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Hidden in plain sight: Systematic review of Indo-West Pacific Siphonariidae uncovers extensive cryptic diversity based on comparative morphology and mitochondrial phylogenetics (Mollusca, Gastropoda)

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Abstract

This study combines phylogenetic analyses of mitochondrial DNA sequences with comparative morphological analyses to revise the taxonomy of 101 nominal siphonariid species from the Indo-West Pacific belonging to the genera *Siphonaria* Sowerby I, 1823 and *Williamia* Monterosato, 1884. We have examined preserved specimens that have been newly collected at 462 sites across Australasia, the Indo-West Pacific, and in temperate zones of the northern and southern Pacific. Critically, our sampling includes topotypic specimens of 98 nominal species. The study area covered herein extends between the latitudes of 60°N and 55°S and the longitudes of 37°E and 175°W. We have sequenced two mitochondrial genes (COI and 16S) from 546 individuals and conducted a phylogenetic analysis including additional sequences from GenBank. We also studied the anatomy of 436 individuals using dissections and scanning electron microscopy. This study offers a comprehensive documentation and taxonomic assessment of type specimens for nearly all examined nominal species. Our taxonomic revision leads us to accept 88 species, which are thoroughly redescribed. 52 nominal species are treated as synonyms of earlier names, 41 of which are newly synonymized herein. Thirteen species names are deemed unavailable or invalid under the rules of zoological nomenclature, and six names are considered as *nomina dubia* or *nomina inquirenda*, notably including the oldest name, *Patella laciniosa*, which was widely used previously. In addition, we describe 40 new species. We have identified eleven species with broad distributions in the IWP and beyond and four species with more limited distributions than previously accepted. Notably, many species have narrow ranges, some being single island endemics. To stabilize taxonomic names, we have designated neotypes for seven species (*Siphonaria sipho* Sowerby I, 1823, *Patella japonica* Donovan, 1824, *S. obliquata* Sowerby I, 1825, *Pileopsis radiata* Blainville, 1826, *S. radians* H. Adams & A. Adams, 1855, *S. incerta* Deshayes, 1863, and *S. tasmanica* Tenison Woods, 1877) and lectotypes for 25 species (*Patella javanica* Lamarck, 1819, *S. albicante* Quoy & Gaimard, 1833, *S. atra* Quoy & Gaimard, 1833, *S. capensis* Quoy & Gaimard, 1833, *S. denticulata* Quoy & Gaimard, 1833, *S. diemenensis* Quoy & Gaimard, 1833, *S. guamensis* Quoy & Gaimard, 1833, *S. plana* Quoy & Gaimard, 1833, *S. plicata* Quoy & Gaimard, 1833, *S. punctata* Quoy & Gaimard, 1833, *S. viridis* Quoy & Gaimard, 1833, *S. savignyi* Krauss, 1848, *S. cancer* Reeve, 1856, *S. bifurcata* Reeve, 1856, *S. funiculata* Reeve, 1856, *S. kurracheensis* Reeve, 1856, *S. lirata* Reeve, 1856, *S. scabra* Reeve, 1856, *S. belcheri* Hanley, 1858, *S. nuttallii* Hanley, 1858, *S. nigerrima* Smith, 1903, *S. madagascariensis* Odhner, 1919, *S. alba* Hubendick, 1943, *M. lentulus* Iredale, 1940, *H. monticulus* Iredale, 1940 and *M. oppositus* Iredale, 1940).

Key words: Panpulmonata, *Siphonaria*, *Williamia*, taxonomy, nomenclature, endemism, anatomy

Introduction

The Siphonariidae are pulmonate limpet gastropods with an ovate, asymmetrical, and ribbed shell. These snails commonly occur on intertidal and subtidal rocky shores throughout the tropical, subtropical, and temperate zones around the world extending into the subpolar zones (i.e., up to latitudes of about 60° N and 55°S). We have identified 232 nominal species-group taxa within the Siphonariidae globally, excluding fossil taxa as well as subsequent incorrect spellings of original names (51) through an exhaustive literature search, which included also previously published taxonomic treatments (e.g., Hubendick 1946, White & Dayrat 2012, MolluscaBase Eds. 2021 accessed 15 April 2021). Many of these taxa were originally described by early taxonomists between the 1820s and 1860s with an almost exclusive focus on shell characters. An additional burst of taxonomic descriptions occurred in the 1940s. Again, species were then usually described with nearly exclusive emphasis on conchological features and to a lesser extent under consideration of additional features, such as radular characters. Frequently, species descriptions were based on comparatively few specimens, without an appropriate documentation of the amounts of intraspecific morphological variation. Subsequently, species boundaries have been extended to include samples collected from other locations than the type localities of described species based on conchological similarity with any of these earlier described taxa. Over time, changing assumptions about the diagnostic value of certain features, the amount of morphological variability within single species, and simple misidentifications have created a legacy of taxonomic chaos that has severely impacted our ability to identify species, delimit their distributions, and study their diversity and evolution.

These deeply rooted problems are epitomised by some lingering key taxonomic issues, which have remained unresolved for decades. For example, the identity and taxonomic relationships of some of the earliest described, and presumably most widespread nominal species, such as *Siphonaria laciniosa* (Linnaeus, 1758), *Siphonaria sipho* Sowerby I, 1823, *Siphonaria crenata* Blainville, 1827, *Siphonaria javanica* (Lamarck, 1822), *Siphonaria atra* Quoy & Gaimard, 1833, and *Siphonaria normalis* Gould, 1846 have remained questionable for the uncertain diagnostic value of shell characters (e.g., Dayrat *et al*. 2014, Güller *et al.* 2015). Hubendick (1945, 1946) provided the first comprehensive revision of the Siphonariidae, which he subsumed in the now unaccepted taxon 'Patelliformia', a non-monophyletic group that also included the 'Gadiniidae' (= Trimusculidae), an unrelated family of limpet-like gastropods. Hubendick (1945, 1946) delineated species exclusively by their shell and suggested a revised classification based on assessments of shell, radular, and reproductive characters. Within the genus *Siphonaria* Sowerby I, 1823, he recognised two subgenera, *Siphonaria* and *Liriola*, and five sections within each of these subgenera. Subsequently, Morrison (1972: 51) provided a revised classification with emphasis on shell shape and reproductive strategies, which was subsequently followed by Christiaens (1980a: 78). While different modes of larval development have been documented in *Siphonaria* (e.g., Chambers & McQuaid 1994a, 1994b), the reproductive strategies of most species remain unknown. Hubendick (1946: 5, 61) and Simone & Seabra (2017: 148) also indicated that the currently available information on the anatomy of species is generally inadequate to support a sound classification.

Molecular phylogenetic studies of siphonariids are still in their infancy, which poses a challenge in delineating natural groups. Teske *et al*. (2007) were among the first to use DNA sequence data to elucidate the taxonomy of four sympatric species in South Africa. Uncovering high amounts of intra-specific plasticity, they found that shell characters alone were not sufficient to correctly delimit species. Similarly, molecular phylogenetic analyses have been instrumental in uncovering cryptic species from the north Atlantic (Kawauchi & Giribet 2011, Giribet & Kawauchi 2015) as well as in revising the taxonomy of South American (Güller *et al.* 2015) and sub-Antarctic siphonariids (González-Wevar *et al.* 2018).

The most comprehensive molecular work to date is that of Dayrat *et al.* (2014), who sequenced 123 specimens from 93 locations throughout the Indo-West Pacific. They recovered 41 clades (called units **1** to **41**; these clade identifiers are also used herein), which were presumed to represent distinct species. While some of these units could readily be connected to certain species names for exhibiting recognisable shell groups, most of these units could not be confidently identified for being essentially indistinguishable from one another. Consequently, species names as traditionally conceived of were applied to several distinct clades each. In these cases, Dayrat *et al*. (2014) referred to species groups, such as the *normalis* group (units **12** to **14**), the *laciniosa* group (units **19** to **24**), and the *atra* group (units **30** to **41**), for example. It was considered likely that these species groups contained several shell-wise cryptic species that were difficult to distinguish. For sake of convenience and consistency, we continue to refer to these informal species groups throughout the present work.

