species *Bucconia attenuata* (= *Scaphander attenuatus*; see *S. cancellatus* section) from Indonesia (a synonym of *S. cancellatus*), but mentioned that the latter had larger, more attenuate shells. Kuroda *et al.* (1971) transferred the species to the genus *Nipponoscaphander* with no explanation, and the name *N. teramachii* was later used to report unidentified *Nipponoscaphander* species from China (Guangyu 1997, Qi 2004). More recently, Hori (2017) assigned this species to the genus *Scaphander* but without any explanation.

Type material: Untraceable.

Material examined: **Japan**: Tosa Bay, three spcs, two sequenced, one dissected and sequenced, ZMBN 131891, H = 5–6 mm; Nansei Islands, five spcs, one dissected, NSMT Mo-95253, H = 4.1–6 mm; eight spcs, NSMT Mo-95254, H = 1.3–8.5 mm; East China Sea, west of Takara Islands, three spcs, three sequenced, ZMBN 131888, H = 7–8 mm.

Diagnosis: Shell ovoid to sub-rectangular, dirty white. Spiral sculpture composed of ovoid punctations forming striations. Apex rounded. Posterior edge of outer lip rounded, rising slightly above apex. Rachidian teeth H-shaped. Prostate oval, separated from penial chamber by short prostatic duct. Penial chamber lined with soft longitudinal ridges.

Shell (Fig. 19): Maximum H observed = 31 mm. Shell ovoid to sub-rectangular, only one whorl visible. Aperture wide, as long as shell, narrowing posteriorly. Spire slightly umbilicate in juveniles. Posterior edge of outer lip rounded, protruding slightly beyond apex. Parietal wall covered with white callus; thick, smooth in anterior half; thin to inconspicuous in posterior half. Spiral sculpture composed of punctuated striations. Punctations well defined, ovoid, distinct. Thin, dirty white periostracum. Shell dirty white.

Radula (Fig. 20A–C): Radular formula 14 × 1.1.1 (H = 6 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth H-shaped, with upper cusps more developed, squarish.

Digestive tract (Fig. 20D, E): Salivary glands thin; surface smooth. Paired gizzard plates sub-triangular to kidney-shaped.

Male reproductive system (Fig. 20F, G): Penial chamber cylindrical, widening towards prostatic duct, lined with soft longitudinal

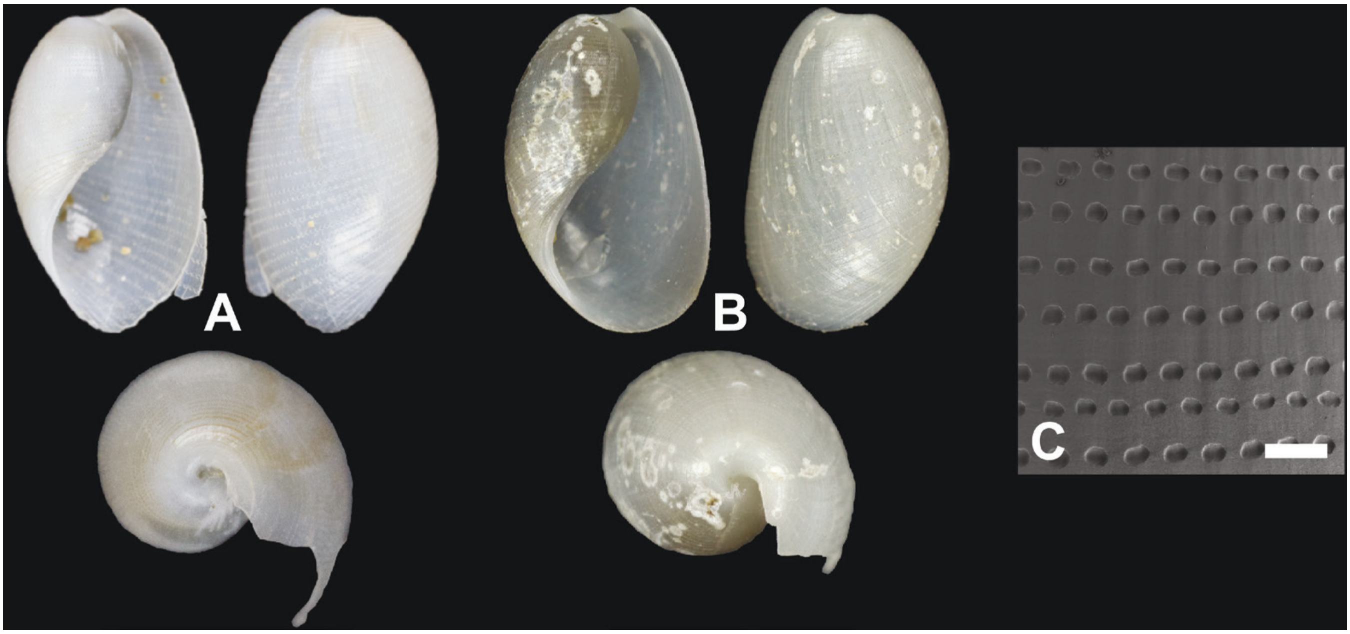

Figure 19. Shells and SEM image of the shell sculpture of *Scaphander teramachii*. A, Japan, Tosa Bay (ZMBN 131891, H = 6 mm). B, Japan, East China Sea, west of Takara Island (ZMBN 131888, H = 8 mm). C, Japan, Tosa Bay (ZMBN 131891, H = 6 mm). Scale bar: C = 200 µm.

ridges. Muscular penial papilla absent. Penial chamber separated from prostate by short prostatic duct, widening towards prostate. Prostate oval, rounded at end.

Ecology: Found between 100 and 1533 m depth. Feeds on foraminifera and small molluscs (bivalves and gastropods) (Habe 1964; present study).

Distribution (Fig. 21): Tosa Bay, Japan (Habe 1954, 1964, Hasegawa and Okutani 2011, Hori 2017; present study) to China Sea (Hori 2017; present study).

Remarks: As Habe (1954) remarked in the original description of *S. teramachii*, the adult form of the species bears a strong resemblance to congeneric *S. cancellatus*, whose posterior edge of the outer lip rises in a more pronounced wing and whose aperture is generally wider. However, it is demonstrated in this study that the shells of *S. cancellatus* depict great variability (see *S. cancellatus* section), making the separation of these two species based on shell characters difficult. In addition, both species have similar internal features, such as an eversible penial chamber lined by warts. Despite our efforts, the type material for *S. teramachii* could not be located and is likely to be untraceable. Two shell labelled as 'possible' types are housed at the National Museum of Nature and Science in Tokyo (NSMT Mo-38721); however, these are larger than the specimen mentioned in the original description (Habe 1954, Hasegawa and Okutani 2011; present study) and differ slightly in shape from Habe (1954)'s drawing by being more inflated anteriorly and generally less elongate, with a periostracum orange in colour. The periostracum was originally described as white, which is the same colour observed by us in newly collected material. Based on these features, the shells labelled as 'possible' types housed at the NSMT are here assigned to the species *S. cancellatus*, which was also recorded in Japan (as *Bucconia attenuata*) by the original descriptor of *S. teramachii* (Habe 1955).

In this study, it was possible to amplify and sequence DNA only from smaller, probably juvenile, white *S. teramachii* from Japan. The lack of DNA sequences from the resembling *S. cancellatus* from Japan hindered a sound comparative study of the shells of the two species, and any differences pointed out between them warrant caution. The name *Nipponoscaphander teramachii* has been used to report specimens from the South China Sea (Guangyu 1997, Qi 2004) and the Philippines (Poppe 2010). However, examination of the illustrations provided in those works revealed that the depicted specimens are not conspecific with *S. teramachii*, but do belong to the genus *Nipponoscaphander*. Therefore, the distribution of *S. teramachii* is here considered to be restricted to Japan.

This species showed higher than average intraspecific variability for *COI*, with uncorrected *p*-distances of 0%–3.9%. However, no anatomical differences were observed in the morphological study of these sequenced specimens.

Scaphander otagoensis Dell, 1956

(Figs 8, 22, 23; Table 2)

Scaphander otagoensis Dell, 1956: 143–144, fig. 208; Powell 1979, 84; Lörz *et al.* 2012: 41.

Scaphander cf. *otagoensis* 1—Siegwald *et al.* 2022.

Taxonomic history: Scaphander otagoensis was described by Dell (1956) from shells collected off southern regions of the North and South Islands of New Zealand.

Type material: Scaphander otagoensis Dell, 1956—**New Zealand**: off Otago Peninsula, Karitane Canyon, Portobello *Alert* station 54-17, 45°37'30"S, 171°06'00"E, 475–640 m, holotype, *MNZ M.9141*, H = 13.6 mm, images seen (Fig. 22A, G); six paratypes, MNZ M.9140, H = 4–7 mm, images seen; Taiaroa Canyon, *Alert*, station B.S.190, 45°45'24"S, 171°05'00"E, 549 m, one paratype, MNZ M.10565, H = 9 mm, images seen (Fig. 22B).

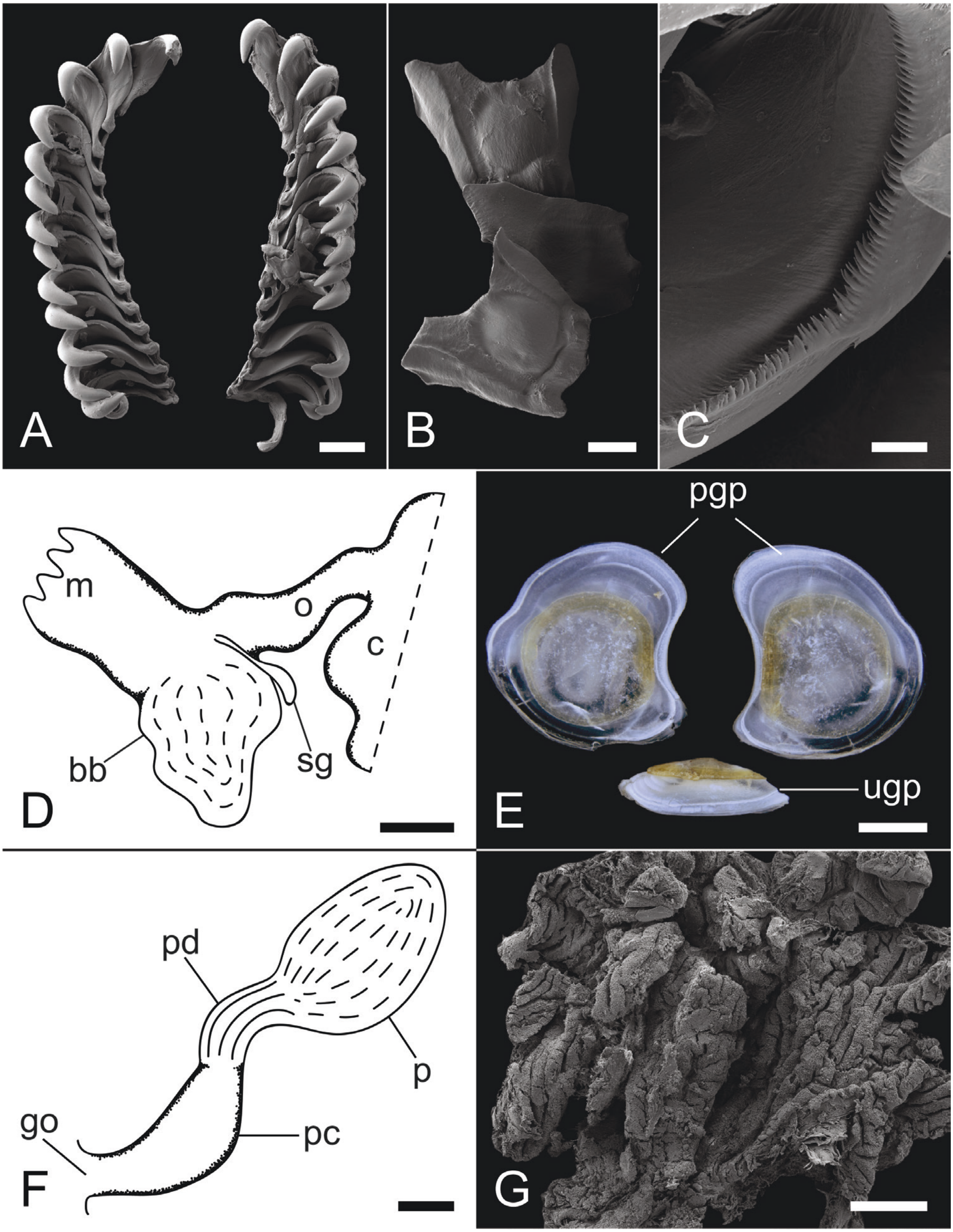

Figure 20. Anatomical details of *Scaphander teramachii*. A, radula, Japan, East China Sea, west of Takara (ZMBN 131888, H = 8 mm). B, rachidian teeth (ZMBN 131888, H = 8 mm). C, detail of lateral teeth (ZMBN 131888, H = 8 mm). D, anterior part of digestive tract (ZMBN 131888, H = 8 mm). E, gizzard plates (ZMBN 131888, H = 8 mm). F, male reproductive system, Japan, Nansei Islands (NSMT Mo-95253, H = 6 mm). G, penial chamber lining (ZMBN 131888, H = 8 mm). Scale bars: A = 100 μm; B = 20 μm; C = 10 μm; D = 500 μm; E, F = 1 mm; G = 200 μm.

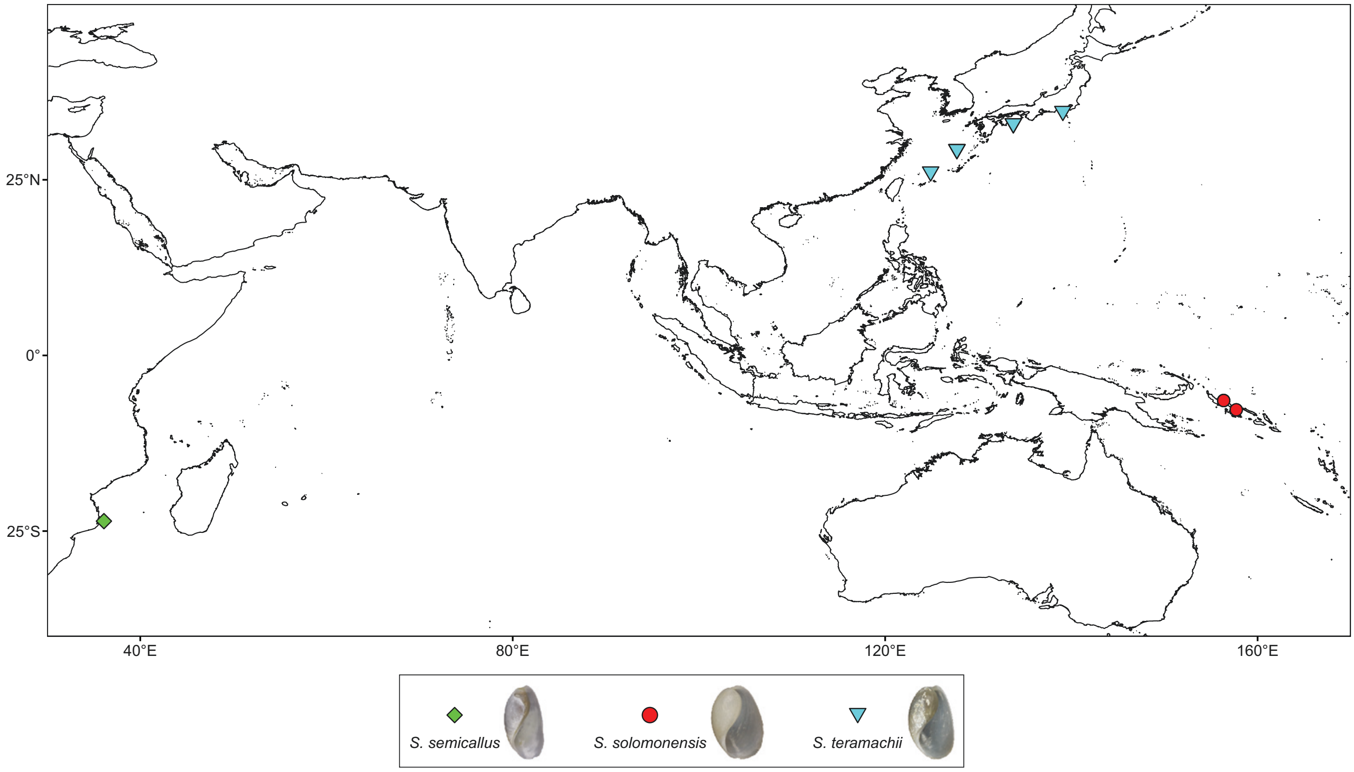

Figure 21. Geographical distribution of ***Scaphander semicallus***, ***Scaphander solomonensis***, and *Scaphander teramachii*. Geographical records are based on studied material and reliable literature records.

Other material examined: **New Zealand:** North Island, east-northeast of Cape Palliser, head of Pahaua Canyon, 10 spcs, two dissected and sequenced, one dissected, MNZ M.301800, H = 21–27 mm; east-southeast of Cape Palliser, seven spcs, two sequenced, MNZ M.301817, H = 18–28 mm; five spcs, one dissected and sequenced, NIWA 63032, H = 25–31 mm; northwest of Chatham Islands, one spc., sequenced, NIWA 30182, H = 10 mm; Western Chatham Rise, northeast of Mernoo Bank, four spcs and 22 sh., two dissected, MNZ M.059714, H = 6–37 mm; South Island, southeast of Cape Campbell, two spcs, one sequenced, NIWA 63804, H = 17, 26 mm.

Diagnosis: Shell elongate, covered by thick, pale orange to brownish periostracum. Spiral sculpture composed of variable rows of rectangular punctations. Spire concealed; posterior edge of outer lip rising above apex. Rachidian teeth sub-rectangular, elongate. Prostate cylindrical. Penial papilla absent. Penial chamber bulged and lined with soft warts around prostatic duct entrance.

Shell (Fig. 22): Maximum H observed = 37 mm. Shell elongate to pyramidal, only one whorl visible. Aperture as long as shell, narrowing posteriorly. Spire concealed. Posterior edge of outer lip rising slightly above apex. Parietal wall covered with thick, smooth white callus. Spiral sculpture composed of punctuated striations. Punctations rectangular, in rows of variable sizes. Thick, pale orange to brownish periostracum. Shell dirty white to pale yellow.

Radula (Fig. 23A–C): Radular formula 21 × 1.1.1 (H = 28 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth sub-rectangular, elongate, with cusps slightly curved inwards.

Digestive tract (Fig. 23D, E): Salivary glands long, thin, surface uneven. Paired gizzard plates sub-triangular to kidney-shaped.

Male reproductive system (Fig. 23F, G): Penial chamber cylindrical, lined with soft longitudinal ridges towards genital opening, bulged around prostatic duct entrance, lined with warts and wrinkles. Muscular papilla absent. Penial chamber separated from prostate by short prostatic duct. Prostate cylindrical, rounded at end.

Ecology: Found between 964 and 1793 m depth (Lörz *et al.* 2012; present study). Feeds on foraminifera (present study).

Distribution (Fig. 8): Eastern New Zealand (Dell 1956, Morley and Hayward 2009, Rowden *et al.* 2016; present study).

Remarks: The shell of *S. otagoensis* is similar to those of *S. interruptus* and *S. amygdalus*, especially in their juvenile forms. The three species occur around New Zealand, with their bathymetric ranges overlapping. However, *S. otagoensis* has a more pronounced pyramidal shell, with straighter lateral edges, a posterior part more acute, and a notable darker periostracum. The overall shape of the shell of *S. interruptus* is similar but with lateral and posterior edges slightly more rounded, and the S-curve of its parietal wall and aperture is more pronounced. The shell of *S. amygdalus* is more oval than *S. otagoensis*, with a noticeable narrowing of the posterior edge of the shell, giving it an almond shape. *Scaphander interruptus* differs anatomically by

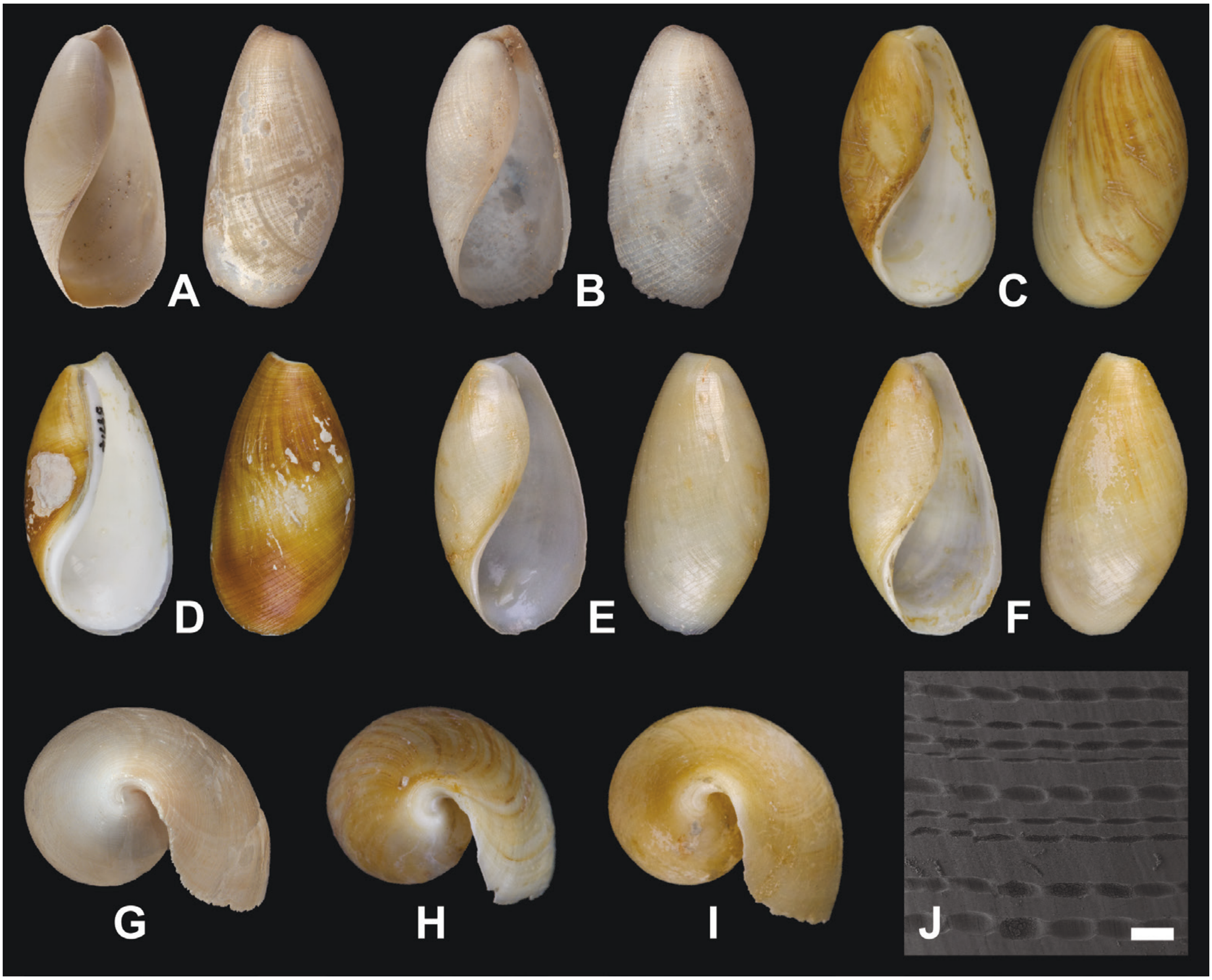

Figure 22. Shells and SEM image of the shell sculpture of *Scaphander otagoensis*. A, New Zealand, off Otago Peninsula, Karitane Canyon (holotype, *MNZ M.9141*, H = 13.6 mm; images courtesy of the MNZ). B, New Zealand, Taiaroa Canyon (paratype, MNZ M.10565, H = 9 mm; images courtesy of the MNZ). C, New Zealand, North Island, east-northeast of Cape Palliser (MNZ M.301800, H = 24 mm). D, New Zealand Western Chatham Rise, northeast of Mernoo Bank (MNZ M.059714, H = 39 mm). E, New Zealand, South Island, southeast of Cape Campbell (NIWA 63804_A, H = 17 mm). F, New Zealand, east-southeast of Cape Palliser (NIWA 63032_A, H = 28 mm). G, New Zealand, off Otago Peninsula, Karitane Canyon (holotype, *MNZ M.9141*, H = 13.6 mm; image courtesy of the MNZ). H, New Zealand, North Island, east-northeast of Cape Palliser (MNZ M.301800, H = 24 mm). I, New Zealand, east-southeast of Cape Palliser (NIWA 63032_A, H = 28 mm). J, New Zealand Western Chatham Rise, northeast of Mernoo Bank (MNZ M.059714, H = 39 mm). Scale bar: J = 200 μm.

lacking warts lining the deeper part of the penial chamber, but *S. otagoensis* and *S. amygdalus* have similar internal features, which makes distinction based on anatomical characters challenging (see *S. amygdalus* and *S. interruptus* sections). These sister species are distinct genetically, with uncorrected *p*-distances for *COI* estimated at 9.01%–10.03% between *S. otagoensis* and *S. interruptus*, 10.14%–11.76% between *S. interruptus* and *S. amygdalus*, and 11.91%–13.39% between *S. otagoensis* and *S. amygdalus*.

Scaphander grandis (Minichev, 1967)

(Figs 15, 24, 25; Table 2)

Meloscaphander grandis Minichev, 1967: 130–134, figs 25–29; 1969: 43.

Scaphander grandis—Chaban *et al.* 2019a: 385–397, figs 1–6; 2019b: 12.

Scaphander interruptus—Valdés and McLean 2015: (in part) 119–121, figs 2–5, 9, 10.

Taxonomic history: Minichev (1967) described the species under the genus *Meloscaphander* from three specimens collected by the Russian ship *Vityaz* off South Alaska. He remarked on the similarity of these specimens to the shell and anatomy of *Scaphander*, but assigned them to *Meloscaphander* based on their visible spire. This species was redescribed and analysed phylogenetically by Chaban *et al.* (2019a), resulting in its reassignment to the genus *Scaphander*. Examination of the shells of the specimens studied anatomically by Valdés and McLean (2015) in their

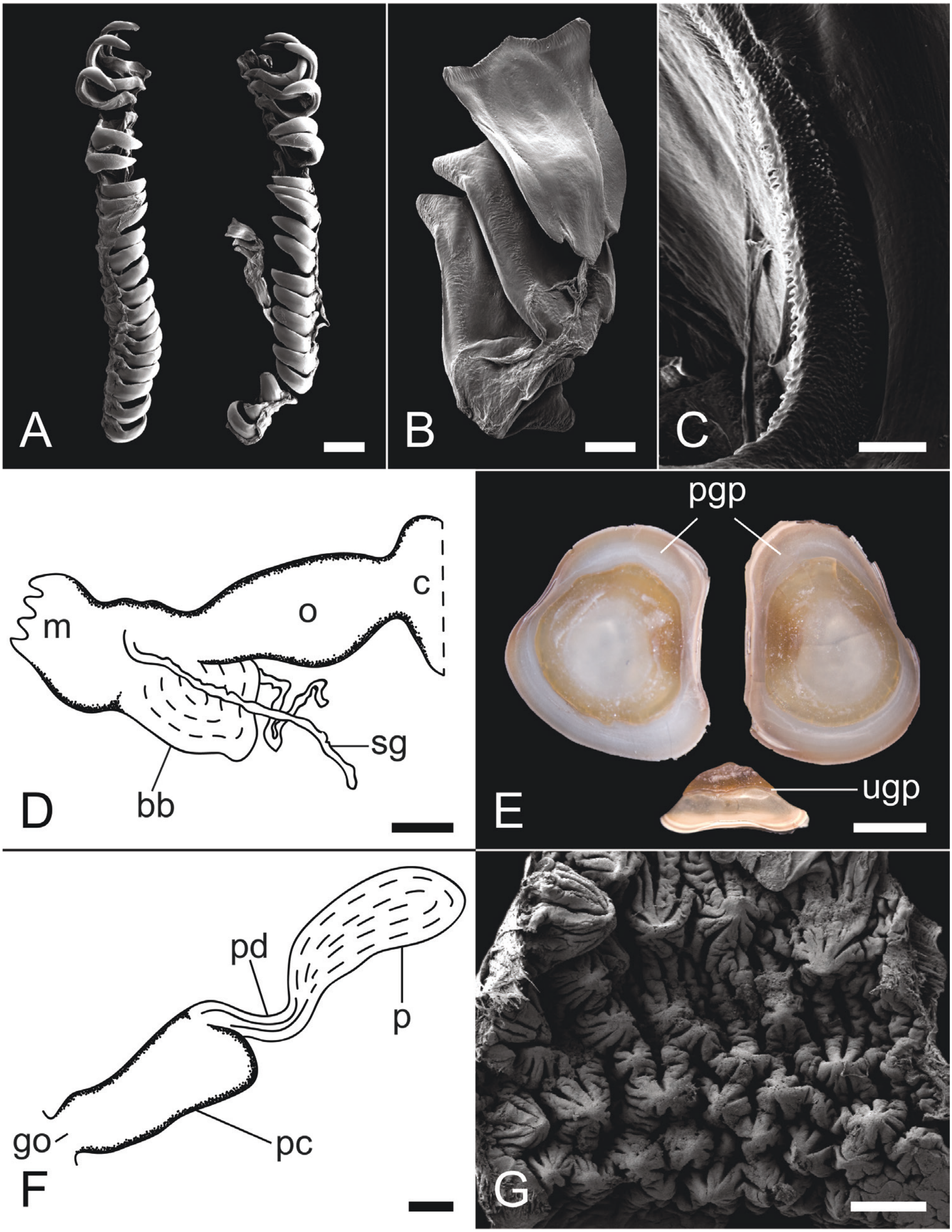

Figure 23. Anatomical details of *Scaphander otagoensis*. A, radula, New Zealand, North Island, east-northeast of Cape Palliser, head of Pahaua Canyon (MNZ M.301800/1). B, rachidian teeth (MNZ M.301800/1). C, detail of lateral teeth (MNZ M.301800/1). D, anterior part of digestive tract, New Zealand, North Island, east-southeast of Cape Palliser (NIWA 63032_A, H = 28 mm). E, gizzard plates, New Zealand, Western Chatham Rise, northeast of Mernoo Bank (MNZ M.059714/1). F, male reproductive system (MNZ M.059714/1). G, penial chamber lining (MNZ M.059714/1). Scale bars: A, G = 200 μm; B = 30 μm; C = 100 μm; D, F = 1 mm; E = 3 mm.

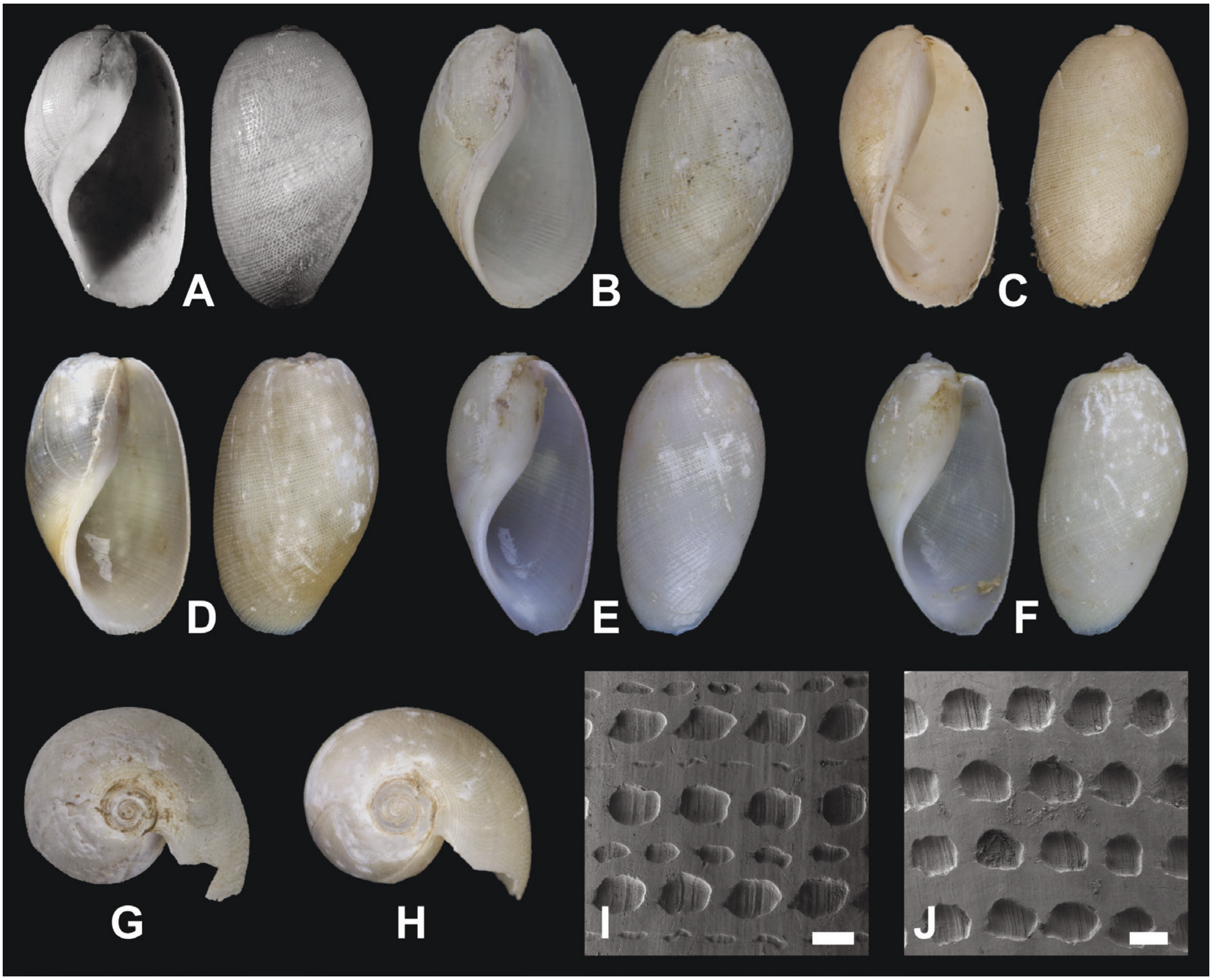

Figure 24. Shells and SEM images of the shell sculpture of *Scaphander grandis*. A, Northwestern Pacific, south of Alaska (holotype, *Meloscaphander grandis*, *ZISP 1/62440*, H = 33 mm; images adapted from Chaban *et al.* 2019a). B, USA, CA, Santa Barbara County, west of Point Arguello (LACM 1972-264.1, H = 29.5 mm). C, USA, CA, Santa Barbara County, west of Point Arguello (LACM 1972-261.9, H = 20 mm). D, Northeastern Pacific, Kurile-Kamchatka Abyssal Plain (ZSM Mol 20210097, H = 21 mm). E, Northeastern Pacific, Kurile-Kamchatka Abyssal Plain (ZSM Mol 20 210 094, H = 25 mm). F, Northeastern Pacific, Kurile-Kamchatka Abyssal Plain (ZSM Mol 20 210 096, H = 23 mm). G, USA, CA, Santa Barbara County, west of Point Arguello (LACM 1972-264.1, H = 29.5 mm). H, Northeastern Pacific, Kurile-Kamchatka Abyssal Plain (ZSM Mol 20210097, H = 21 mm). I, Northeastern Pacific, Kurile-Kamchatka Abyssal Plain (ZSM Mol 20210095, H = 24 mm). J, Northeastern Pacific, Kurile-Kamchatka Abyssal Plain (ZSM Mol 20 150 062, H = 29 mm). Scale bars: I, J = 200 μm.

redescription of *S. interruptus* revealed that these specimens instead belonged to *S. grandis.* The shells of *S. interruptus* are distinct, for example, by lacking a visible spire (see the Remarks in this sections for a discussion).