Based on the lessons from previous studies, we realized that an integrative taxonomic approach was required to resolve the taxonomic status of these potentially cryptic species complexes correctly; an approach that draws on the assessment of shell characters in combination with comparative anatomical and molecular phylogenetic information. Furthermore, to fully disentangle the confusing taxonomy at the species level, it has been critical to examine topotypic material for as many nominal species as possible to correctly attribute these names to the species so delineated. The present revision is primarily concerned with all nominal species that have previously been reported from the Australian Exclusive Economic Zone (Australian EEZ) and adjacent waters, including both accepted species and their supposed synonyms. Currently, three genera and 16 species of siphonariids are accepted to occur in Australian waters (Stanisic 1998: 1068). However, through the body of taxonomic literature, altogether 149 nominal species-group taxa, occurring throughout the Pacific and Indian Oceans, have been related to these taxa through proposed synonymies. We revise the taxonomy of all these taxa based on studies of types, freshly collected topotypic material, and supplementary samples, both dry and ethanol preserved, by using an integrative approach that considers morphological (shell), anatomical (digestive and reproductive features) as well as molecular phylogenetic evidence.

At present, the most speciose genus of Siphonariidae in Australian waters is *Siphonaria*, which encompasses twelve currently accepted species. Less taxonomically diverse are *Pugillaria* Iredale, 1924 with three species as well as *Benhamina* Finlay, 1926 and *Williamia* Monterosato, 1884 each containing a single accepted species, *B. obliquata* (Sowerby, 1825) and *W. radiata* (Pease, 1861), respectively (e.g., Jenkins 2018).

Several species of *Siphonaria* as presently delineated are thought to be rather widespread within the Indo-West Pacific (IWP), with reported ranges extending to the shores of eastern Africa, Madagascar, the Arabian Peninsula, India, the Indo-Malay Archipelago, Japan, several Pacific Islands, and New Zealand. Wherever possible, we aimed to test these purportedly wide species distributions by examining specimens from these shores. Other species, however, are considered to have more restricted distributions within the Australian region (Stanisic, 1998). All known species of *Pugillaria* are endemic to the southern part of the Australian shelf, with *Pugillaria stowae* (Verco, 1906) being the most widespread species while both *Pugillaria oblia* Jenkins, 2018 and *Pugillaria emergens* Jenkins, 2018 are known from a few occurrences only (Jenkins 2018).

Williamia has been systematically revised by Marshall (1981). Accordingly, the only Recent species in the region has a planktonic larva and is widespread throughout the IWP with occurrences in Hawaii, Japan, and New Zealand among others. Most recently, *Williamia* has been shown to be the sister taxon of *Siphonaria* in a phylogenomic study of the Panpulmonata (Krug *et al*. 2022: 4, figs 1–2). Together, both genera form an isolated evolutionary lineage within the Panpulmonata > Pneumopulmonata, the Siphonariidae.

Materials and methods

Materials. This study is based on the examination of many newly collected, ethanol preserved samples from 419 locations (304 from around the Australian mainland as well as several islands in the Australian EEZ, and 115 from throughout the IWP (Table S1, Supplementary materials).

The sampling was designed to target the type locality of each nominal species under study to obtain topotypic material suitable for anatomical and molecular examination. Throughout this revision, we specifically refer to topotypes for specimens that have been collected at the type locality of a nominal species and that closely match its shell morphology as based on comparison

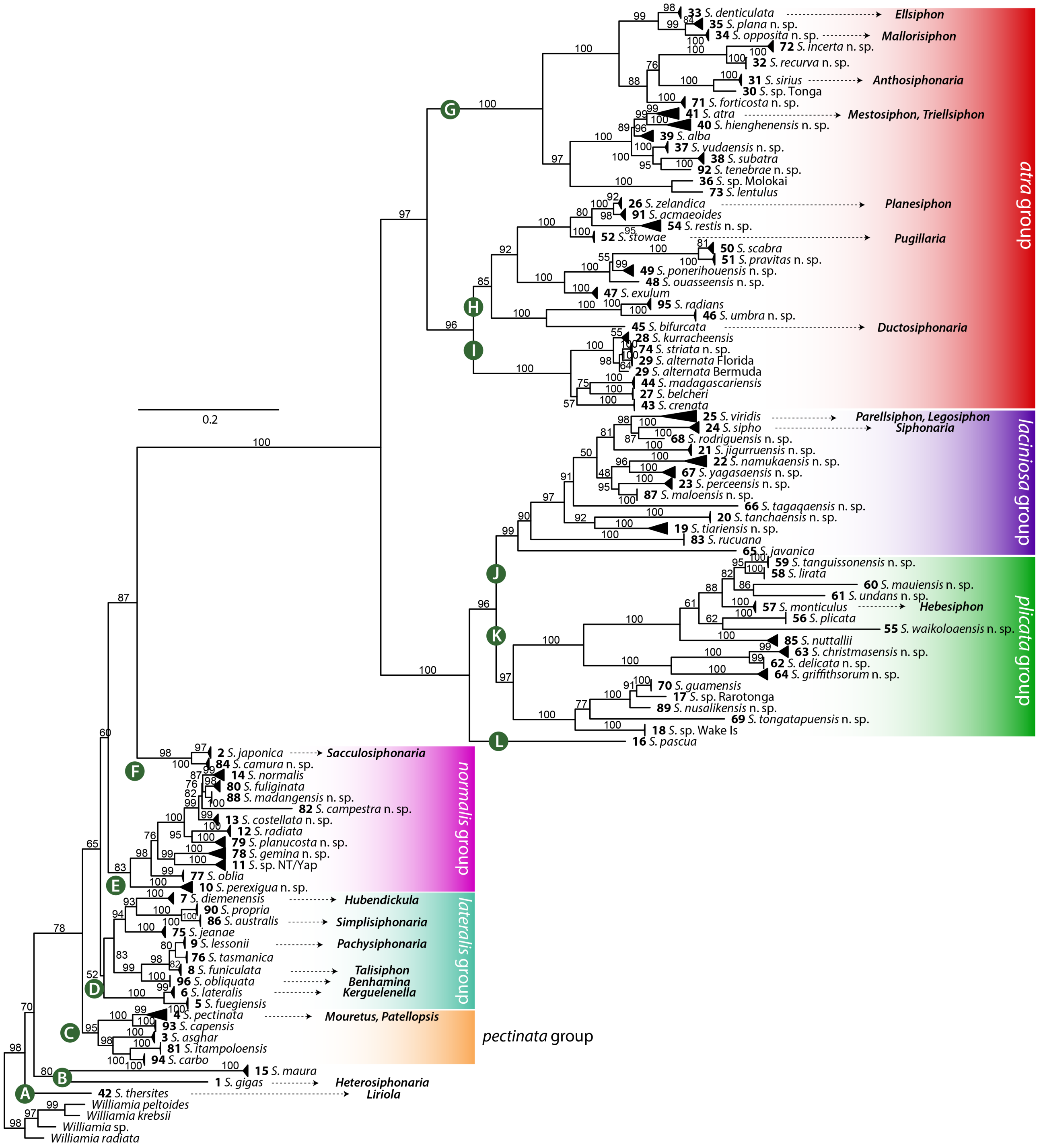

FIGURE 1. Maximum Likelihood phylogram based on analyses of a concatenated sequence data set of 16S and COI. Branches are collapsed at the species level. Branch labels give unit numbers and accepted species names. Numbers on branches indicate branch support employing 10,000 ultrafast bootstraps. Available genus-group names are shown next to their type species. Scale bar indicating modelled sequence divergence.

with original descriptions and types. To supplement our own samples, we included both ethanol-fixed and dry shell samples from various museums, including relevant types. Where type specimens were not accessible to us, we used photographs of type specimens instead. Overall, our sampling included specimens representing almost all nominal species previously recorded from the IWP. Crucially, it included topotypes from 79 out of 99 nominal species covered herein. All specimens newly sampled for this study have been collected under the necessary permits from the relevant jurisdictions.