Type material: Meloscaphander grandis Minichev, 1967—**Northwestern Pacific**: south of Alaska, *Vityaz* cruise 29, station 4158, 46°56’06”N, 143°58’54”W, 4665 m, holotype, *ZISP 1/62440*, H = 33 mm, images seen (Fig. 24A).

Other material examined: **Kurile-Kamchatka Abyssal Plain**: one spc., dissected, ZSM Mol 20210094, H = 25 mm; one spc., sequenced, ZSM Mol 20210053, H = 24 mm; one spc., dissected and sequenced, ZSM Mol 20150062, H = 29 mm; one spc., dissected and sequenced, ZSM Mol 20210096, H = 23 mm; one spc., dissected, ZSM Mol 20210095, H = 24 mm; one spc., dissected, ZSM Mol 20210097, H = 21 mm; one spc., ZSM Mol 20210098, H = 19 mm; two spcs, ZSM Mol 20150050, H = 20 mm; two spcs, ZSM Mol 20150051, H = 24–28 mm; three spcs, ZSM Mol 20150052, H = 20–25 mm; 17 spcs, ZSM Mol 20150053, H = 16–23 mm; three spcs, ZSM Mol 20150056, H = 18–19 mm; one spc., ZSM Mol 20150057, H = 27 mm; one spc., ZSM Mol 20150059, H = 21 mm; four spcs, ZSM Mol 20150063, H = 18–24 mm. **USA**: California, Santa Barbara County, 230 km west of Point Arguello, one sh. (broken), LACM 1995-21.9, H = 24.5 mm; one sh. (broken), LACM 1991-131.3, H = 25 mm; one sh. (broken), LACM 1993-74.1, H = 25 mm; one sh. (broken), LACM 1991-130.2, H = 24 mm; one spc., dissected, LACM 1991-133.3, H = 29 mm; one sh. (broken), LACM 1993-21.10, H = 11 mm; off Oregon, Tufts Abyssal Plain, one sh., LACM 1972-262.7,

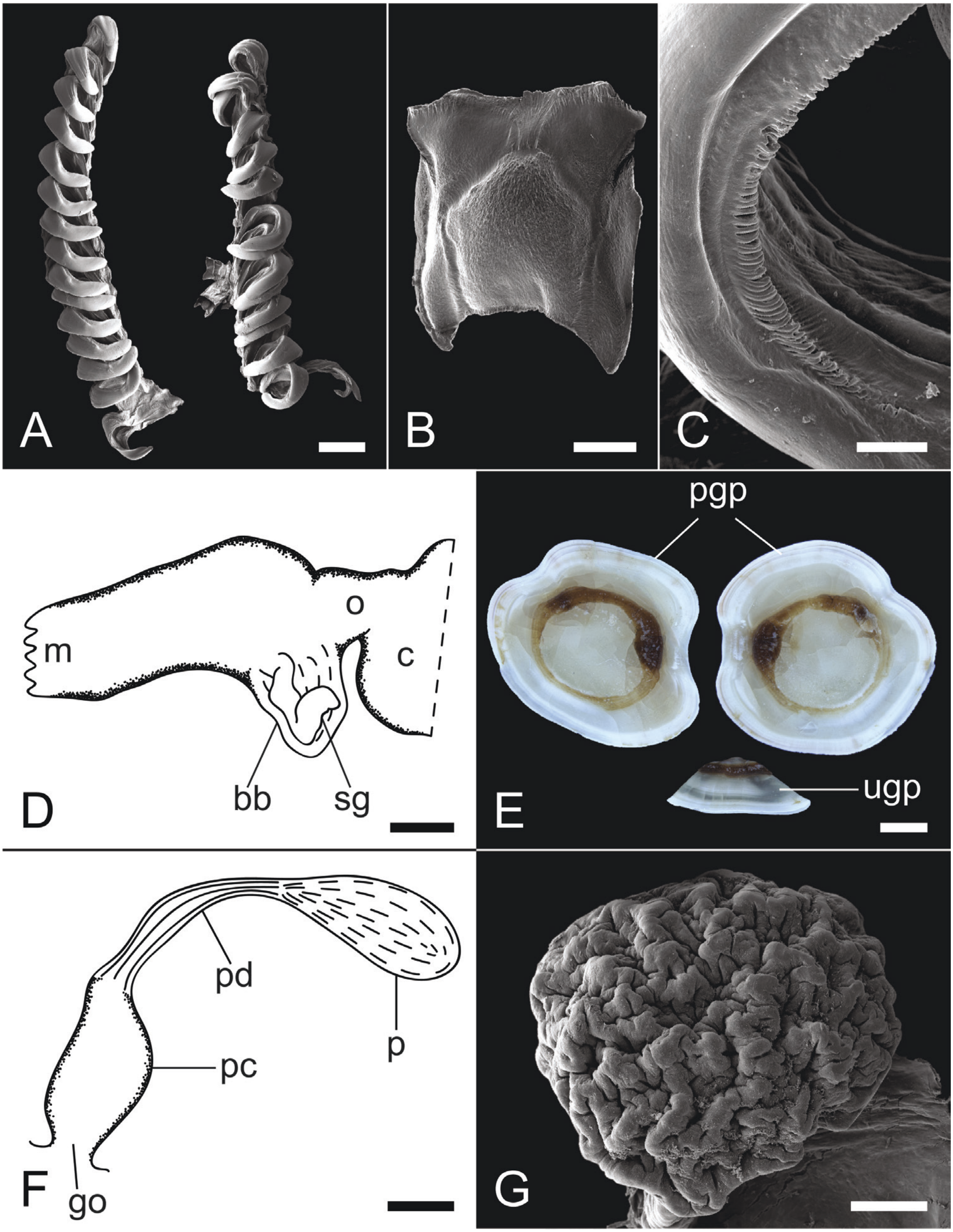

Figure 25. Anatomical details of *Scaphander grandis*. A, radula, Northeastern Pacific, Kurile-Kamchatka Abyssal Plain (ZSM Mol 2021095, H = 24 mm). B, rachidian teeth, Northeastern Pacific, Kurile-Kamchatka Abyssal Plain (ZSM Mol 201 210 097, H = 21 mm). C, detail of lateral teeth (ZSM Mol 2021095, H = 24 mm). D, anterior part of digestive tract, Northeastern Pacific, Kurile-Kamchatka Abyssal Plain (ZSM Mol 20 210 094, H = 25 mm). E, gizzard plates, Northeastern Pacific, Kurile-Kamchatka Abyssal Plain (ZSM Mol 20 150 062, H = 29 mm). F, male reproductive system, Northeastern Pacific, Kurile-Kamchatka Abyssal Plain (ZSM Mol 20 210 096, H = 23 mm). G, penial papilla (ZSM Mol 20 210 094, H = 25 mm). Scale bars: A = 200 μm; B = 20 μm; C = 15 μm; D, F = 1 mm; E = 2 mm; G = 100 μm.

H = 26.5 mm; one sh., LACM 1972-264.1, H = 29.5 mm; one sh., LACM 1972-265.9, H = 10 mm; two spcs, LACM 1972-263.7, H = 25.5–28 mm; four spcs, one dissected, LACM 1972-261.9, H = 14.5–21 mm; one spc., LACM 1972-272.7, H = 12 mm; one spc., LACM 1972-270.8, H = 8 mm; one sh., LACM 1972-266.6, H = 13 mm.

Diagnosis: Shell ovoid, elongate. Spiral sculpture composed of rows of irregular sub-rectangular punctuations. Spire small, flat or slightly raised, partly separated from body whorl by a suture widening into a narrow groove along upper part of parietal wall. Outer lip rounded posteriorly, forming a shoulder level with or below apex. Parietal wall with thickened callus, smooth white. Rachidian teeth sub-rectangular, broad. Prostate oval to cylindrical, short, separated from penial chamber by long, thin prostatic duct. Penial papilla bulbous, covered with wrinkles.

Shell (Fig. 24): Maximum H observed = 33 mm. Shell ovoid, elongate. Aperture wide, nearly as long as shell, narrowing posteriorly. Spire small, flat or partly raised, made of three to four whorls. Suture partly separating spire from body whorl, widening in a narrow groove along uppermost part of parietal wall. Posterior edge of outer lip joining body whorl immediately below spire in acute-like shoulder. Parietal wall covered with thick, smooth white callus. Spiral sculpture composed of punctuated striations. Punctations irregularly shaped, sub-rectangular. Thin, translucent periostracum. Shell white.

Radula (Fig. 25A–C): Radular formula 22 × 1.1.1 (H = 28 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth sub-rectangular, broad, with upper cusps curved inwards.

Digestive tract (Fig. 25D, E): Salivary glands medium long; surface uneven. Paired gizzard plates irregularly ovoid to sub-quadrate.

Male reproductive system (Fig. 25F, G): Penial chamber cylindrical, lined with soft longitudinal ridges. Muscular penial papilla, bulbous, covered in wrinkles. Penial chamber separated from prostate by long, thin prostatic duct. Prostate cylindrical to oval, rounded at end.

Ecology: Found between 3585 and 5427 m depth. Feeds on foraminifera, diatoms, and small bivalves and gastropods (Chaban *et al.* 2019a; present study).

Distribution (Fig. 15): Northern Pacific; Northeastern Pacific Abyssal Plain, south of Alaska (Minichev 1967, Chaban *et al.* 2019a) down to offshore Santa Barbara, California (present study), to Northwestern Pacific Abyssal Plain along the Kurile-Kamchatka Trench (Chaban *et al.* 2019a, 2019b; present study).

Remarks: This species is distinguishable from most other *Scaphander* species by its visible spire and the presence of a shoulder in the posterior edge of the outer lip of the shell. *Scaphander tortuosus* nom. nov. [= *Scaphander sibogae* (Schepman, 1913)] and *Scaphander planeticus* Dall, 1908 are the only other known *Scaphander* representatives with a distinct shell shoulder, but both species present enough conchological differences from *S. grandis* to be kept separate, because they are both significantly more ovate and less elongate than *S. grandis*.

Valdés and McLean (2015) considered *S. interruptus* to be the only species of *Scaphander* present in the Eastern Pacific and described its anatomy. In this study, we examined the material listed in their article and noticed the presence of a spire in the shell of the specimens used for the anatomical dissections, which *S. interruptus* lacks. After comparison of these shells with the type material for *S. grandis* and further anatomical observations, we concluded that the specimens dissected by Valdés and McLean (2015) are conspecific with *S. grandis*.

Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020

(Figs 15, 26, 27; Table 2)

Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020.

Taxonomic history: This was, until the present work, the most recent species described of the genus *Scaphander* and was, up to now, cited in the literature only in the original description (Siegwald *et al.* 2020).

Type material: Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020—**Argentina**: Argentine Sea, off Mar del Plata (38°04’38.76”S, 53°34’46.32”W to 38°01’35.16”S, 53°39’58.32”W), holotype, dissected and sequenced, *MACNIn 42431*, H = 26.5 mm; one paratype, dissected and sequenced, ZMBN 127881, H = 24.3 mm; four paratypes, one dissected and sequenced, one sequenced, ZMBN 127882, H = 17.8, rest of shells greatly damaged; one paratype, MACNIn 42432, shell damaged.

Other material examined: **Australia**: Tasmania, Freycinet Commonwealth Marine Reserve, one spc., dissected and sequenced, AM C.590963, H = 24 mm; six spcs and four sh., AM C.482170, H = 14–32 mm; one spc., sequenced, AM C.519366, H = 23 mm; Bass Strait, one spc., dissected and sequenced, AM C.594398, H = 25 mm; one spc., sequenced, AM C.594399, H = 27 mm; 14 spcs, AM C.590964, H = 15.5–25 mm; Victoria, East Gippsland Commonwealth Marine Reserve, four spcs, AM C.590960, H = 18–25 mm; one spc., dissected and sequenced, AM C.590967, H = 27 mm; New South Wales, Hunter Commonwealth Marine Reserve, one spc., sequenced, AM C.482252, H = 14 mm; Jervis Commonwealth Marine Reserve, one spc., dissected and sequenced, AM C.590966, H = 20 mm; three spcs, AM C.590958, H = 21–25 mm.

Diagnosis: Shell ovoid to sub-rectangular, white. Spiral sculpture composed of rows of large polygonal punctations. Spire small, flat or slightly raised, partly separated from body whorl by suture widening into groove along parietal wall. Outer lip rounded posteriorly, forming a shoulder inserted below, level, or above apex. Rachidian teeth subquadrate. Prostate cylindrical, separated from penial chamber by thin prostatic duct. Penial papilla bulbous to elongate, covered with warts and wrinkles.

Shell (Fig. 26): Maximum H observed = 31 mm. Shell ovoid to sub-rectangular. Aperture wide, as long as shell, narrowing posteriorly. Small flat or partly raised spire made of three to four whorls. Deep suture partly separating spire from body whorl, widening into a protruding groove along the upper

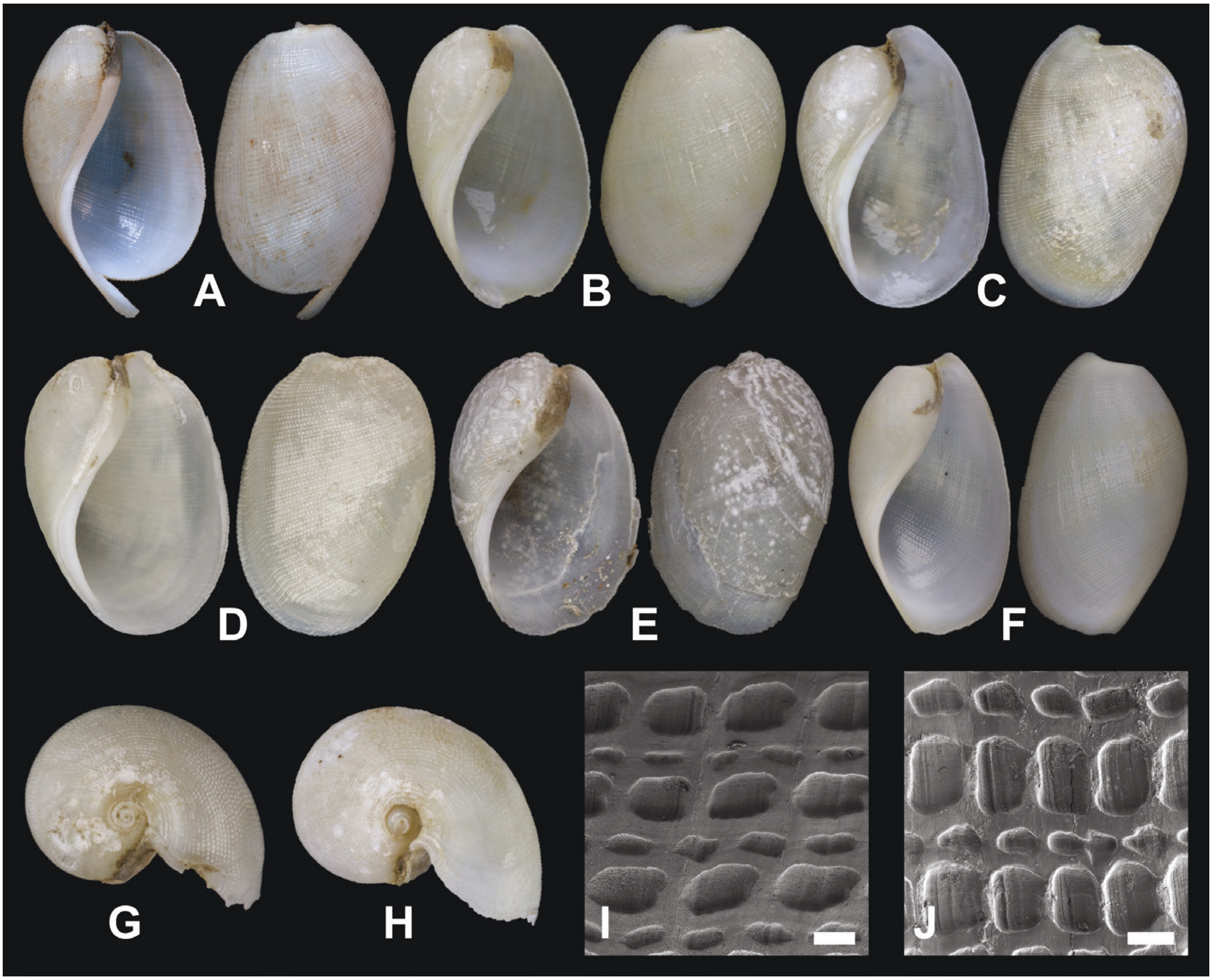

Figure 26. Shells and SEM images of the shell sculpture of *Scaphander meridionalis*. A, Argentina, off Mar del Plata (holotype, *MACNIn 42431*, H = 26.5 mm). B, Australia, Tasmania, Freycinet Commonwealth Marine Reserve (AM C.519366, H = 23 mm). C, Australia, Bass Strait (AM C.594398, H = 25 mm). D, Australia, New South Wales, Jervis Commonwealth Marine Reserve (AM C.590966, H = 20 mm). E, Australia, New South Wales, Hunter Commonwealth Marine Reserve (AM C.482252, H = 14 mm). F, Argentina, off Mar del Plata (paratype, ZMBN 127881, H = 24.3 mm). G, Australia, New South Wales, Jervis Commonwealth Marine Reserve (AM C.590966, H = 20 mm). H, Australia, Bass Strait (AM C.594398, H = 25 mm). I, Argentina, off Mar del Plata (paratype, ZMBN 127881, H = 24.3 mm). J, Australia, Tasmania, Freycinet Commonwealth Marine Reserve (AM C.519366, H = 23 mm). Scale bars: I, J = 200 µm.

part (one-quarter) of the parietal wall. Posterior edge of outer lip joining body whorl in a rounded shoulder, sometimes protruding beyond apex. Parietal wall covered with thick, smooth white callus. Spiral sculpture composed of punctuated striations. Punctations large, sub-rectangular. Thin, translucent periostracum. Shell white.