Project collection locations are identified in the format [Abbreviated Locality-site identifier] (e.g., LHI02-3, Q50-2). All text references to examined samples indicate preservation status (p = preserved samples, d = dry shells, PH = photographic record) and number of specimens

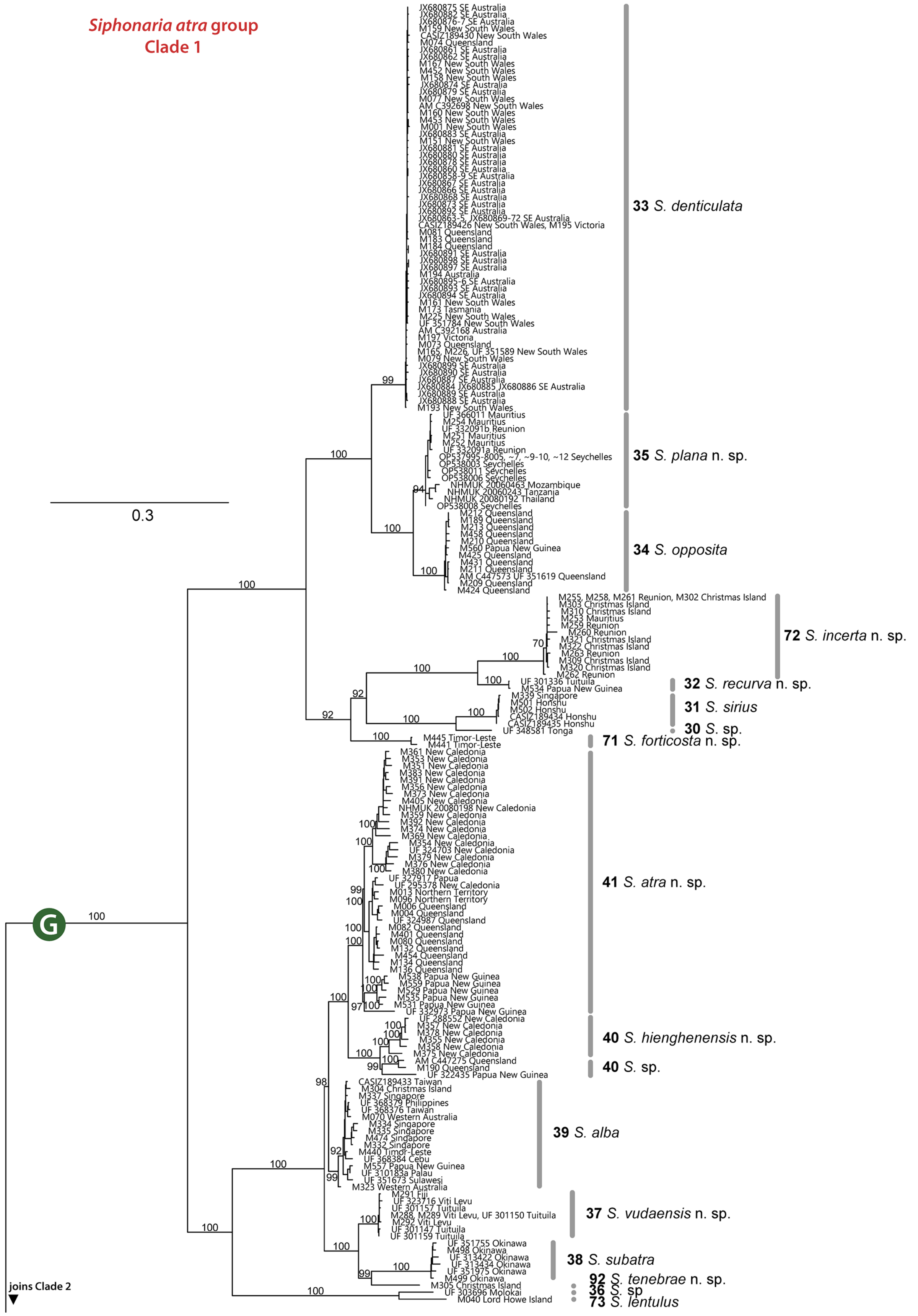

FIGURE 2. Maximum Likelihood phylogram (partial, species not collapsed). Clades G–I (*atra* group) of the tree shown in Fig. 1. Branch labels give specimen identifiers for new sequences or Genbank accession numbers for imported sequences from other studies and geographic regions (see Tables S1–S2 for details). Identical haplotypes are merged into single tips. Numbers on branches indicate branch support by employing 10,000 ultrafast bootstraps. Clade names give unit numbers and accepted species names. Scale bar indicating modelled sequence divergence. Figure spread over two pages.

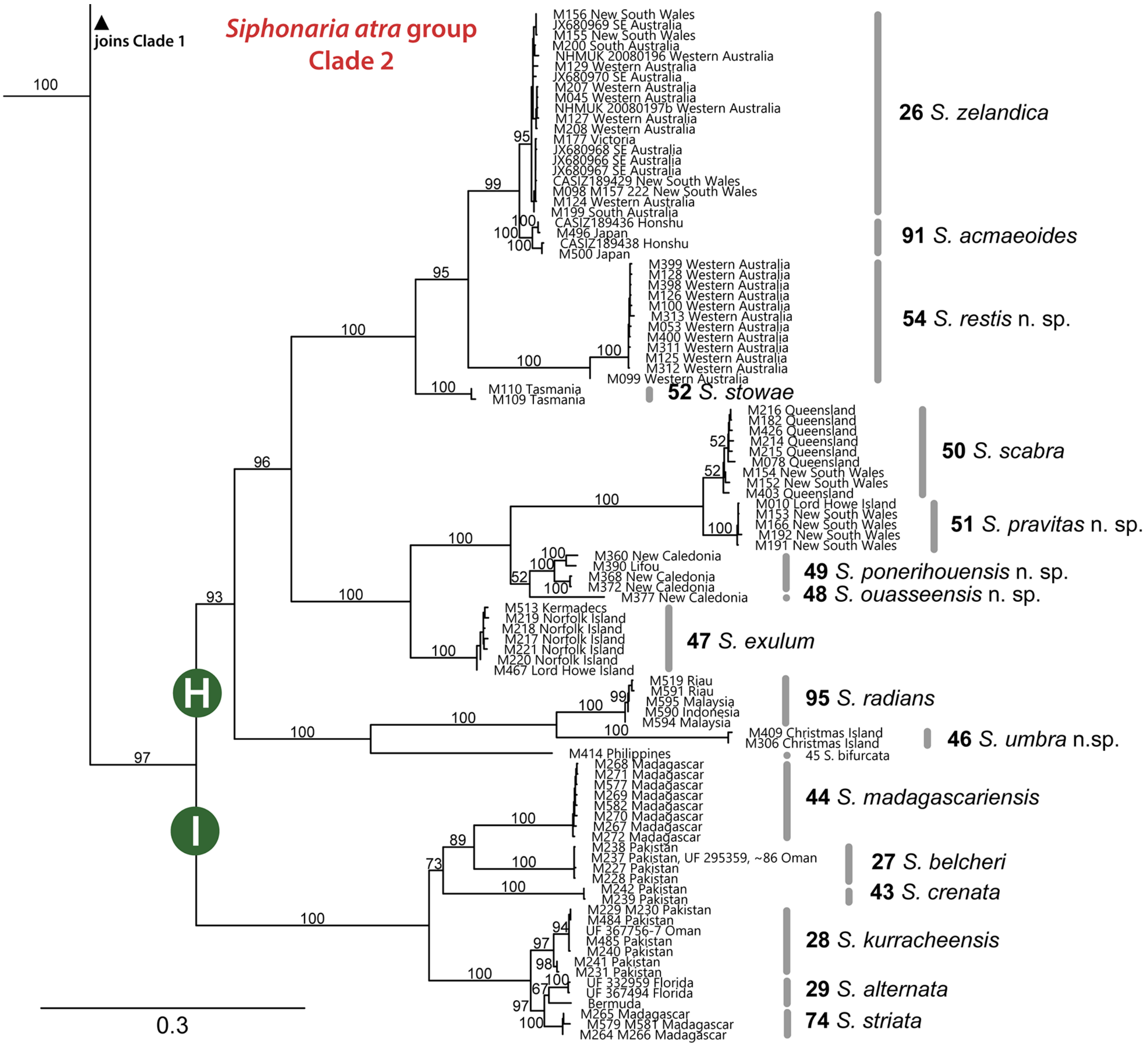

FIGURE 2. Continued.

studied. For reference, each examined specimen has been assigned a project-based specimen identifier for samples used for anatomical investigation ([SK] identifiers) and DNA sequencing ([M] identifiers). Both shell and soft bodies have been retained separately under these identifiers. Specimen identifiers are cross-referenced to the relevant museum lots (Table S1, Supplementary materials).

Abbreviations used. Institutions: AM, Australian Museum, Sydney, Australia; ANSP, Academy of Natural Sciences Philadelphia, Philadelphia, USA; AWMM, Auckland War Memorial Museum, Auckland, New Zealand; BPBM, Bernice Pauahi Bishop Museum, Honolulu, Hawaii, United States; BU, Bahria University, Karachi Campus, Pakistan; CBG, Centre for Biodiversity Genomics, University of Guelph, Ontario, Canada; CM, Canterbury Museum, Christchurch, New Zealand; GNS, GNS Sciences, Lower Hutt, New Zealand; ZCR, Lee Kong Chian Natural History Museum, Singapore; MAGNT, Museum and Art Gallery of the Northern Territory, Darwin, Australia; MBM, Marine Biological Museum, Chinese Academy of Sciences, China; MCZ, The Louis Agassiz Museum of Comparative Zoology, Harvard University in Cambridge, Massachusetts, USA; MHNG, Muséum d'Histoire naturelle de Genève, Geneva, Switzerland; MNHN, Muséum national d'Histoire naturelle, Paris, France; MV, Museums Victoria, Melbourne, Australia; NHMUK, Natural History Museum of the United Kingdom, London, United Kingdom; NMNZ, National Museum of New Zealand Te Papa, Wellington, New Zealand; NRM, Swedish Museum of Natural History, Stockholm, Sweden; OIST, Okinawa Institute of Science and Technology, Japan; PMNH, Pakistan Museum of Natural History, Islamabad, Pakistan; PUP, Polytechnic University of Philippines, Manila, Philippines; QM, Queensland Museum, Brisbane, Australia; RBCM, Royal British Columbia Museum, Victoria, Canada; SAM, South Australian Museum, Adelaide, Australia; TMAG, Tasmanian Museum and Art Gallery, Hobart, Australia; USNM, Smithsonian National

Museum of Natural History, Washington, USA; UUZM, Uppsala University, Museum of Evolution, Uppsala, Sweden; WAM, Western Australian Museum, Perth, Australia.

Geographic abbreviations. CI, Christmas Island, Indian Ocean, Australia; CKI, Cocos (Keeling) Island Group, Indian Ocean, Australia; GBR, Great Barrier Reef, Queensland, Australia; IWP, Indo-West Pacific; LHI, Lord Howe Island, Australia; MI, Macquarie Island, Australia; NC, New Caledonia; NI, Norfolk Island, Australia; NSW, New South Wales, Australia; NT, Northern Territory, Australia; NZ, New Zealand; PNG, Papua New Guinea; Qld, Queensland, Australia; SA, South Australia; Tas, Tasmania, Australia; Vic, Victoria, Australia; WA, Western Australia, Australia.

Shell characters. sl, longitudinal shell length at shell edge; sh, shell height, maximum distance from shell edge to highest apical point; sw, shell width at shell edge; ap.p, posterior apex offset, distance of the apex from the anterior shell edge; ap.l, lateral apex offset, distance of the apex from the right/siphonal ridge shell edge; nr, number of ribs; ADM, adductor muscle; CMS, cephalic muscle scar; BK, broken shell; ER, eroded shell; n, number in sample; SD, standard deviation.

Anatomy. AG, albumen gland; AL, length of animal; AO, accessory organ; BC, bursa copulatrix; BD, bursal duct; BM, buccal mass; CD, common duct (= spermoviduct); ED, epiphallus duct; EG, epiphallus gland; F1, flagellum 1; F2, flagellum 2; GA, genital atrium; GP, genital pore; HD, hermaphrodite duct; HG, hermaphrodite gland; MA, muscle-attachment (= 'retractor muscle' in Hubendick 1946: 11); MG, mucus gland; RAM, right adductor muscle; RS, reproductive system; SPM, spermatophore; SV, seminal vesicle.

Other abbreviations. TS, Topotypic specimen; TSs, topotypic specimens.

Anatomical and morphological studies. All samples have preliminarily been identified to morphospecies based on their shell morphology using comparisons with type specimens and under consideration of previous taxonomic treatments and revisions. These morphological candidate species are referred to as groups and were consistent with the '*laciniosa*', '*atra*' and '*normalis*' groups identified by Dayrat *et al.* (2014). This shell-based taxonomic concept was expanded on to include the '*plicata*', '*lateralis*', and '*pectinata*' groups. To investigate whether these shell-based groups could be further subdivided, we completed morpho-anatomical examinations on selected specimens from across the distributional range of each group. We included specimens representing the full range of shell variation exhibited within each sample to ensure that they exhibited consistent morphological and anatomical traits and to recognise possibly cryptic species. All descriptions of external morphology are based on freshly preserved specimens except where noted. We performed anatomical dissections of the reproductive system, including extraction and documentation of spermatophores. Anatomical drawings were produced using a stereo microscope with camera lucida. Point-to-point dimensions were measured using digital calipers and curved dimensions were measured using a Koizumi Comcurve 8 (precision 0.1 mm). We use the following terminology for reproductive system structures: epiphallic parts (also called distal parts; i.e., GA, AO, EG, ED and F1) and hermaphroditic parts (i.e., HG, HD, AG, SV, MG CD, BC and BD). Shells, radulae, and jaws were mounted on specimen stubs, coated with gold, and examined under a scanning electron microscope (Hitachi S-3400N EM). Unless otherwise indicated, photographs depict the anterior of shells in right-aligned dorsal and ventral views as well as the right-facing lateral views. The terminology used for shell geometry, including abbreviations, follows Jenkins (2018: 2, fig. 1). The following shell characters were quantified: length (sl), width (sw), height (sh), number of ribs (nr), and anterior (ap.p) and lateral (ap.l) distances. Extremely worn or juvenile shells were not measured except type specimens. Shell length was categorised as small (length < 15 mm), medium (length between 15 and 30 mm), and large (length > 30 mm). Shell height profile was categorised as a ratio of shell height: shell length as low (sh/sl < 0.25), medium (sh/sl between 0.25 and 0.33), and high (sh/sl > 0.33) aligning with methods described by Hubendick (1946: 11, figs 1–11) and Dayrat *et al.* (2014: 248). Posterior and lateral apex offset were categorised as ratios of sl/ap.p and sw/ap.l as central (< 1), weakly offset (1–3), and strongly offset (> 3), respectively.