Radula (Fig. 27A–C): Radular formula 17 × 1.1.1 (H = 24.3 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth sub-quadrate, slightly wider on one end, with pointed cusps.

Digestive tract (Fig. 27D, E): Salivary glands long, surface uneven. Paired gizzard plates sub-rectangular.

Male reproductive system (Fig. 27F, G): Penial chamber cylindrical, lined with soft longitudinal ridges. Muscular penial papilla, bulbous to elongate, covered in warts and wrinkles. Penial chamber separated from prostate by thin prostatic duct. Prostate cylindrical, rounded at end.

Ecology: Found between 2338 and 2952 m depth. Feeds on foraminifera, smaller bivalves, gastropods, and tubicolous polychaetes (Siegwald *et al.* 2020; present study).

Distribution (Fig. 15): Argentina in the Southwestern Atlantic Ocean (Siegwald *et al.* 2020) and Southeastern Australia between New South Wales, Tasmania, and Victoria (present study).

Remarks: The shell of *S. meridionalis* is similar to the ones of *S. grandis* from the Northern Pacific Ocean and the Atlantic species *S. imperceptus*. However, the spire groove is remarkably less prominent in the latter. Furthermore, *S. meridionalis*

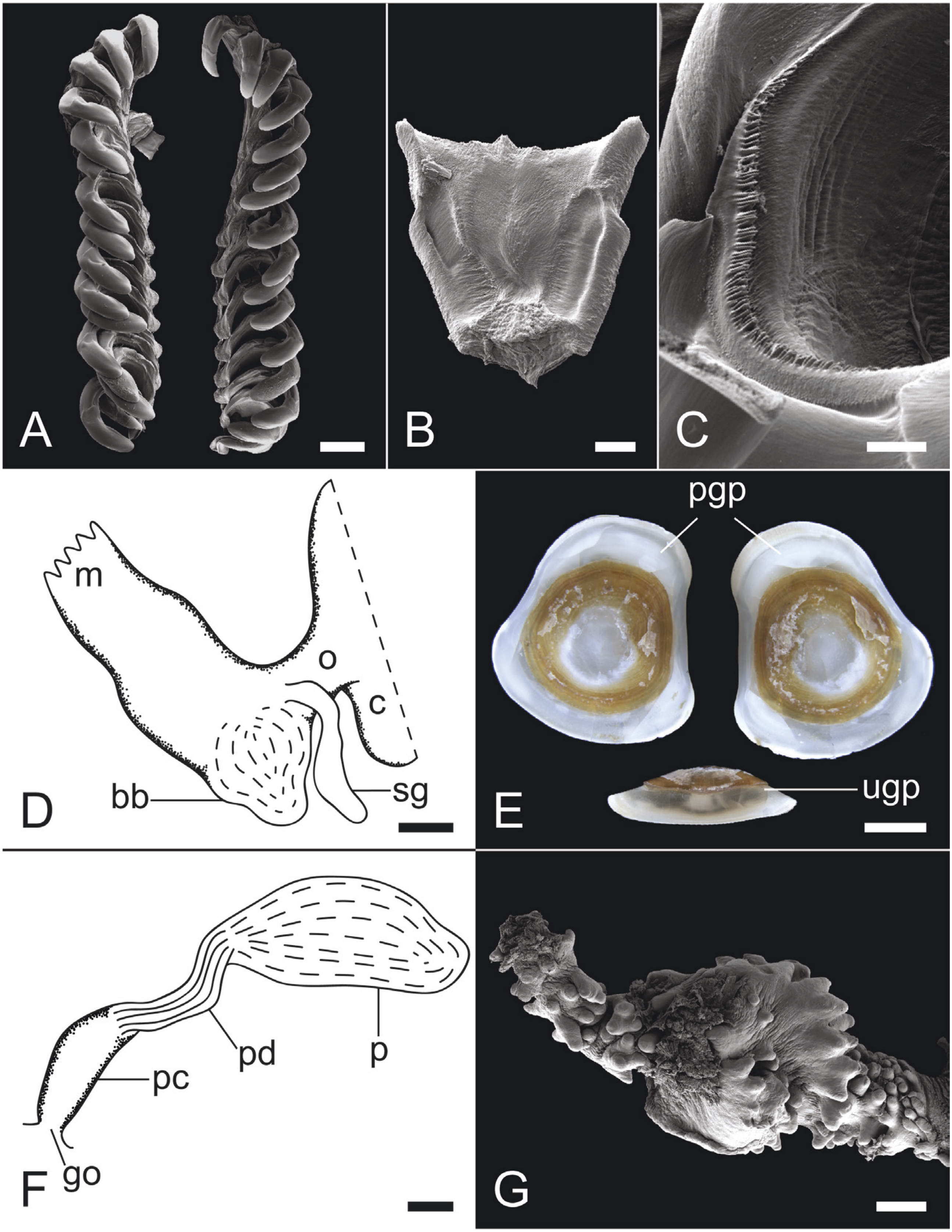

Figure 27. Anatomical details of *Scaphander meridionalis*. A, radula, Australia, Tasmania, Freycinet Commonwealth Marine Reserve (AM C.48270, H = 24 mm). B, rachidian teeth (AM C.48270, H = 24 mm). C, detail of lateral teeth (AM C.48270, H = 24 mm). D, anterior part of digestive tract, Australia, Victoria, East Gippsland Commonwealth Marine Reserve (AM C. C.590967, H = 27 mm). E, gizzard plates (AM C. C.590967, H = 27 mm). F, male reproductive system (AM C.563068, H = 27 mm). G, SEM of penial papilla (AM C.563068, H = 27 mm). Scale bars: A, G = 200 μm; B = 20 μm; C = 10 μm; D, F = 1 mm; E = 2 mm.

is molecularly distinct from *S. grandis* (*COI* uncorrected *p*-distances estimated at 5.02%–7.09% between these species). It was not possible to extract DNA successfully from the available samples of *S. imperceptus*, but according to its original description by Bouchet (1975), *S. imperceptus* has a bifid penis, which is lacking in *S. meridionalis*.

Scaphander meridionalis is also a rare case of a benthic gastropod with Pacific–Atlantic distribution (Zaharias *et al.* 2020, Siegwald *et al.* 2022). It has so far been recorded only from Argentina and Australia, and such striking wide disjunct distribution suggests possible undersampling across the southern regions of the Indo-West Pacific Ocean, but also certainly high dispersal capabilities likely to be related to a planktotrophic development. An alternative hypothesis is a human-mediated introduction.

Several specimens from Australia were hosting specimens of parasitic pycnogonids in their mantle cavity. Only the legs of the pycnogonids were protruding from the *Scaphander* shell, and their proboscis and chelifores were piercing into the gut of the snails. Some snails were found hosting up to 12 pycnogonid individuals. This is similar to what was observed for *Ascorhynchus endoparasiticus* Arnaud, 1978 found in *Scaphander punctostriatus* (Arnaud 1978). The pycnogonid specimens found in *S. meridionalis* also seem to belong to *Ascorhynchus*.

Scaphander tortuosus nom. nov.

(**Figs 14, 15; Table 2**)

Meloscaphander sibogae Schepman, 1913: 464, pl. 31, figs 5–9.
Scaphander sibogae—Chaban *et al.* 2019a: 397.

ZooBank LSID: urn: lsid::zoobank.org:act:19B569B7-0264-448C-AD90-E151A2AAB9AB

Etymology: Latin, *tortuosus*; convoluted. Named for the complexity of its taxonomic history and its visible spire.

Taxonomic history: Schepman (1913) introduced the genus *Meloscaphander* for this species, which he described as *M. sibogae*, based on a single specimen from Indonesia, collected during the *Siboga* expedition. He described an anatomy very similar to *Scaphander*, but included the species in a separate genus owing to a different shell shape with a visible spire. Chaban *et al.* (2019a) synonymized *Meloscaphander* with *Scaphander*, rendering *Scaphander sibogae* (Schepman, 1913) [= *M. sibogae* Schepman, 1913] an unavailable homonym name of *Scaphander sibogae* Schepman, 1913, given that the previous names have no synonyms available (see *S. sibogae* and *S. cancellatus* sections for complementary information and discussion). Therefore, in accordance with the principle of priority (ICZN 1999a: art. 23.3.5) and rules for replacement of junior homonyms (ICZN 1999b: art. 60.3), we here introduce the replacement name *Scaphander tortuosus* nom. nov. for *Meloscaphander sibogae* Schepman, 1913. Following recommendation 60A (ICZN 1999a,b), the type material of *Meloscaphander sibogae* Schepman, 1913 is maintained as the type material of *S. tortuosus* nom. nov.

Type material: Meloscaphander sibogae Schepman, 1913—**Indonesia**: Banda Sea, Sulawesi, *Siboga* expedition, station 221, 6°24′00"S, 124°39′00"E, 2798 m, holotype, *ZMA. MOLL.136944*, H = 16 mm, images seen (Fig. 14B).

Diagnosis: Shell ovoid, yellowish, wider in upper half, with small, slightly raised spire. Spiral sculpture composed of punctuated striations.

Shell (Fig. 14): Maximum H observed = 16 mm. Shell ovoid, wider towards posterior end. Aperture wide, nearly as long as body whorl, narrowing posteriorly. Small raised spire of four whorls. Posterior edge of outer lip joining body whorl immediately below spire in soft shoulder. Parietal wall covered with thick, smooth white callus. Spiral sculpture composed of punctuated striations. Punctations ovoid, in rows of variable size.

Radula: Lateral teeth curved, with fine denticulation on one of the edges (Schepman 1913).

Digestive tract: Paired gizzard plates subquadrate, with rounded corners (Schepman 1913).

Male reproductive system: Unknown.

Ecology: Found at 2798 m.

Distribution (Fig. 15): Banda Sea, off Southeast Sulawesi Island, Indonesia (Schepman 1913).

Remarks: To our knowledge, only one representative (the holotype) of the species has ever been sampled. It shares the visible spire of *S. grandis* and *S. imperceptus* (both also originally described under the genus *Meloscaphander*), *S. meridionalis*, and *Scaphander obnubilus*. However, considering the variability of shells observed in those species, only the study of additional shells, anatomical details, and ideally DNA sequences could clarify the status of this species.

Scaphander amygdalus sp. nov.

(**Figs 8, 28, 29; Table 2**)

Scaphander cf. *otagoensis* 3—Siegwald *et al.* 2022.

ZooBank LSID: urn: lsid:zoobank.org:act:77914A80-336C-4D73-9155-1E7782C0D529

Etymology: Latin, *amygdalum*; almond. Named after its almond-shaped shell.

Type material: **Australia**: New South Wales, Hunter Commonwealth Marine Reserve, holotype, dissected and sequenced, *AM C.563070*, H = 29 mm. **New Zealand**: between the South Island and the Chatham Islands, 43°58′55.2″S, 179°37′40.8″E, one paratype, sequenced, NIWA 48567, H = 13 mm.

Other material examined: **Australia**: New South Wales, Hunter Commonwealth Marine Reserve, one spc., AM C.590965, H = 27 mm; three spcs, AM C.519357, H = 17–21 mm; one spc., AM C.600442, H = 32 mm; Central Eastern Commonwealth Marine Reserve, one spc., dissected and sequenced, AM C.519351, H = 27 mm. **New Zealand**: west of the North Island, one spc., sequenced, NIWA 30512, H = 9 mm; off Kahurangi, three spcs, one sequenced, NIWA 30374, H = 10–13 mm; one spc., sequenced, NIWA 30469, H = 9 mm; northeast of Christchurch, one spc., sequenced, NIWA 30258, H = 20 mm;

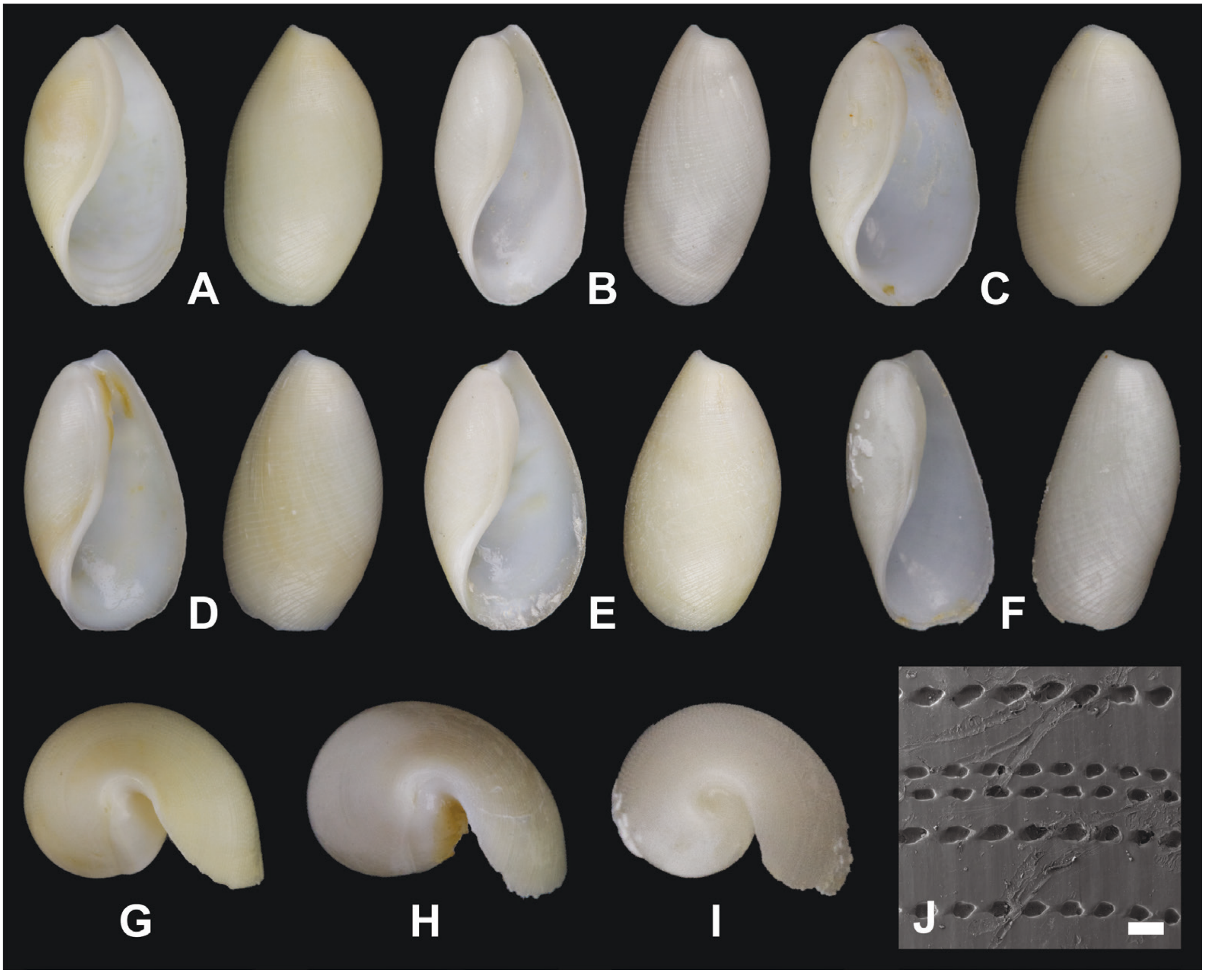

Figure 28. Shell and SEM image of the shell sculpture of ***Scaphander amygdalus***. A, Australia, New South Wales, Hunter Commonwealth Marine Reserve (holotype, *AM C.563070*, H = 29 mm). B, New Zealand (paratype, NIWA 48567, H = 13 mm). C, Australia, New South Wales, Central Eastern Commonwealth Marine Reserve (AM C.519351, H = 27 mm). D, New Zealand (NIWA 30258, H = 20 mm). E, Australia, New South Wales, Hunter Commonwealth Marine Reserve (AM C.590965, H = 27 mm). F, New Zealand (NIWA 30469, H = 9 mm). G, Australia, New South Wales, Hunter Commonwealth Marine Reserve (holotype, *AM C.563070*, H = 29 mm). H, New Zealand (NIWA 30258, H = 20 mm). I, New Zealand (NIWA 30469, H = 9 mm). J, Australia, New South Wales, Central Eastern Commonwealth Marine Reserve (AM C.519351, H = 27 mm). Scale bar: J = 200 µm.

one spc., sequenced, NIWA 30235, H = 8 mm; one spc., sequenced, NIWA 30291, H = 8.5 mm.

Diagnosis: Shell elongate to oval, covered by thin, cream-coloured periostracum. Spiral sculpture composed of ovoid punctations in rows. Spire concealed; posterior edge of outer lip rising slightly above apex. Rachidian teeth sub-rectangular. Prostate short, cylindrical. Penial papilla absent. Penial chamber bulged and lined with soft warts around prostatic duct entrance.

Shell (Fig. 28): Maximum H observed = 29 mm. Shell elongate to oval, widest around centre, only one whorl visible. Aperture wide, as long as shell, narrowing posteriorly. Spire concealed. Posterior edge of outer lip rising slightly above apex. Parietal wall covered with thick, smooth white callus. Spiral sculpture composed of punctuated striations. Punctations ovoid, separate. Periostracum thin, translucent to cream coloured. Shell dirty white to pale yellow.

Radula (Fig. 29A–C): Radular formula 19 × 1.1.1 (H = 29 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth sub-rectangular, with cusps acutely curved inwards.

Digestive tract (Fig. 29D, E): Salivary glands medium long, surface uneven. Paired gizzard plates sub-triangular to kidney-shaped.

Male reproductive system (Fig. 29F, G): Penial chamber cylindrical, lined with soft longitudinal ridges towards genital opening, bulged around prostatic duct entrance, lined with soft warts. Muscular papilla absent. Penial chamber separated

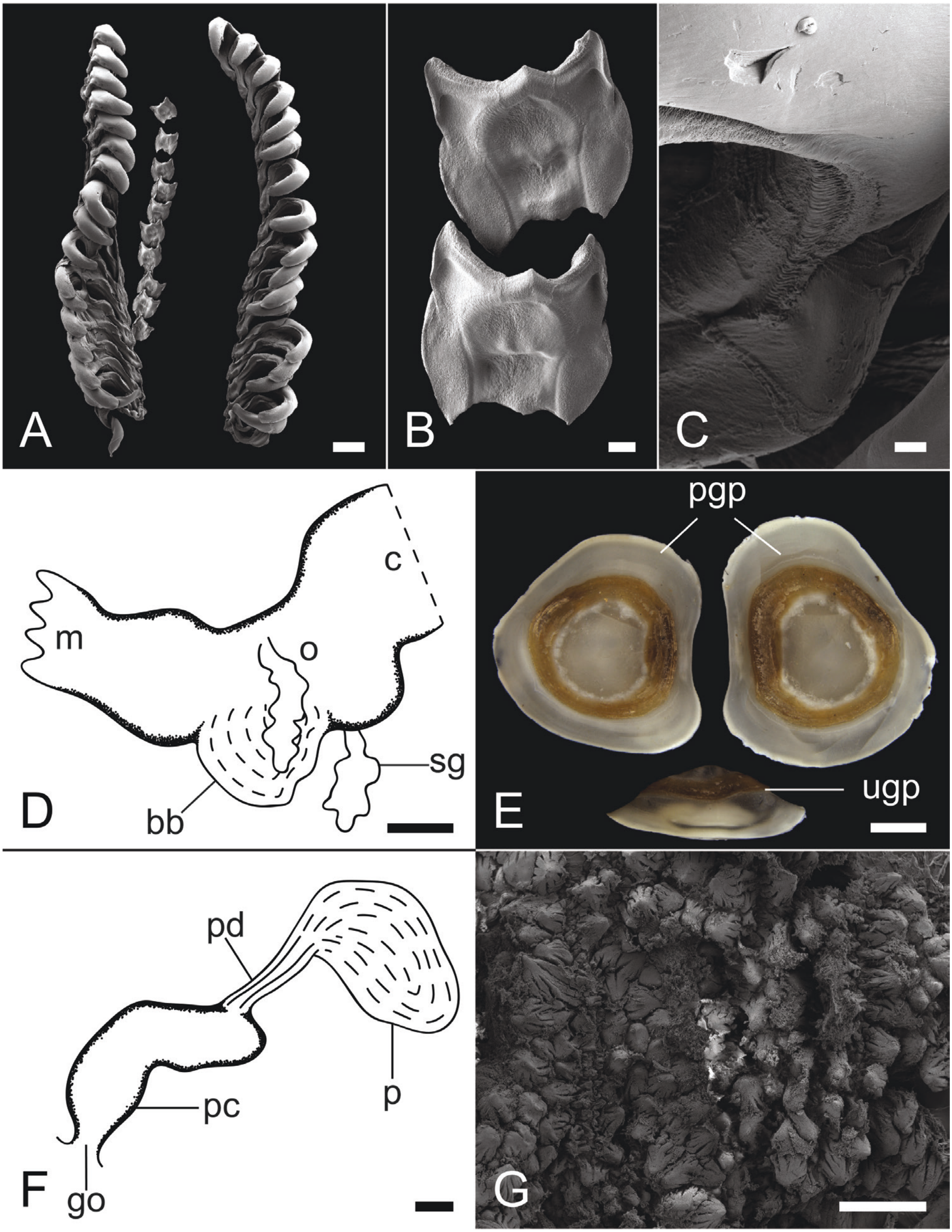

Figure 29. Anatomical details of ***Scaphander amygdalus***. A, radula, Australia, New South Wales, Central Eastern Commonwealth Marine Reserve (holotype, *AM C.563070*, H = 29 mm). B, rachidian teeth (holotype, *AM C.563070*, H = 29 mm). C, detail of lateral teeth (holotype, *AM C.563070*, H = 29 mm). D, anterior part of digestive tract, Australia, New South Wales, Central Eastern Commonwealth Marine Reserve (AM C.519351, H = 27 mm). E, gizzard plates (AM C.519351, H = 27 mm). F, male reproductive system (holotype, *AM C.563070*, H = 29 mm). G, lining of penial chamber (holotype, *AM C.563070*, H = 29 mm). Scale bars: A = 200 μm; B = 20 μm; C = 10 μm; D, F = 1 mm; E = 2 mm; G = 500 μm.

from prostate by thin prostatic duct. Prostate short, cylindrical, rounded at end.

Ecology: Found between 531 and 1257 m depth. Feeds on foraminifera (present study).

Distribution (Fig. 8): Southeastern Australia to Western and Eastern New Zealand.

Remarks: This species showed higher than average intraspecific variability for *COI*, with uncorrected *p*-distances of 0.18%–3.22%. However, no significant conchological or anatomical differences were noticed when studying the morphology of these sequenced specimens.

The shell of this species is similar in shape to the shell of *S. otagoensis* and *S. interruptus*, two sympatric species. However, *p*-distances between those species were unquestionably high (10.14%–11.76% between *S. amygdalus* and *S. interruptus*, 11.91%–13.39% between *S. amygdalus* and *S. otagoensis*, and 9.01%–10.03% between *S. otagoensis* and *S. interruptus*), and *S. amygdalus* is wider and more centrally rounded, with the rachidian teeth of *S. amygdalus* being noticeably wider and more indented than those of the other two. The shell of *S. amygdalus* is also similar to elongate forms of *S. mundus* but has a more oval shape and pronounced narrowing at both anterior and posterior ends.

Scaphander cornus **sp. nov.**

(Figs 3, 30, 31; Table 2)

Scaphander mundus—Valdés 2008 (in part): 674–676, figs 40B, 42A, B.

Scaphander sp.1—Siegwald *et al.* 2022.

ZooBank LSID: urn:lsid:zoobank.org:act:BA92D17E-7185-487F-A1E1-88CDDCBF6BD5

Etymology: Latin, *cornu*; horn. Named after the shape of the posterior wing of the shell, which resembles a small horn.

Type material: **Australia**: Victoria, East Gippsland Commonwealth Marine Reserve, holotype, dissected and sequenced, *AM C.590968*, H = 23 mm; Bass Strait, one paratype, sequenced, AM C.563069, H = 34 mm.

Other material examined: **Australia:** Victoria, East Gippsland Commonwealth Marine Reserve, one spc., AM C.590962, H = 27 mm; New South Wales, Jervis Commonwealth Marine Reserve, one spc., dissected and sequenced, AM C.519368, H = 26 mm; Bass Strait, one spc., dissected and sequenced, AM C.590959, H = 30 mm. **New Caledonia:** Loyalty Basin, one sh., MNHN-IM-2010-2061, H = 27 mm.

Diagnosis: Shell ovoid, white. Spiral sculpture composed of sub-rectangular punctuations. Apex rounded. Posterior edge of outer lip rising above apex, in sharp curved wing. Rachidian teeth sub-rectangular. Prostate ovoid. Penial papilla absent. Penial chamber lined with soft warts around prostatic duct entrance.

Shell (Fig. 30): Maximum H observed = 34 mm. Shell ovoid, only one whorl visible. Aperture wide, as long as shell, narrowing posteriorly. Spire concealed. Posterior edge of outer lip rising in

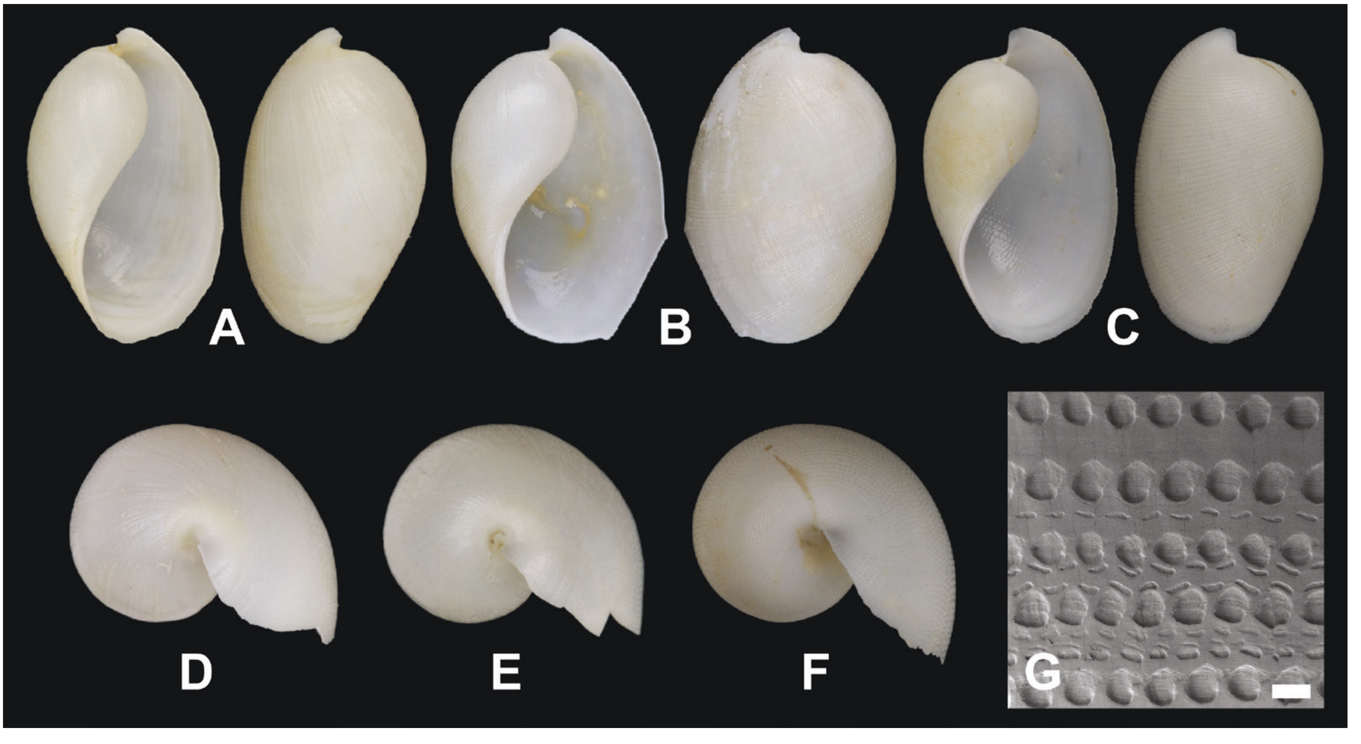

Figure 30. Shells and SEM image of the shell sculpture of ***Scaphander cornus***. A, Australia, Victoria, East Gippsland Commonwealth Marine Reserve (holotype, *AM C.590968*, H = 23 mm). B, Australia, Bass Strait (AM C.590959, H = 30 mm). C, New Caledonia, Loyalty Basin (MNHN-IM-2010-2061, H = 27 mm). D, Australia, Bass Strait (paratype, AM C.563069, H = 34 mm). E, Australia, New South Wales, Jervis Commonwealth Marine Reserve (AM C.519368, H = 26 mm). F, New Caledonia, Loyalty Basin (MNHN-IM-2010-2061, H = 27 mm). G, Australia, Bass Strait (AM C.590959, H = 30 mm). Scale bar: G = 200 μm.

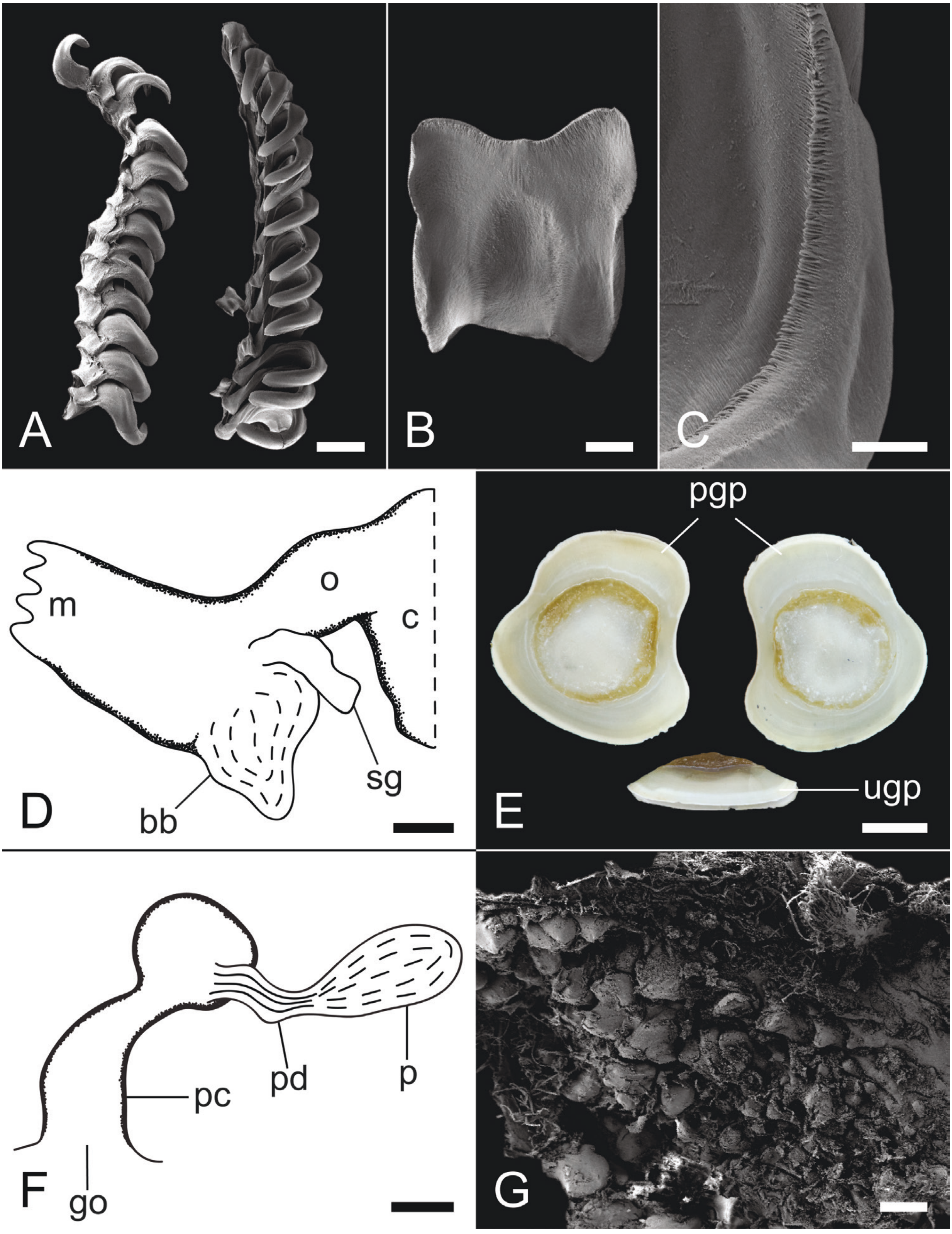

Figure 31. Anatomical details of ***Scaphander cornus***. A, radula, Australia, New South Wales, Jervis Commonwealth Marine Reserve (AM C.519368, H = 26 mm). B, rachidian teeth (AM C.519368, H = 26 mm). C, detail of lateral teeth (AM C.519368, H = 26 mm). D, anterior part of digestive tract, Australia, Bass Strait (AM C.590959, H = 30 mm). E, gizzard plates (AM C.590959, H = 30 mm). F, male reproductive system, Australia, Victoria, East Gippsland Commonwealth Marine Reserve (holotype, *AM C.590968*, H = 23 mm). G, lining of penial chamber (AM C.590959, H = 30 mm). Scale bars: A, G = 200 μm; B, C = 20 μm; D, F = 1 mm; E = 3 mm.

sharp curved wing protruding well beyond apex. Parietal wall covered with slight, smooth white callus. Spiral sculpture composed of punctuated striations. Punctations sub-rectangular, of variable shape and size. Thin, translucent periostracum. Shell white.

Radula (Fig. 31A–C): Radular formula 16 × 1.1.1 (H = 30 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth sub-rectangular, with rounded cusps.

Digestive tract (Fig. 31D, E): Salivary glands medium long; surface uneven. Paired gizzard plates kidney-shaped.

Male reproductive system (Fig. 31F, G): Penial chamber cylindrical, widening towards prostatic duct, lined with soft longitudinal ridges towards genital opening, bulged and lined with warts around prostatic duct entrance. Prostatic duct short. Muscular penial papilla absent. Prostate ovoid.

Ecology: Found between 2338 and 2760 m depth. Feeds on foraminifera (present study).

Distribution (Fig. 3): Southeastern Australia and New Caledonia.