Molecular studies and phylogenetic analyses. Genomic DNA was extracted from small pieces of foot muscle and/or mantle tissue of ethanol preserved samples by use of a QIAGEN DNA extraction kit for animal tissue (Qiagen, Hilden) following the standard procedure of the manual. An approximately 430 base pair long fragment of the mitochondrial 16S rRNA gene (16S) and a 658 base pair long fragment of the mitochondrial cytochrome c oxidase subunit 1 gene (COI) were amplified by PCR using the primers 16Sar and 16Sbr for 16S (Palumbi *et al.* 1996) and LCO1490 and HCO2198 (Folmer *et al.* 1994) or Lobo-F1 and Lobo-R1 (Lobo *et al.* 2013) for COI. PCR reactions were performed in 25 µl volumes using standard protocols with annealing temperatures of 50–55°C and elongation times of 60 s, each. Both strands of PCR fragments were purified, and cycle sequenced by use of the PCR primers. Electropherograms were corrected for misreads and forward and reverse strands were merged into one contig using CodonCode Aligner v. 3.6.1 (CodonCode Corp., Dedham, MA). Additional DNA sequences produced by previous phylogenetic studies (e.g., Colgan & da Costa 2013; Dayrat *et al.* 2014, Giribet & Kawauchi 2016, González-Wevar *et al.* 2018, Ossenbrügger *et al.* 2023) have been retrieved from Genbank and included in our sequence dataset. Sequences were aligned using the online version of MAFFT (version 7) available at www.http://mafft.cbrc.jp/alignment/server/ by employing the iterative refinement method G-INS-I (Katoh *et al.* 2002). Pairwise genetic distances between sequences were calculated by using the phylogenetic software MEGA7 (Kumar *et al.* 2016) under the option 'pairwise deletion of gaps'. The final sequence alignments of 16S and COI were concatenated into one partitioned data set. Four data partitions were designated, one for each codon position in COI and one for the 16S fragment. Phylogenetic relationships were estimated by employing a Maximum Likelihood-based method of tree reconstruction using the program IQ-TREE 2.2 (Nguyen *et al.* 2015). This analysis was performed using the integrated model finder function and the merge function (Kalyaanamoorthy *et al.* 2017). Nodal support of the ML tree was estimated by performing 10,000 ultrafast bootstrap repeats (Minh *et al.* 2013).

Sequences of *Williamia* spp. were used as outgroup to root the phylogenetic tree based on the established sister group relationship of *Siphonaria* and *Williamia* (Krug *et al*. 2022) (see Table S2 for a list of all used sequences including GenBank registration numbers). All newly generated sequences have been deposited with GenBank under the accession numbers PQ042508-PQ042972 and PQ036203-PQ036717 Table S2). We identified 'molecular operational taxonomic units' (MOTU's; in the following referred to simply as 'units' following the terminology of Dayrat *et al*. (2014)) on the topology of the Maximum Likelihood (ML) tree by delimiting distinct sequence clusters that were separated from each other by long branches and receiving high nodal support (bootstrap value > 90%). All unit numbers used in Dayrat *et al.* (2014: **1** to **41**) are maintained herein while new units have been assigned numbers from **42** onwards. Pairwise genetic distances in COI and 16S by were calculated by employing the Kimura-2-parameters model (Kimura 1980) as implemented in MEGA11 (Tamura *et al.* 2021). Of all possible sequence pairs, we recorded the highest intraspecific (i.e., the maximum distance between any two sequences within a single molecular unit) and the lowest interspecific distances (i.e., the minimum distance between any two sequences from two different genetic units).

Species delimitation. Our operational criterion for the delimitation of species was to test whether candidate species were simultaneously phenotypically and genotypically distinct from each other (Sites & Marshall, 2004). Candidate species were initially delimited by grouping specimens into morphospecies using general shell morphology and reproductive anatomy by considering the previous taxonomy and the known or purported distribution of species. We formulated a second set of species hypotheses based on the clustering of samples in the molecular phylogeny into 'units' by incorporating the sequence data set and unit designations of Dayrat *et al.* (2014). We considered every sample or cluster of samples as a molecular MOTU that formed a well-supported clade (by means of basal branch length and nodal support). We then assessed whether such units also represented anatomically and morphologically coherent groups that could be consistently distinguished from one other. At first, we checked for agreement between morphotypes and units. In cases where morphospecies and units agreed with another, we considered these so delineated groups to represent distinct species. We assigned available taxon names to these groups based on morphological similarity and concurrent distribution with type specimens with relying on anatomical and molecular data gathered from topotypes. If such candidate species could not be matched up with previously described nominal species, we describe these species as new taxa. In some cases, morphospecies and molecular units did not match initially. In these cases, we critically assessed the morphology and sequenced additional specimens where possible. If conflicts could not be resolved, we opted for the most inclusive delineation of species and refrained from splitting such groups taxonomically.

Results

Morphological analyses. We have examined 4,187 specimens (568 dissected) newly collected from 443 locations representing 80 accepted species, both previously accepted and described herein as new, with 38 holotypes and 5 neotypes (Table S1). A further 2,898 museum specimens from 193 locations have been examined including 11 holotypes and 2 neotypes. The detailed results of our morphological examinations are documented in the systematic part of this work further below.

Molecular analyses. The final concatenated dataset contained sequences of 875 specimens of *Siphonaria* spp. and 4 specimens of *Williamia* spp. These sequences included concatenated COI and 16S sequences representing 349 individuals that were retrieved from GenBank as well as new sequences from 529 individuals produced herein (with sample identifiers M001 to M601).

Generally, the COI sequences had a length of 658 bp. The 16S sequences were between 395 and 452 bp long. The 16S alignment comprises a total of 527 bp. Several individuals included in the concatenated sequence dataset are represented by only one of the two gene fragments. However, for 640 samples sequences of both fragments are available. Translating the COI nucleotide sequences into amino acid sequences did not produce any stop codons. The integrated model finder of IQ-tree identified GTR+F+I+G4 for 16S as well as TIM+F+ASC+R4, GTR+F+I+G4, and GTR+F+R3 for the three codon positions in COI as the best-fit model scheme by means of the Bayesian Information Criterion. Prior to analysing the concatenated sequence dataset, we performed two separate phylogenetic analyses for each of the gene fragments to check for incongruences and rule out possible mix-ups of sequences. The final analysis of the concatenated sequences produced a phylogenetic tree with a statistically mostly well-supported branching pattern (Fig. 1).

This tree contained 96 distinct, well-supported and well-individualized, genetic clusters (i.e., units). These included the 41 distinct sequence clusters (= 'units') identified by Dayrat *et al.* (2014) and 55 additional units (labelled **42** to **96**), which were not represented in that study. Each of these units contained sequences from between one and 68 individuals.

The principal topology of the ML consensus tree generally well supported by means of 10,000 ultrafast bootstrap replicates. Owing to its large size, the entire tree is shown here with the topology collapsed at the unit level (Fig. 1). We found that the Alaskan species *Siphonaria thersites* Carpenter, 1864 (unit 42) represents the sister species of all other *Siphonaria* species included in our analysis. The next offshoot is formed by the two Caribbean species *Siphonaria gigas* Sowerby I, 1825 (unit 1) and *S. maura* (unit 15). The four successively next more derived offshoots form the informal *normalis* group, a collective term first coined by Dayrat *et al.* (2014) for three independent clades. We here expand this term to include several additional clades not contained in Dayrat *et al.*'s (2014) original tree. However, we note that the *normalis* group as so delimited is non-monophyletic as it encompasses two individual clades (E and F) that are not in a sister-group relationship with one another (Fig. 1). The *normalis* group encompasses 28 units, most of which have been identified as distinct species. These species contain the type species of nine nominal genus-group taxa (*Sacculosiphonaria*, *Hubendickula*, *Simplisiphonaria*, *Pachysiphonaria*, *Talisiphon*, *Benhamiana*, *Kerguellenella*, *Mouretus*, and *Patellopsis*).