Remarks: Scaphander cornus is remarkably similar to its sister species *S. nobilis*, but has a slightly more rounded shell and lacks a penial papilla. It is also similar to *S. mundus*, another white-shelled species found in Eastern Australia and New Caledonia. This resemblance led, for example, Valdés (2008) to include specimens of this new species among the lots used in his redescription of *S. mundus*. However, *S. mundus* has a less rounded, more elongated shell, with a thinner, less curved wing at the posterior edge of the outer lip of the shell. The species *S. cornus* also seems to dwell in deeper bottoms (2338–2760 m) than *S. mundus* (900–1800 m).

***Scaphander obnubilus* sp. nov.**

(Figs 15, 32, 33; Table 2)

Scaphander sp.3—Siegwald *et al.* 2022.

ZooBank LSID: urn:lsid:zoobank.org:act:68312AEC-383B-431B-A5DD-3609B2342F66

Etymology: Latin, *obnubilus*; clouded, concealed. Named for the subtle differences between its shell and the shell of its sister species.

Type material: **Australia:** Bass Strait, holotype, dissected and sequenced, *AM C.482192*, H = 20 mm; New South Wales, Jervis Commonwealth Marine Reserve, one paratype, dissected and sequenced, AM C.519273, H = 16 mm.

Other material examined: **Australia:** Bass Strait, one spc., sequenced, AM C.590969, H = 15 mm.

Diagnosis: Shell ovoid, white. Spiral sculpture composed of sub-rectangular to ovoid punctuated striations. Small, flat spire partly separated from body whorl by a suture widening into a groove along upper part of parietal wall. Outer lip rounded posteriorly, slightly protruding beyond apex. Smooth white callus thickening the parietal wall. Rachidian teeth sub-quadrate, with upper cusps pointing outwards. Prostate cylindrical, separated from penial chamber by short prostatic duct. Penial papilla cylindrical, covered with warts and wrinkles.

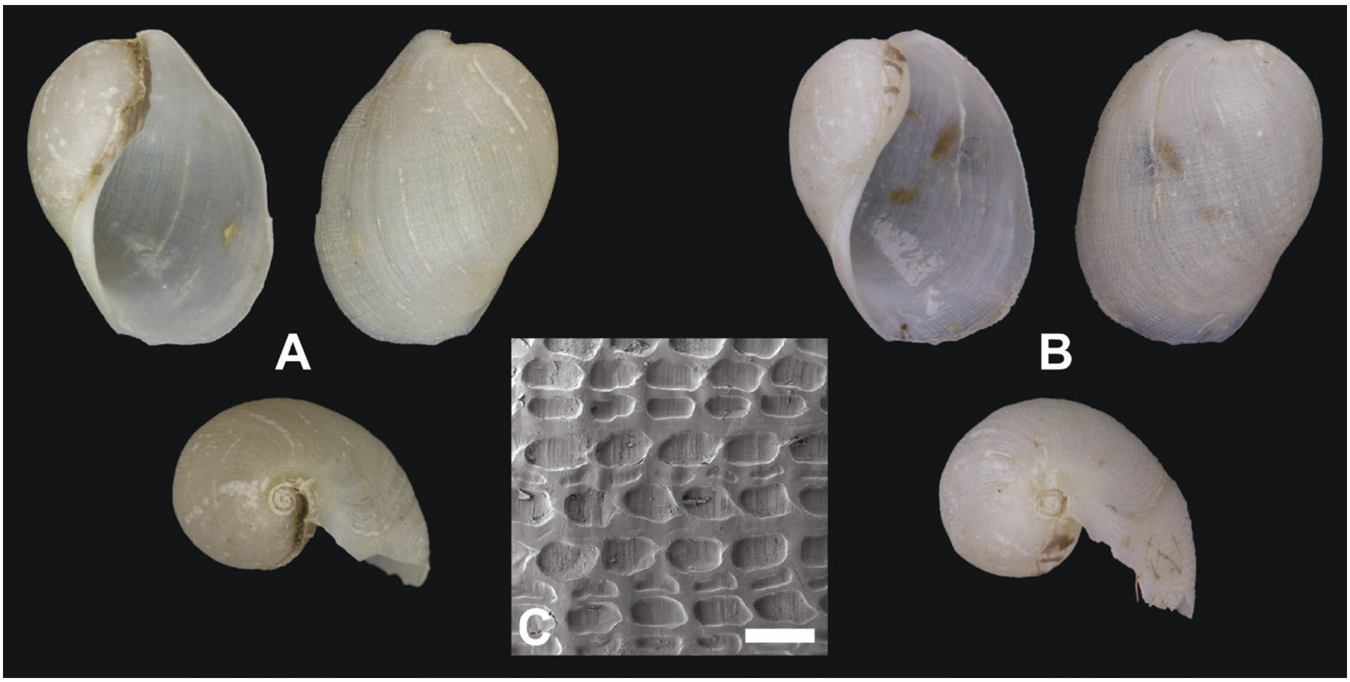

Figure 32. Shells and SEM image of the shell sculpture of ***Scaphander obnubilus***. A, Australia, Bass Strait (holotype, *AM C.482192*, H = 20 mm). B, C, Australia, New South Wales, Jervis Commonwealth Marine Reserve (paratype, AM C.519273, H = 16 mm). Scale bar: C = 400 μm.

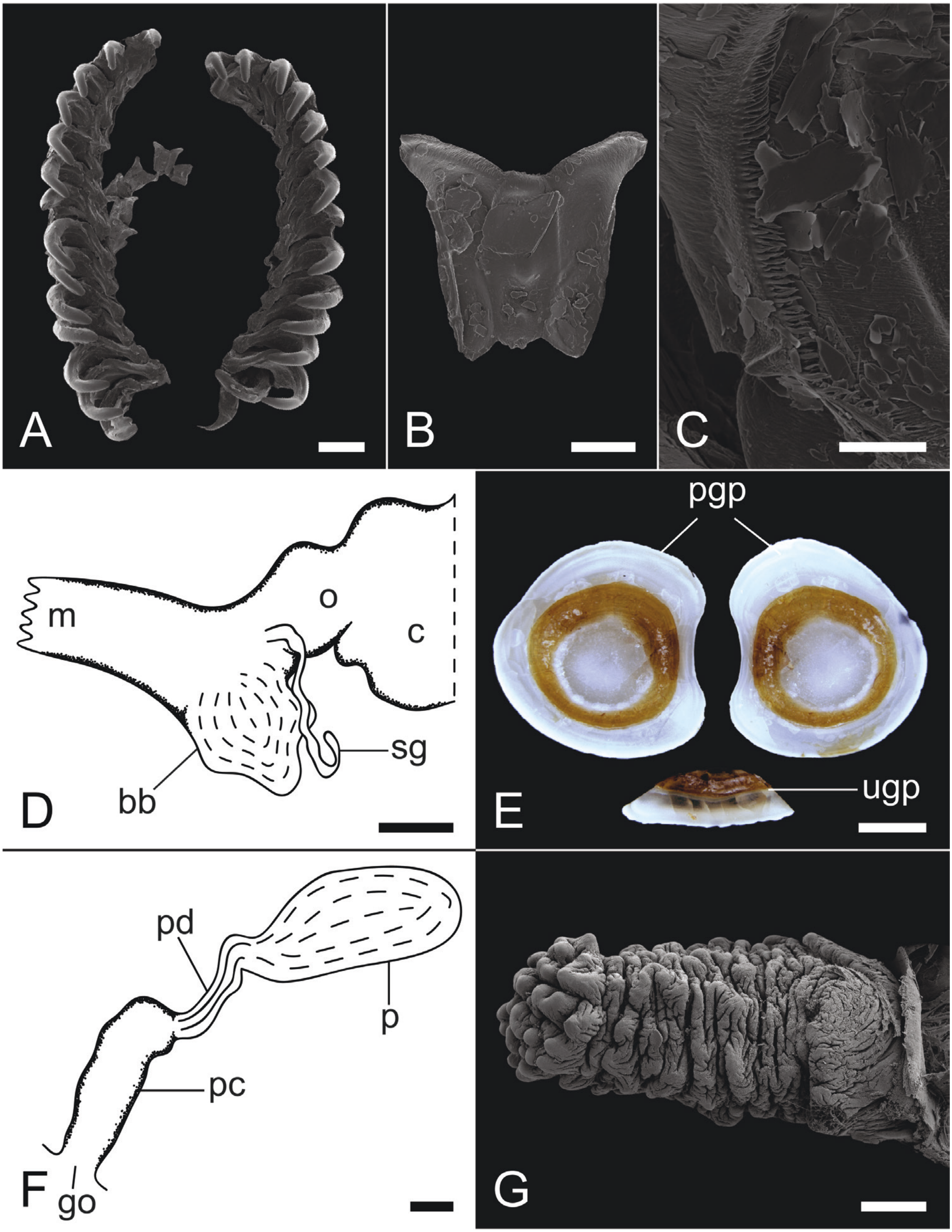

Figure 33. Anatomical details of ***Scaphander obnubilus***. A, radula, Australia, New South Wales, Jervis Commonwealth Marine Reserve (paratype, AM C.519273, H = 16 mm). B, rachidian teeth (paratype, AM C.519273, H = 16 mm). C, detail of lateral teeth (paratype, AM C.519273, H = 16 mm). D, anterior part of digestive tract (paratype, AM C.519273, H = 16 mm). E, gizzard plates, Australia, Bass Strait (holotype, *AM C.482192*, H = 20 mm). F, male reproductive system (holotype, *AM C.482192*, H = 20 mm). G, penial papilla (holotype, *AM C.482192*, H = 20 mm). Scale bars: A, G = 200 µm; B = 40 µm; C = 20 µm; D, F = 1 mm; E = 2 mm.

Shell (Fig. 32): Maximum H observed = 20 mm. Shell ovoid. Aperture wide, as long as shell, narrowing towards posterior. Small flat spire of three to four whorls. Suture partly separating the spire from the body whorl, widening into a groove along upper part of the parietal wall. Posterior edge of outer lip joining body whorl immediately below spire in rounded shoulder rising beyond apex. Parietal wall covered with thick, smooth white callus. Spiral sculpture composed of punctuated striations. Punctuations ovoid to sub-rectangular, of variable size. Thin, translucent periostracum. Shell white.

Radula (Fig. 33A–C): Radular formula 15 × 1.1.1 (H = 16 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth sub-quadrate, with broad cusps pointing sharply outwards on one end.

Digestive tract (Fig. 33D, E): Salivary glands long, thin; surface smooth. Paired gizzard plates sub-triangular to kidney-shaped.

Male reproductive system (Fig. 33F, G): Penial chamber cylindrical, lined with soft longitudinal ridges between genital opening and prostatic duct. Penial papilla muscular, cylindrical, covered in warts and wrinkles. Penial chamber separated from prostate by thin prostatic duct, widening towards prostate. Prostate cylindrical, rounded at end.

Ecology: Found between 2636 and 2760 m depth. Feeds on foraminifera (present study).

Distribution (Fig. 15): Australia, between the southern part of New South Wales and the Bass Strait.

Remarks: The shell of *S. obnubilus* is similar to other spire-bearing species of *Scaphander* from the Pacific, such as *S. grandis*, *S. meridionalis*, *S. planeticus*, and *S. tortuosus*. However, the outer lip of *S. obnubilus* does not form a shoulder against the body whorl as in *S. grandis*, *S. planeticus*, and *S. tortuosus*, but is rounded and rises slightly above the apex instead. The shells of *S. meridionalis* show remarkable variability (Fig. 26), but they never depict such a wide and curved aperture as in *S. obnubilus*. Furthermore, the uncorrected *p*-distances for *COI* of these two species range from 5.78% to 6.87%.

***Scaphander semicallus* sp. nov.**

(Figs 21, 34, 35; Table 2)

Scaphander sp.2—Siegwald *et al.* 2022.

ZooBank LSID: urn:lsid:zoobank.org:act:3E290146-3337-43B2-9B7A-D367D0DAEE9C

Etymology: Latin, *semi*; half, *callum*; callus. Named after the callus covering only the anterior half of the parietal wall of the shell.

Type material: **Mozambique**: offshore of Inhambane, 23°35′12.6″S, 36°05′52.8″E, 1092–1195 m, holotype, dissected and sequenced, *MNHN-IM-2013-52464*, H = 16 mm.

Diagnosis: Shell, elongate, grey-white. Spiral sculpture composed of small, separate ovoid punctations. Apex rounded, with posterior edge of outer lip rising above it in a small wing. Rachidian teeth X-shaped. Prostate cylindrical, separated from penial chamber by prostatic duct. Muscular penial papilla absent.

Shell (Fig. 34): Maximum H observed = 16 mm. Shell elongate, only one whorl visible. Aperture as long as shell, narrowing posteriorly. Spire concealed. Posterior edge of outer lip rising in small wing beyond apex. Parietal wall covered with thick, smooth white callus in anterior half. Spiral sculpture composed of punctuated striations. Punctations ovoid, separate. Thin, translucent to beige periostracum. Shell grey-white.

Radula (Fig. 35A–C): Radular formula 13 × 1.1.1 (H = 16 mm). Lateral teeth curved, with weak denticulation on inner edge. Rachidian teeth X-shaped, with developed cusps, squarish ends.

Digestive tract (Fig. 35D, E): Salivary glands short and small; surface uneven. Paired gizzard plates kidney-shaped.

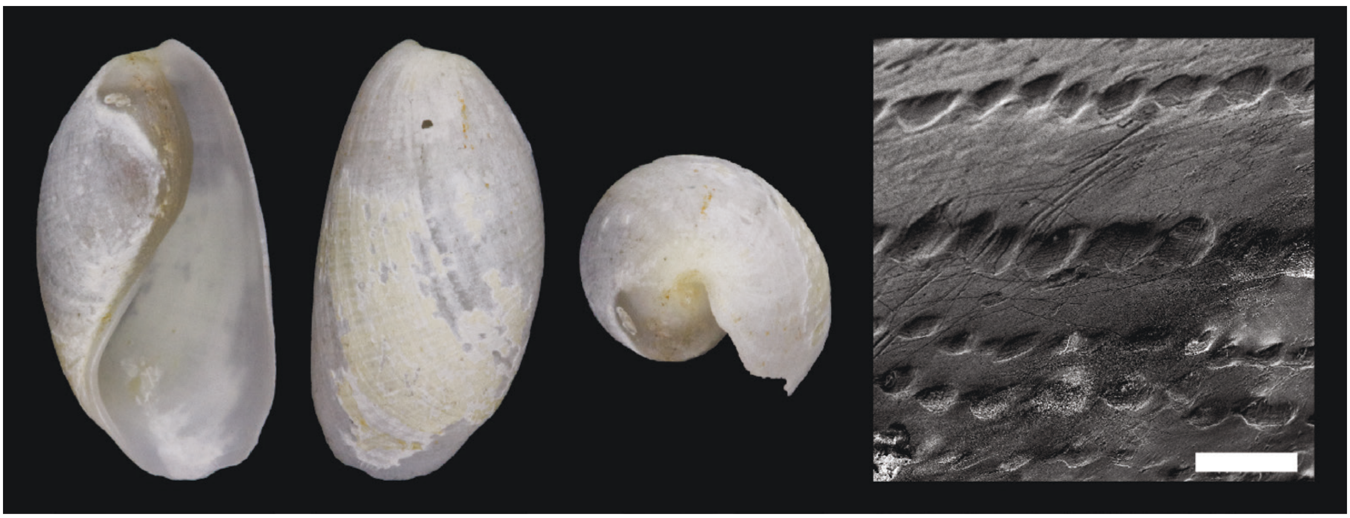

Figure 34. Shell and SEM image of the shell sculpture of ***Scaphander semicallus***, Mozambique, off Inhambane (holotype, *MNHN-IM-2013-52464*, H = 16 mm). Scale bar: 100 µm.

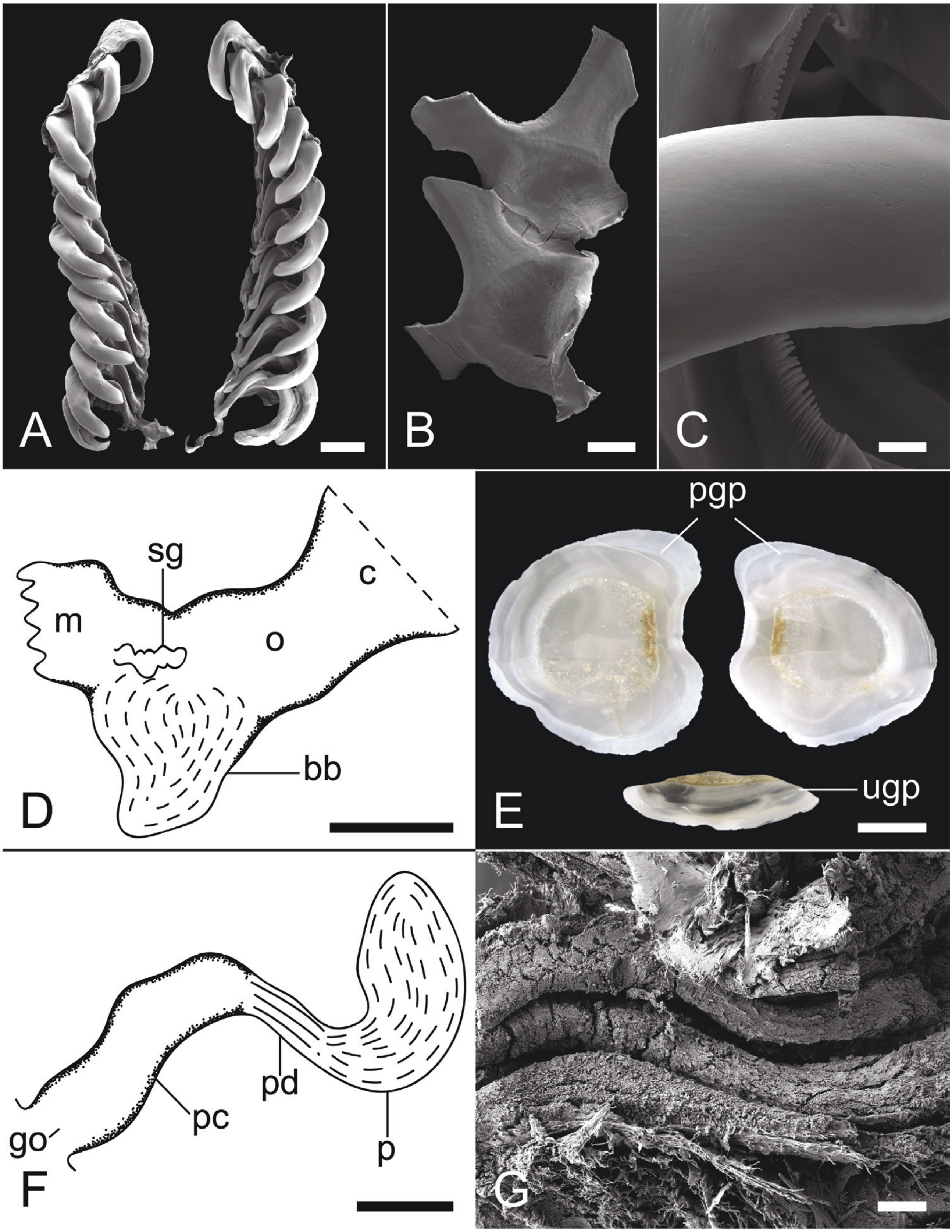

Figure 35. Anatomical details of ***Scaphander semicallus***, Mozambique, offshore Inhambane (holotype, *MNHN-IM-2013-52464*, H = 16 mm). A, radula. B, rachidian teeth. C, detail of lateral teeth. D, anterior part of digestive tract. E, gizzard plates. F, male reproductive system. G, lining of penial chamber. Scale bars: A, G = 100 μm; B = 20 μm; C = 10 μm; D, F = 1 mm; E = 2 mm.