The crown of the phylogenetic tree is separated from the abovementioned clades by a remarkably long basal branch. It consists of two main clades: One of these clades is here identified as the *atra* group following Dayrat *et al.*'s (2014) initial terminology. The second clade is made up of *S. pascua* (unit 16), sister pair of the so-called *laciniosa* and *plicata* groups (Fig. 1). Individual sub-trees with an un-collapsed topology are shown for the *atra* group (Fig. 2), the *laciniosa* and *plicata* groups (Fig 3), and the *normalis* group (Fig. 4).

We estimated genetic divergences within and between units by means of pairwise K-2-P distances in COI across all sequence pairs by recording the maximum distances within and the minimum distances between units (Tables S3–S8). Except for two outliers, the maximum distances within units were generally below 6.9%. In fact, the median of all maximum within-unit distances was 1.4% while the top 95% percentile of all within-unit distances was below or equal to 3.4 % (Fig. 5). The two outliers with highest within-unit distances were unit 40 with 12.7% and unit 41 with 10.4%. We found very limited overlap between the maximum within-unit and the minimum between-unit distances. The latter were generally above 6.5% (= lower 99%-percentile). There have been two outliers: The minimum distance between units 80 and 88 was 4.6% and that between units 14 and 88 was 5.6%. However, the median of all minimum distances between different units was 23% while 95% of all minimum between-unit distances were above 20%. Consequently, there was a statistically significant difference between the distances within and between units (Fig. 5). Pairwise distances in 16S revealed, on average, a nearly linear relationship with pairwise COI distances (Fig. 6). This knowledge is used to assess the genetic distinctiveness of unit when COI sequences are lacking.

Summary of the revised taxonomic classification. In the revised taxonomy of *Siphonaria* in the IWP as proposed herein we accept two genera, *Siphonaria* and *Williamia*. Among the taxa revised herein, we accept altogether 88 species in *Siphonaria* including 40 species that are newly described. We refer to six informal species groups that contain more closely related species that share some morpho-anatomical similarities. These species and species groups are as follows:

Siphonaria Sowerby I, 1823

- *atra* group

S. alternata (Say, 1826) [not revised herein], ***S. crenata*** Blainville, 1827 (= *S. rosea* Hubendick, 1943), ***S. atra*** Quoy & Gaimard, 1833 (= *S. albicante* Quoy & Gaimard, 1833, *S. albicans* Lamarck, 1836, *Mestosiphon eumelas* Iredale, 1940, *Triellsiphon acervus* Iredale, 1940, *S. currumbinensis* Hubendick, 1955), ***S. denticulata*** Quoy & Gaimard, 1833 (= *Ellsiphon marza* Iredale, 1940), ***S. plana*** Quoy & Gaimard, 1833 (= *S. ferruginea* Reeve, 1856), ***S. zelandica*** Quoy & Gaimard, 1833 (= *S. baconi* Reeve, 1856, *S. zebra* Reeve, 1856, *Planesiphon elegans* Iredale, 1940), ***S. radians*** H. Adams & A. Adams, 1855 (= *S. radiata* A. Adams & Reeve, 1850), ***S. bifurcata*** Reeve, 1856, ***S. kurracheensis*** Reeve, 1856, ***S. scabra*** Reeve, 1856, ***S. exulum*** Hanley, 1858 (= *S. exulorum* Hanley 1858, *S. raoulensis* Oliver, 1915, *S. cheesemani* Oliver, 1915, *S. macauleyensis* Oliver, 1915, *S. macauleyensis perplexa* Oliver, 1915, *S. amphibia* Oliver, 1915, *Parellsiphon innocuus* Iredale, 1940), ***S. belcheri*** Hanley, 1858, ***S. incerta*** Deshayes, 1863 (= *S. parcicostata* Deshayes, 1863), ***S. acmaeoides*** Pilsbry, 1894 (= *S. acmaeoides paulae* Christiaens, 1980), ***S. sirius*** Pilsbry, 1894, ***S. subatra*** Pilsbry, 1904, ***S. stowae*** Verco, 1906 (= *Pugillaria stowae comita* Iredale, 1924), ***S. madagascariensis*** Odhner, 1919, ***S. opposita*** (Iredale 1940), ***S. lentula*** (Iredale, 1940), ***S. alba*** Hubendick, 1943, ***S. emergens*** (Jenkins, 2018), ***S. cacao* sp. nov.**, ***S. caubianensis* sp. nov.**, ***S. forticosta* sp. nov.**, ***S. hienghenensis* sp. nov.**, ***S. ouasseensis* sp. nov.**, ***S. bourailensis* sp. nov.**, ***S. pravitas* sp. nov.**, ***S. recurva* sp. nov.**, ***S. restis* sp. nov.**, ***S. striata* sp. nov.**, ***S. tenebrae* sp. nov.**, ***S. umbra* sp. nov.**, ***S. vudaensis* sp. nov.**

- *laciniosa* group

S. javanica (Lamarck, 1819), ***S. sipho*** Sowerby I, 1824 (= *S. exigua* Sowerby I, 1823, *S. radiata* Gray, 1824, *S. cornuta* Gould, 1846, *S. siquijorensis* Reeve, 1856, *S. luzonica* Reeve, 1856, *S. corrugata* Reeve, 1856, *S. sipho elatior* Schrenck, 1867, *S. sipho intermedia* Schrenck, 1867, *S. sipho depressior* Schrenck, 1867), ***S. viridis*** Quoy & Gaimard, 1833 (= *S. punctata* Quoy & Gaimard, 1833, *Parellsiphon zanda* Iredale, 1940, *Parellsiphon promptus* Iredale, 1940, *Legosiphon optivus* Iredale, 1940, *Legosiphon mirificus* Iredale, 1940, *Legosiphon densatus* Iredale, 1940), ***S. savignyi*** Krauss, 1848, ***S. rucuana*** Pilsbry, 1904, ***S. kudatensis* sp. nov.**, ***S. jiigurruensis* sp. nov.**, ***S. maloensis* sp. nov.**, ***S. namukaensis* sp. nov.**, ***S. caledonica* sp. nov.**, ***S. poindimiensis* sp. nov.**, ***S. rodriguensis* sp. nov.**, ***S. tagaqaensis* sp. nov.**, ***S. tanchaensis* sp. nov.**, ***S. yagasaensis* sp. nov.**

- *plicata* group

S. guamensis Quoy & Gaimard, 1833, ***S. plicata*** Quoy & Gaimard, 1833 (= *S. tongensis* Hubendick,

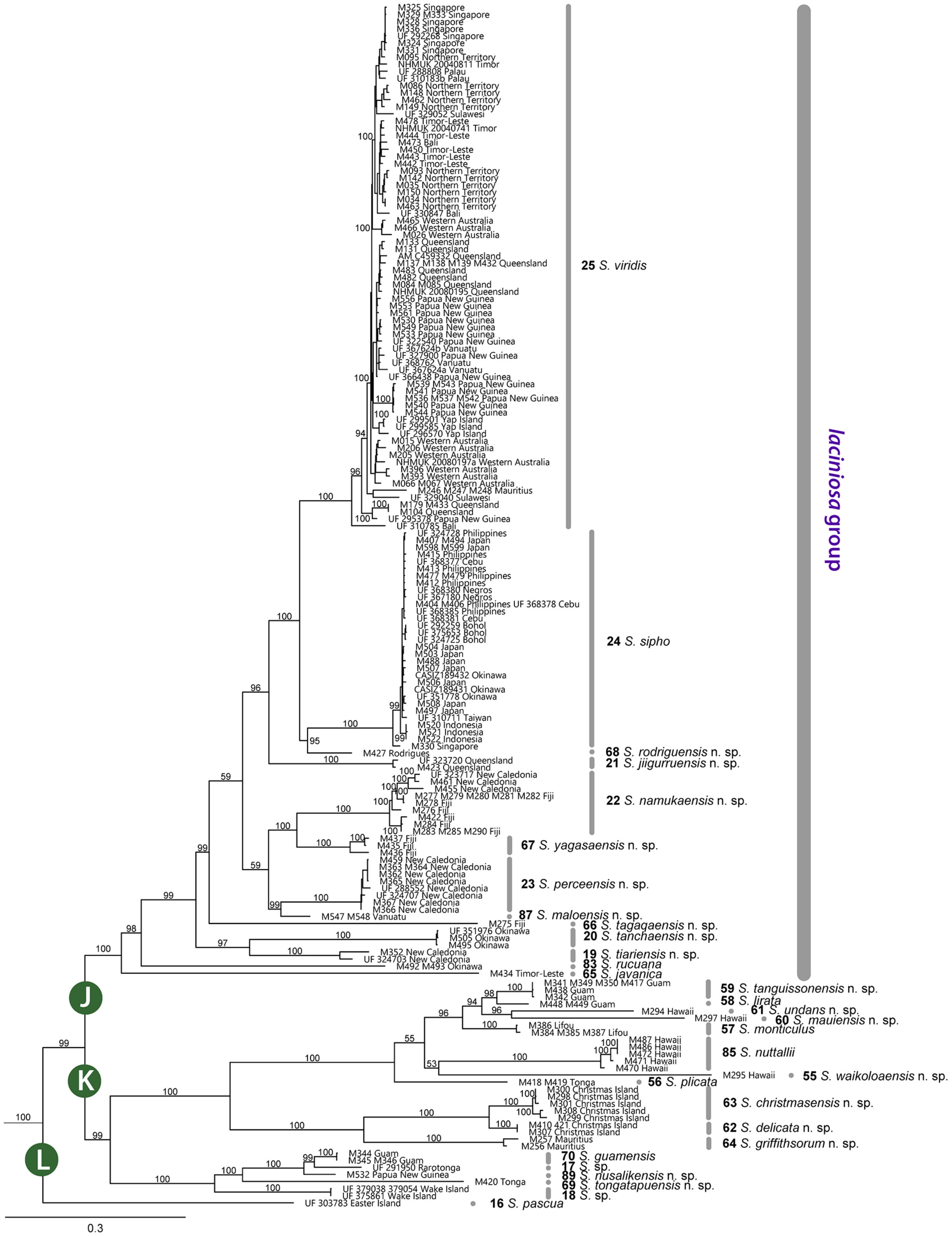

FIGURE 3. Maximum Likelihood phylogram (partial, species not collapsed). Clades J–L (*laciniosa* and *plicata* groups) of the tree shown in Fig. 1. Branch labels give specimen identifiers for new sequences or Genbank accession numbers for imported sequences from other studies and geographic regions (see Tables S1–S2 for details). Identical haplotypes are merged into single tips. Numbers on branches indicate branch support by employing 10,000 ultrafast bootstraps. Clade names give unit numbers and accepted species names. Scale bar indicating modelled sequence divergence.

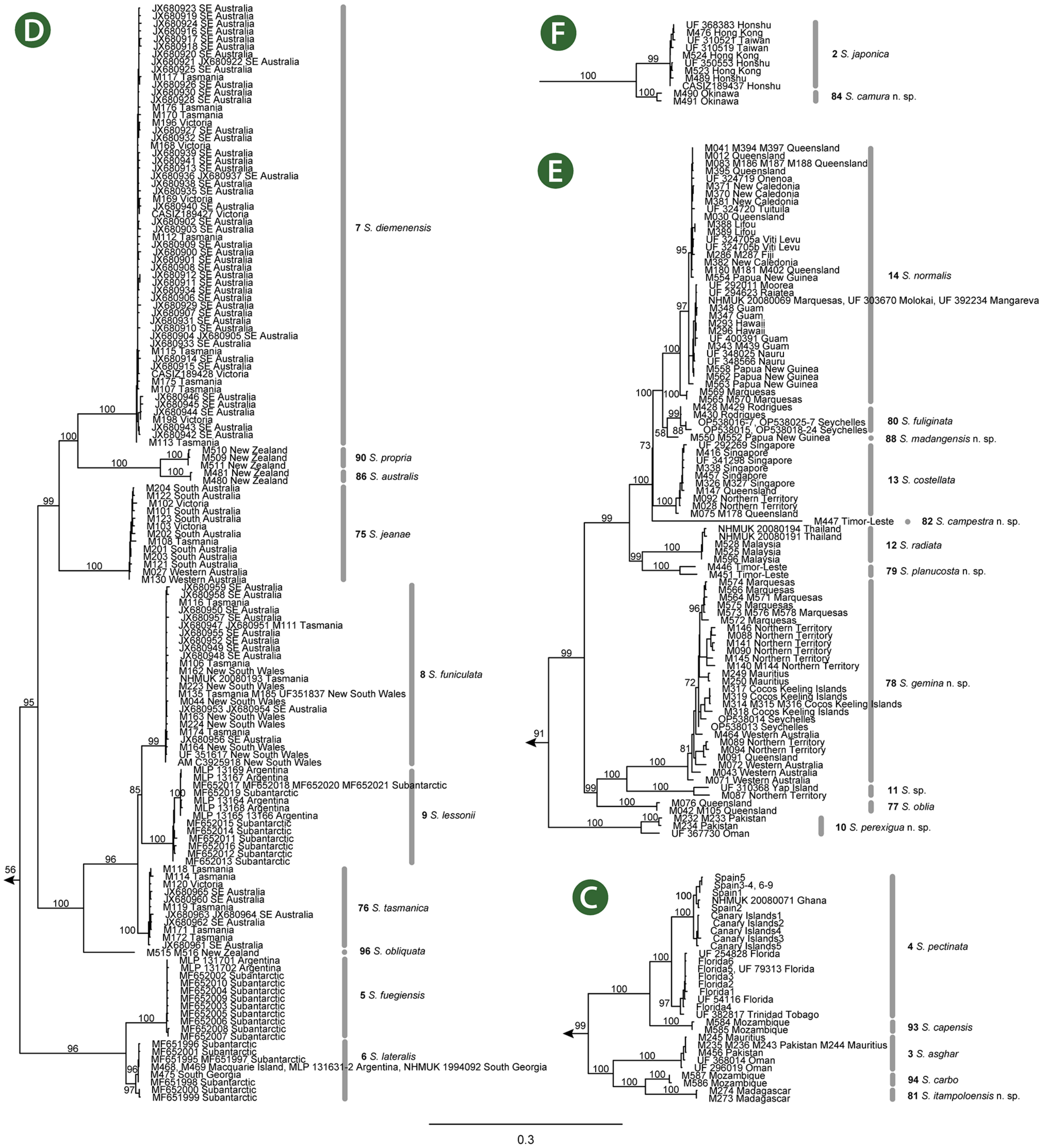

FIGURE 4. Maximum Likelihood phylogram (partial, species not collapsed). Clades C–F (*normalis*, *lateralis* and *pectinata* groups) of the tree shown in Fig. 1. Branch labels give specimen identifiers for new sequences or Genbank accession numbers for imported sequences from other studies and geographic regions (see Tables S1–S2 for details). Identical haplotypes are merged into single tips. Numbers on branches indicate branch support by employing 10,000 ultrafast bootstraps. Clade names give unit numbers and accepted species names. Scale bar indicating modelled sequence divergence.