Male reproductive system (Fig. 35F, G): Penial chamber cylindrical, lined internally with longitudinal ridges between genital opening and prostatic duct. Eversible penial papilla located at prostatic duct entrance; penial papilla thin, with apical tip rounded, covered in soft warts and wrinkles. Penial chamber separated from prostate by thin prostatic duct, widening towards prostate. Prostate oval, rounded at end.

Ecology: Found between 1092 and 1195 m depth. Feeds on foraminifera (present study).

Distribution (Fig. 21): Mozambique in the Western Indian Ocean.

Remarks: This species is known from a single specimen collected in Mozambique at bathyal depths. Its elongate shell is similar to the non-angular form of the Atlantic *Scaphander gracilis* Watson, 1883 (Locard 1897, Siegwald and Malaquias 2022), but can be distinguished easily by its parietal callus, which covers only the anterior half of the parietal wall, instead of the entire wall as in *S. gracilis*. Based on estimates of *COI* uncorrected *p*-distances, the two species are 9.27% distinct. The X-shape of the rachidian teeth of *S. semicallus* is, so far, unique among the genus.

Scaphander solomonensis sp. nov.

(Figs 21, 36, 37; Table 2)

Scaphander sp.4—Siegwald *et al.* 2022.

ZooBank LSID: urn:lsid:zoobank.org:act:AB362B0B-586D-4B6D-892C-B42C4F841A04

Etymology: After its type locality, the Solomon Islands.

Type material: **Solomon Islands**: northwest of Choiseul, holotype, dissected and sequenced, *MNHN-IM-2019-7924*, H = 12 mm; northwest of Isabel, one paratype, dissected and sequenced, MNHN-IM-2013-52483, H = 11 mm.

Other material examined: **Solomon Islands**: northwest of Choiseul, one spc., dissected and sequenced, MNHN-IM-2013-52480, H = 7 mm; one spc., MNHN-IM-2019-11703, H = 11 mm; northwest of Isabel, one spc., sequenced, MNHN-IM-2019-7923, H = 10 mm; one spc., MNHN-IM-2013-52481, H = 10 mm.

Diagnosis: Shell ovoid to attenuate, dirty white. Spiral sculpture composed of punctuated grooves or rows of distinct punctuations. Apex rounded. Posterior edge of outer lip rising above apex, in a small rounded wing. Rachidian teeth quadrate to H-shaped. Prostate cylindrical, separated from penial chamber by prostatic duct. Penial chamber lined with soft longitudinal ridges.

Shell (Fig. 36): Maximum H observed = 12 mm. Shell ovoid to attenuate, only one whorl visible. Aperture wide, as long as shell, narrowing posteriorly. Apex rounded, spire slightly umbilicate. Posterior edge of outer lip rising in small rounded wing protruding beyond apex. Parietal wall covered with white callus; thick, smooth in anterior half; thin to inconspicuous in posterior half. Spiral sculpture composed of punctuated striations or grooves. Punctations ovoid, separate or interconnected in spiral grooves of uneven width. Thin, white to translucent periostracum. Shell dirty white.

Radula (Fig. 37A–C): Radular formula 17 × 1.1.1 (H = 11 mm). Lateral teeth curved, with fine denticulation on inner edge.

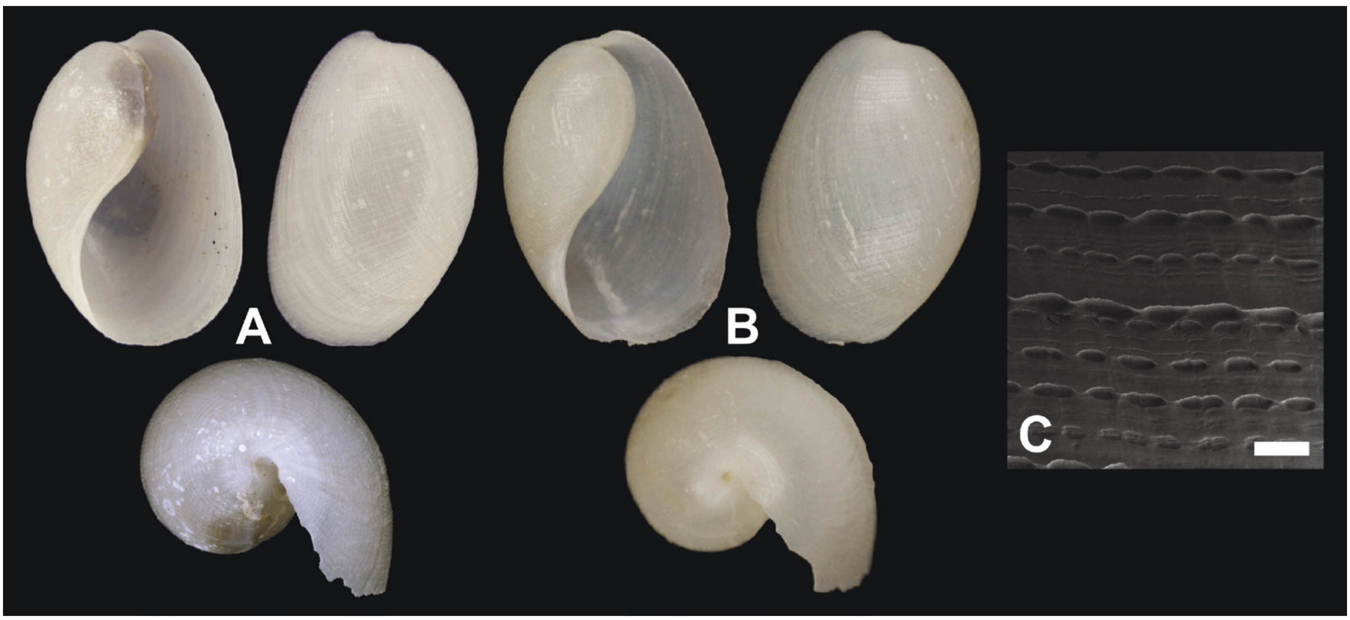

Figure 36. Shells and SEM image of the shell sculpture of ***Scaphander solomonensis***. A, Solomon Islands, northwest of Choiseul (holotype, *MNHN-IM-2019-7924*, H = 12 mm). B, Solomon Islands, northwest of Choiseul (paratype, MNHN-IM-2013-52483, H = 11 mm). C, Solomon Islands, northwest of Isabel (MNHN-IM-2019-7923, H = 10 mm). Scale bar: C = 200 μm.

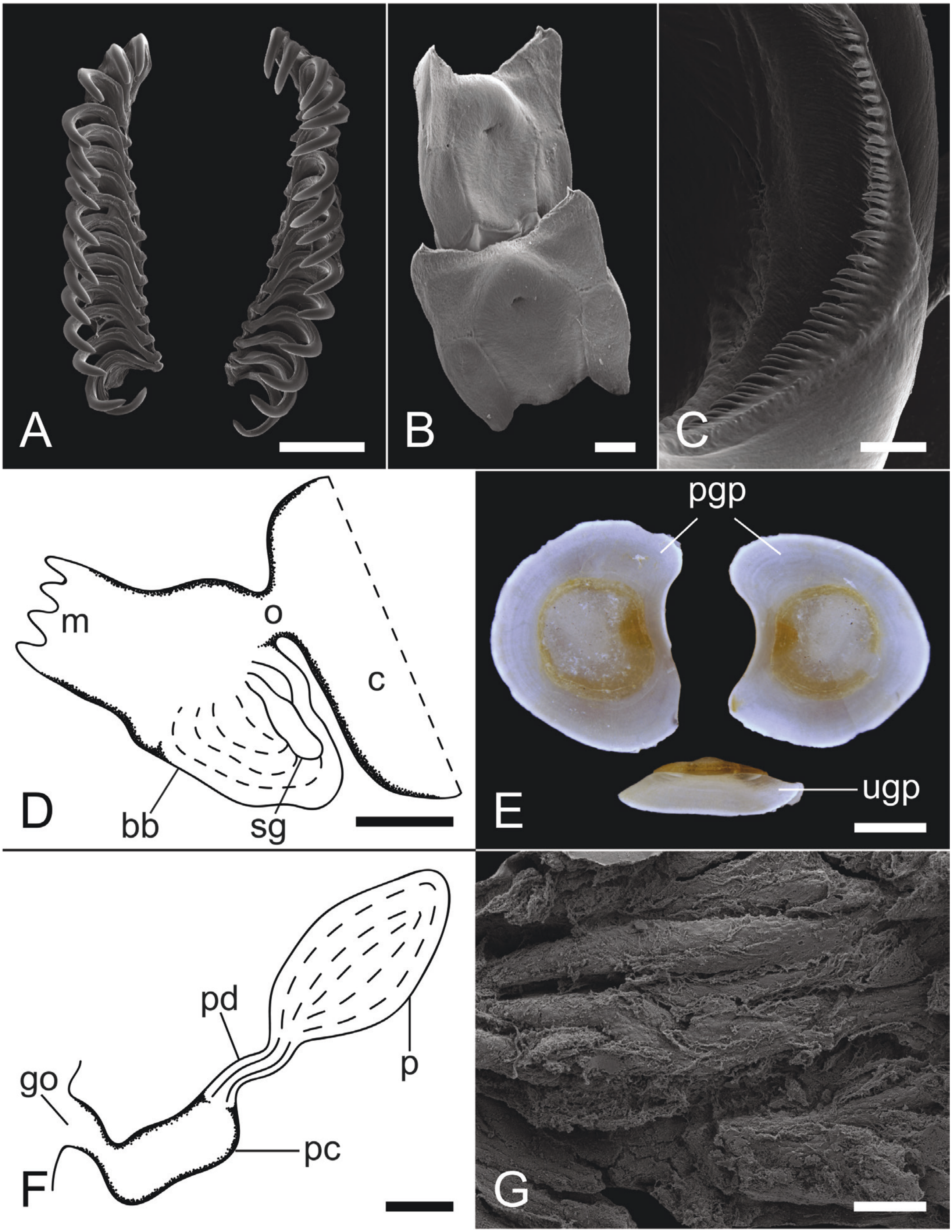

Figure 37. Anatomical details of ***Scaphander solomonensis***. A, radula, Solomon Islands, northwest of Choiseul (paratype, MNHN-IM-2013-52483, H = 11 mm). B, rachidian teeth, Solomon Islands, northwest of Choiseul (MNHN-IM-2013-52480, H = 7 mm). C, detail of lateral teeth, Solomon Islands, northwest of Choiseul (holotype, *MNHN-IM-2019-7924*, H = 12 mm). D, anterior part of digestive tract (MNHN-IM-2013-52480, H = 7 mm). E, gizzard plates (MNHN-IM-2013-52480, H = 7 mm). F, male reproductive system (holotype, *MNHN-IM-2019-7924*, H = 12 mm). G, lining of penial chamber (MNHN-IM-2013-52480, H = 7 mm). Scale bars: A = 200 μm; B, C = 10 μm; D, F = 500 μm; E = 1 mm; G = 100 μm.

Rachidian teeth sub-rectangular to H-shaped, with upper cusps curved inwards.

Digestive tract (Fig. 37D, E)*:* Salivary glands medium long; surface smooth. Paired gizzard plates sub-triangular to kidney or crescent-shaped.

Male reproductive system (Fig. 37F, G)*:* Penial chamber cylindrical, narrower towards genital opening, widening towards prostatic duct, lined with soft longitudinal ridges. Muscular papilla absent. Penial chamber separated from prostate by thin prostatic duct, widening towards prostate. Prostate cylindrical, distal end narrower.

Ecology: Found between 718 and 1100 m depth. Feeds on foraminifera (present study).

Distribution (Fig. 21)*:* Solomon Islands (present study).

Remarks: Scaphander solomonensis resembles its sister species *S. teramachii* from Japan, but has a wider and more ovate shell. In addition, the wart structure lining the penial chamber of *S. teramachii* was not found in *S. solomonensis*, which has soft longitudinal ridges lining the interior of the chamber.

Remarks on taxa originally assigned to *Scaphander* but of doubtful or different taxonomic affiliation

Adams (1862) described six species of *Scaphander* from the Seas of China and Japan, with short Latin descriptions, no measurements of the shells, and no illustrations. Despite our efforts, we could not locate any type material for these species.

(1) *Nipponoscaphander japonicus* (Adams, 1862) [original designation *Scaphander japonicus* Adams, 1862]

Remarks: The species *S. japonicus* Adams, 1862 was assigned to the genus *Bucconia* by Kuroda and Habe (1954), who provided illustrations of specimens identified by Adams. These authors later transferred the species to the newly described genus *Nipponoscaphander* erected based on *S. japonicus* (Kuroda *et al.* 1971). Later, the species has been ascribed arbitrarily either to *Scaphander* (Valdés 2008, Poppe 2010, Hori 2017) or to *Nipponoscaphander* (Guangyu 1997, Qi 2004), but recently, Siegwald *et al.* (2022) confirmed the affiliation of *S. japonicus* with the genus *Nipponoscaphander*, based on molecular phylogenetic evidence.

(2) *Philine cumingii* (Adams, 1862) [original designation *Scaphander cumingii* Adams, 1862]

Remarks: The species *Scaphander cumingii* Adams, 1862 was illustrated and redescribed as *Bucconia cumingii* by Habe (1954), but was afterwards assigned to *Bucconia* (Habe 1955, Hori 2000) and to *Nipponoscaphander* (Kuroda *et al.* 1971, Guangyu 1997). Valdés (2008) concluded that it belongs to the genus *Philine*, based on the anatomical study of specimens.

(3) ?*Philine sieboldii* (Adams, 1862) [original designation *Scaphander sieboldii* Adams, 1862]

Remarks: In the original description of this species, Adams (1862) mentioned that 'The only species at all resembling this is *S. pectinatus*'. *Scaphander pectinatus* is a species that Adams (1855) described originally as *Bulla pectinata* and which was later synonymized with *Philine scabra* (Müller, 1784) (Müller 1784, Lemche 1948, Menke 1954). This would suggest the affiliation of this species in the genus *Philine*.

(4) *Scaphander dilatatus* Adams, 1862 *nomen inquirendum*

(5) *Scaphander elongatus* Adams, 1862 *nomen inquirendum*

(6) *Scaphander sulcatinus* Adams, 1862 *nomen inquirendum*

Remarks: As mentioned above, the descriptions by Adams (1862) of *Scaphander* were brief and elusive and were not accompanied by any illustrations. To our knowledge, the names *S. dilatatus*, *S. elongatus*, and *S. sulcatinus* have not been used after the original descriptions, unless in direct quotations of the work by Adams (1862) (e.g. Pilsbry 1893, Habe 1955). We therefore suggest these names to be considered as *nomina inquirendae*, i.e. names attributed to species of doubtful identity requiring further investigation.

Sabatia takedai (Habe, 1981) [original designation *Nipponoscaphander takedai* Habe, 1981]

Remarks: Re-evaluation of the original description and examination of the type material (NSMT Mo-58234; Habe 1981) of *Scaphander takedai* (Habe 1981) (original designation *Nipponoscaphander takedai* Habe, 1981) showed that it has an ovate shell with a thick tuberculate callus (Fig. 38A). This is a synapomorphy of the genus *Sabatia* (Siegwald *et al.* 2022), and therefore the species is here reassigned to the latter genus.

Scaphander bushirensis (Melvill & Standen, 1901) [original designation *Cylichna bushirensis* Melvill & Standen, 1901]

Remarks: This species was described from the Persian Gulf under the genus *Cylichna* (Melvill & Standen 1901) and was reassigned to the genus *Scaphander* by one of its authors (Melvill 1906). The name *Scaphander bushirensis* (Melvill & Standen, 1901) was subsequently used on a few occasions (e.g. Brouwer *et al.* 2000, Al-Kayat *et al.* 2021) and is today the accepted name for this species (MolluscaBase 2022b). Despite the small size of the shell (H ≈ 9 mm), it is well formed and seems to be an adult. Its robustness, presence of deep spiral striae all over the shell, smooth, thick columella, convex lateral sides, and slight pyriform shape could point to *Scaphander*, but during the present study we did not find any material resembling this shell among worldwide collections from this geographical area, and no adult *Scaphander* species of such small size are known. We maintain here this species in the genus *Scaphander*, but this taxonomic affiliation warrants caution and future confirmation (Fig. 38B).

Scaphander ceylanicus Smith, 1904 [original designation *Scaphander ceylanica* Smith, 1904]

Remarks: This species was described based on an empty shell collected by the *Investigator* off the coast of Sri Lanka. Annandale and Stewart (1909) illustrated the shell collected by the *Investigator* and, based on the interpretation of this illustration

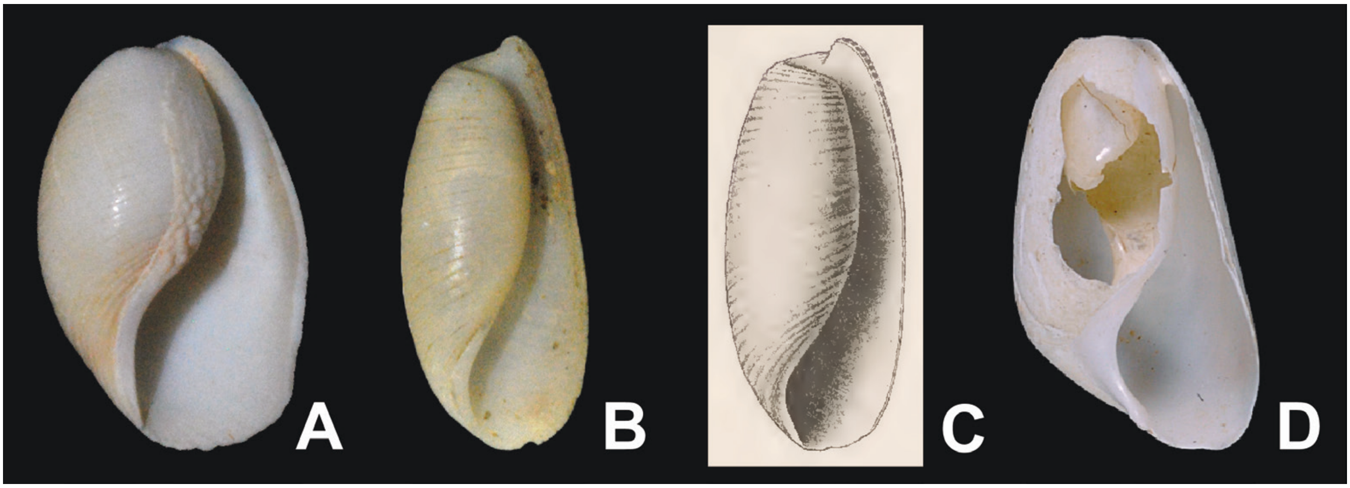

Figure 38. Shells of taxa previously assigned to *Scaphander*. A, *Sabatia takedai*, Hawaii, Oahu Island, off Honolulu (paratype, *Nipponoscaphander takedai*, NSMT Mo-58234, H = 6 mm). B, *Cylichna bushirensis*, Persian Gulf, Bushire (syntype, NHMUK 1901.12.9.55, H = 9 mm). C, *Cylichna ceylanica*, [illustration by Annandale and Stewart (1909) of the original material for *Scaphander ceylanica* collected on the *Investigator*, H = 9 mm]. D, *Cylichnium willetti*, Alaska, Forrester Island (holotype, *Scaphander willetti*, *USNM 216405*, H = 12.5 mm).

(Fig. 38C), we presume that it might represent the same species discussed above, namely *S. bushirensis* (Melvill & Standen, 1901). Nevertheless, until new material is available for study and comparison this remains speculative, and both species names are thus here kept as valid.

Scaphander willetti Dall, 1919

Remarks: Dall (1919) described *Scaphander willetti* based on a broken empty shell of 12 mm height from Forrester Island, Southern Alaska (Fig. 38D). This taxonomic assignment was corroborated by Valdés (2019), but in our opinion, despite the presence of a sculpture made of faint spiral lines of oval pits, the features of this shell do not entirely fit *Scaphander*. The sharp pyriform outline, wide anterior aperture, and flat spire and shoulder are together characters absent in *Scaphander*. However, we feel unable at this stage to ascribe this broken shell confidently to any known genus; therefore, until additional evidence is available, we follow the assessment by Valdés (2019).

Phylogenetics and species delimitation analyses

For the 12S, 18S, and 28S genes, the unmasked alignments yielded better-resolved trees, showing higher node support (Supporting Information, Figs S2–S4, S8–S13). For the 16S gene, the alignment with relaxed Gblocks settings yielded the better-resolved tree with higher node support (Supporting Information, Figs S5–S7). Therefore, the concatenated dataset was composed of the *COI* alignment (658 bp, 93 sequences), the 12S unmasked alignment (350 bp, 50 sequences), the 16S alignment masked with relaxed Gblocks settings (403 bp, 55 sequences), the 18S unmasked alignment (989 bp, 48 sequences), and the 28S unmasked alignment masked with relaxed Gblocks settings (1463 bp, 47 sequences) and included a total of 3863 bp from 93 specimens.

The Bayesian inference analysis retrieved *Scaphander* as monophyletic (PP = 1), but the relationship with its probable sister clade *Sabatia* was not resolved (PP = .71), as was also the case in th study by Siegwald *et al.* (2022) (Fig. 39).

The best-scoring ASAP analysis retrieved 21 molecular *Scaphander* lineages for the three models used. Those were congruent with the previous molecular species hypothesis by Siegwald *et al.* (2022), except for *S. teramachii*, which was split in two based on distribution in the current ASAP analyses (Fig. 39).

Some of the morphologically defined putative species were not supported as a single cluster by the STACEY delimitation analysis when using a PP threshold of .95 (*S. amygdalus*, *S. teramachii*, and *S. watsoni*). However, when applying a lower threshold of .80, all the morphologically defined species were supported as single clusters (Supporting Information, Fig. S14), including *S. teramachii*, which was split by the ASAP analysis.

The *COI* uncorrected *p*-distances ranged from 0% to 3.9% within putative *Scaphander* lineages and from 3.91% to 17.83% between lineages (Supporting Information, Table S2).

DISCUSSION

Historically, the taxonomy and diversity of the genus *Scaphander* has been confusing and elusive. Recent efforts have been made to study its phylogenetics and establish a sound taxonomy, but most studies have a regional focus (Valdés 2008, Eilertsen and Malaquias 2013a, Chaban *et al.* 2019a, Siegwald *et al.* 2020, 2022, Siegwald and Malaquias 2022). In this work, of the 32 extant species currently recognized in MolluscaBase (2022a), 25 were retrieved as valid, three were established as synonyms to accepted species, and two were reassigned to other genera. In addition, five species are newly described from the Indo-West Pacific, bringing the number of worldwide *Scaphander* species to 33; including five cases of *taxon inquirendum* (Table 3).

In most cases, intraspecific *p*-distances for *COI* were inferior to ~1.5%, except for *S. amygdalus* (0.18%–3.22%) and *S. teramachii* (0%–3.9%). The specimens of *S. amygdalus* clustered together in the ASAP analysis, but in the STACEY analysis they clustered together only when using the lower threshold PP value (.85), whereas the specimens of *S. teramachii* were split into two partitions in the ASAP analysis, but clustered together

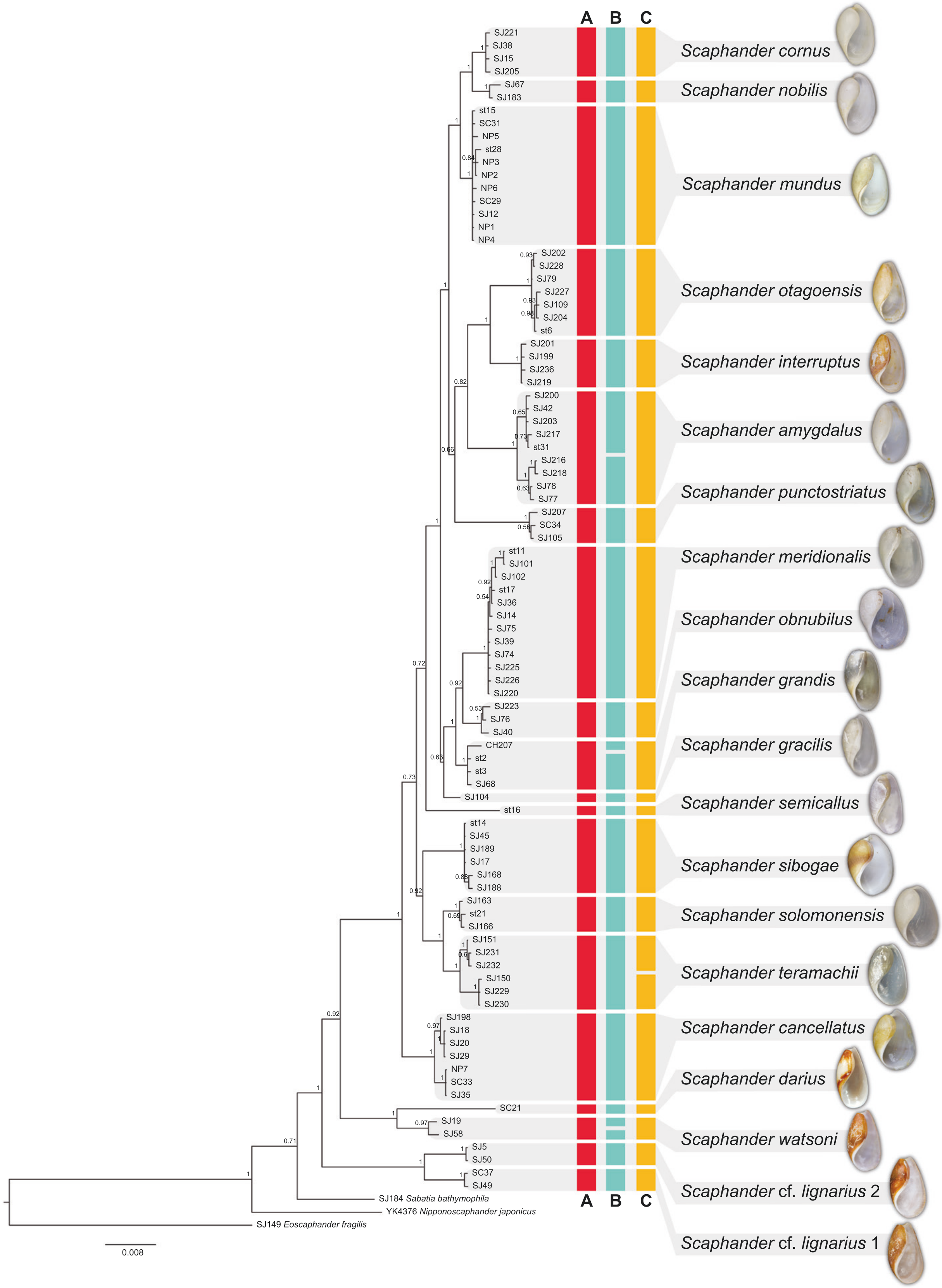

Figure 39. Bayesian phylogeny of *Scaphander* depicting relationships and species diversity of *Scaphander*. Hypothesis based on the combined analysis of the mitochondrial markers *COI*, 12S rRNA, and 16S rRNA, and the nuclear 18S rRNA and 28S rRNA. Numbers above branches represent posterior probabilities from the Bayesian analysis, and bands next to the tree depict the results from the species delimitation methods (A = STACEY with threshold value of .85%; B = STACEY with threshold value of .95%; C = ASAP).

Table 3. Alphabetical list of worldwide accepted species of the genus *Scaphander*.

Species
Scaphander amygdalus
Scaphander andamanicus Smith, 1894
Scaphander bushirensis (Melvill & Standen, 1901)
Scaphander cancellatus Martens, 1902
Scaphander ceylanicus Smith, 1904
Scaphander clavus Dall, 1889
Scaphander cornus
Scaphander darius Marcus & Marcus, 1967
Scaphander dilatatus Adams, 1862 (*taxon inquirendum*)
Scaphander elongatus Adams, 1862 (*taxon inquirendum*)
Scaphander gracilis Watson, 1883
Scaphander grandis (Minichev, 1967)
Scaphander illecebrosus Iredale, 1925
Locard 1897
Scaphander imperceptus (Bouchet, 1975)
Scaphander interruptus Dall, 1890b
Scaphander laetus Thiele, 1925 (*taxon inquirendum*)
Scaphander lignarius (Linnaeus, 1758)
Scaphander meridionalis Siegwald, Pastorino, Oskars & Malaquias, 2020
Scaphander mundus Watson, 1883
Scaphander nobilis Verrill, 1884
Scaphander obnubilus
Scaphander otagoensis Dell, 1956
Scaphander pilsbryi McGinty, 1955 (*taxon inquirendum*)
Scaphander planeticus Dall, 1908
Scaphander punctostriatus (Mighels & Adams, 1842)
Scaphander semicallus
Scaphander sibogae Schepman, 1913
Scaphander solomonensis
Scaphander sulcatinus Adams, 1862 (*taxon inquirendum*)
Scaphander teramachii (Habe, 1954)
Scaphander tortuosus (Siegwald & Malaquias) nom. nov.
Scaphander watsoni Dall, 1881
Scaphander willetti Dall, 1919

in the STACEY analysis, even when using the higher threshold PP value (.95). In both cases, our morphological study did not reveal any significant conchological or anatomical differences between conspecific specimens. As was observed in previous works (Eilertsen and Malaquias 2013a, Chaban *et al.* 2019a, Siegwald *et al.* 2022), the type species for the genus *Scaphander*, the Atlantic *S. lignarius*, was retrieved as two separate lineages, with high intraspecific *p*-distances for *COI*. This suggests that *S. lignarius* might be a cryptic species complex and requires further investigation.

Shell characters such as the shape, spire structure, and posterior end of the outer lip, in combination with the anatomy of the male reproductive system, were found to be the most relevant characters for species delimitation (Table 2); however, those characters did not appear to be clade specific, although a proper cladistic analysis is necessary to retrieve any conclusions soundly. The penial papilla is often not developed in immature specimens (Eilertsen and Malaquias 2013a), and certain species do not possess one even in adult forms but can exhibit distinct warty structures in the penial chamber (e.g. *S. cancellatus* and *S. otagoensis*). Amorim *et al.* (2013) studied the male reproductive apparatus of the cephalaspid gastropod *Bulla striata* Bruguière, 1972 (Bruguière 1972) and concluded that in those snails, the penial chamber functioned as an eversible structure to bring out the penial papilla during copulation. Our morphological study suggests a similar function in *Scaphander* snails, both for species presenting a penial papilla and for species with only warts in the lining of the penial chamber. This view is reinforced by observations made in a fixed specimen of *S. cancellatus*, which presented the warty walls of the penial chamber everted outside the body cavity (Fig. 13).

For some species, only shell material was available (e.g. *S. andamanicus*, *S. illecebrosus*, and *S. interruptus*), with examples of species represented by one single specimen (e.g. *S. planeticus* and *S. tortuosus*, for which the holotype is the only sampled specimen on record). Shell variability was found to be species dependent; for species where we had enough specimens to assess intraspecific variability (≥10 spcs), some showed very conservative shells (such as in *S. sibogae*) but others showed considerable variability (such as in *S. meridionalis*). The latter might render species assignment based on shells alone problematic, especially in species for which few specimens have been sampled and in which shell intraspecific variability has not been studied previously (Eilertsen and Malaquias 2013a, Siegwald *et al.* 2022; present study). Further sampling and acquisition of anatomical and molecular data would shed light on those uncertain cases.

This work provides the first global phylogenetic and taxonomic framework to understand the systematics and evolution of the genus *Scaphander*, contributing overall to a better understanding of deep-sea biodiversity. The worldwide diversity of *Scaphander*, including all species discussed here, comprises 33 species; however, 10 remain known only from their shells, with five considered of doubtful status. About 73% of the known *Scaphander* diversity (24 of the 33 species recognized in this study) are found in the Indo-Pacific. Some species have a restricted distribution range (e.g. *S. otagoensis* only known from New Zealand; *S. teramachii* only known from Japan), whereas other species have amphi-oceanic ranges (e.g. *S. punctostriatus* in the Atlantic; *S. grandis* in the Pacific), and two species are even distributed across ocean basins (*S. meridionalis* and *S. nobilis*) (Table 2). The most diverse region is the Western Pacific (17 species), followed by the Atlantic (12 species) and the Indian Ocean (7 species), and as previously remarked by Siegwald *et al.* (2022), the biogeography of the genus *Scaphander* is not characterized by radiations unique to the Atlantic and eastern Pacific or to the Indo-West Pacific realms, but instead by an apparent polyphyletic pattern, with clades including species from more than one ocean realm. Contrary to shallow-water and costal habitats, little is known about speciation and biogeographical patterns in the deep sea, and this is often attributable to a lack of understanding of deep-sea biodiversity and species distributions. Therefore, the framework provided by this research creates a unique opportunity to address major questions about deep-sea evolution at a global scale.

SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

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CONFLICT OF INTEREST

None declared.

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AUTHOR CONTRIBUTIONS

Manuel António E. Malaquias (conceptualized the work and contributed to the experimental design, writing, and revision of the manuscript). Justine Siegwald (performed the literature review, morphological and molecular work, analyses, identification of the specimens, and writing of the manuscript).

DATA AVAILABILITY

The data underlying this article are available in the article and in its online Supporting Information.

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