1943), ***S. lirata*** Reeve, 1856, ***S. nuttallii*** Hanley, 1858 (= *S. normalis* f. *chirura* Pilsbry, 1920, ***S. monticulus*** (Iredale, 1940), ***S. christmasensis* sp. nov.**, ***S. delicata* sp. nov.**, ***S. griffithsorum* sp. nov.**, ***S. tongatapuensis* sp. nov.**, ***S. mauiensis* sp. nov.**, ***S. nusalikensis* sp. nov.**, ***S. tanguissonensis* sp. nov.**, ***S. undans* sp. nov.**, ***S. waikoloaensis* sp. nov.**

- *normalis* group

S. japonica (Donovan, 1824) (= *S. cochleariformis* Reeve, 1856, *S. alterniplicata* Grabau & King, 1928, *S. corallina* Christiaens, 1980), ***S. radiata*** (Blainville, 1826), ***S. normalis*** Gould, 1846 (= *Planesiphon soranus* Iredale, 1940), ***S. fuliginata*** Reeve, 1856, ***S. oblia*** (Jenkins, 2018), ***S. campestra* sp. nov.**, ***S. camura* sp. nov.**, ***S. costellata***

sp. nov., ***S. gemina*** **sp. nov.**, ***S. madangensis*** **sp. nov.**, ***S. perexigua*** **sp. nov.**, ***S. planucosta*** **sp. nov.**

- *lateralis* group

S. obliquata Sowerby I, 1825 (= *S. scutellum* Deshayes, 1841), ***S. australis*** Quoy & Gaimard, 1833, ***S. diemenensis*** Quoy & Gaimard, 1833, ***S. lateralis*** Gould, 1846 (= *Kerguelenia innominata* Iredale, 1915, *Kerguelenia macquariensis* Powell, 1939), ***S. funiculata*** Reeve, 1856 (= *S. blainvillei* Hanley, 1858, *S. virgulata* Hedley, 1915, *S. oblivirgulata* Hubendick, 1943), ***S. tasmanica*** Tenison Woods, 1877 (= *S. zonata* Tenison Woods, 1878, *Talisiphon tasmanicus nereis* Iredale, 1940, *Talisiphon tasmanicus turritus* Iredale, 1940), ***S. propria*** Jenkins, 1983, ***S. jeanae*** Jenkins, 1984, ***S. fuegiensis*** Güller, Zelaya & Ituarte, 2016 [not revised].

- *pectinata* group

S. pectinata (Linnaeus, 1758) [not revised], ***S. naufragum*** Stearns, 1872 [not revised, included in unit 4], ***S. capensis*** Quoy & Gaimard, 1833 (= *Siphonaria kowiensis* Turton, 1932, *Siphonaria capensis* var. *lineolata* Krauss, 1848, *Siphonaria capensis* forma *kraussi* Hubendick, 1946), ***S. carbo*** Hanley, 1858 (= *S. nigerrima* Smith, 1903, *S. tenuicostulata* Smith, 1903, *S. anneae* Tomlin, 1944), ***S. asghar*** Biggs, 1958, ***S. itampoloensis*** **sp. nov.**

- Species without group assignment

S. gigas Sowerby I, 1825 [not revised], ***S. maura*** Sowerby I, 1835 [not revised], ***S. thersites*** Carpenter, 1864 [not revised], ***S. pascua*** Rehder, 1980 [not revised].

Genus ***Williamia*** Monterosato, 1884
W. peltoides (Carpenter, 1864) [not revised], ***W. radiata*** (Pease, 1861), ***W. krebsii*** (Mörch, 1877) [not revised].

Discussion

Implications for the genus-level classification. Breaking with the historical practice of taxonomic splitting, we synonymize 21 genus-group names associated with *Siphonaria*, introduced by various authors in the past (refer to Fig. 2 for these names and their type species). This decision, grounded in the pursuit of taxonomic stability and supported by available evidence, is not taken lightly. Our contention is that, barring *Siphonaria*, the previously proposed genus-group taxa lack shared morphological characteristics conducive to their unambiguous identification and delineation.

Initially, Dall (1870) proposed the division of *Siphonaria* into two subgenera, *Siphonaria* and *Liriola*, introducing the latter for species like *S. alternata*, *S. thersites*, *S. lateralis*, *S. lessonii*, and *S. peltoides*, based on shell, radular, and anatomical features. However, our molecular phylogeny (Figs 1–4) rejects the taxonomic grouping of these species. Consequently, the purported morphological similarities either represent plesiomorphic traits or result from convergence. Notably, *S. peltoides* is member of *Williamia*, not *Siphonaria*. Subsequently, Hubendick (1945: 55) expanded on Dall's division, creating five sections within each subgenus based on reproductive anatomy and shell morphology. Nevertheless, our analysis revealed that none of these characteristics reliably differentiates the subgenera. Notably, the SPM in *S. thersites*, the type species of *Liriola*, contrasts with the short, sac-like SPM claimed to be typical for *Liriola*. Similarly, the presence of a single genital pore and the BC in this species contradict that opposing character states are typical for *Liriola*. On the other hand, the SPM in several species of *Siphonaria* s. str. is short and sac-like (e.g., *S. tasmanica, S. zelandica, S. acmaeoides, S. funiculata, S. capensis*, and *S. lateralis*).

Through comprehensive comparative studies, we assert that the characters emphasized by Hubendick (1946) lack consistent representation among species, rendering the subdivision of *Siphonaria* into ten groups largely phenetic and unhelpful for recognizing natural groups. The unique features of incomplete shell cover in *S. thersites* and enclosed ducts in the RS distinguish this species from most others the family (a somewhat reduced shell is also observed in *S. obliquata*, which is not closely related, though). The molecular phylogeny places *S. thersites* as sister of all other species included in the tree, suggesting its evolutionary distinctiveness with respect to these species. While this finding may support the treatment of *Liriola* as a distinct taxon after all, it presently stands as monotypic, a status we find less meaningful. Future studies of extralimital species are required to resolve the question if these diagnostic features may be shared by species that are more closely related to *S. thersites*.

Although our mitochondrial phylogeny exhibits substantial structure, caution is warranted in linking genus-group names to specific clades due to insufficient DNA sequence sampling as well as sequence saturation, which can negatively affect the resolution of deeper evolutionary splits among *Siphonaria*. Sequence saturation, particularly in COI, underscores the need to employ additional genetic markers to reliably resolve these deeper phylogenetic relationships before any systematic hypotheses are formalised.

For now, we reference informal species groups, primarily based on shared shell features and clade membership. However, deviations from these shell features among the members of a group are common. For example, *S. zelandica* and *S. acmaeoides*, positioned in the '*atra* group' exhibit characteristics resembling the '*lateralis*' and '*plicata* group', respectively. Similarly, *S. bifurcata* and *S. scabra* ('*atra* group') display RS and shell features akin to both the '*laciniosa*' and '*plicata* group'.

The systematic significance of morpho-anatomy and mitochondrial genetics. Accurate species identification is paramount in nomenclature and taxonomy, serving as the cornerstone for higher-level classifications, as well as the exploration of distributions and biodiversity. Traditionally, siphonariid species have been exclusively characterized based on shell features, leading to the association of specific shell forms with certain taxonomic names, as outlined by Hubendick (1946), for example.

Some of these names featured prominently throughout the taxonomic literature, such as *S. laciniosa*, *S. atra*, *S. normalis*, *S. pectinata*, *S. plicata*, and *S. lateralis*. These species, as previously defined, were commonly considered to have wide distributions (e.g., Habe 1971, Cernohorsky 1972, 1978, Springsteen & Leobrera 1986, Dayrat *et al.* 2014).

However, siphonariids are also notorious for displaying considerable variability in shell characters (e.g., Teske *et al*. 2007, 2011). Notably, distinct shell forms have been identified within the same species, sometimes connected through intermediate forms (Hubendick 1946, Brook 1998, Wood & Gardner 2007, Teske *et al*. 2007, 2011). This conchological variability challenges the historical reliance on shell characteristics for species identification and delimitation; a finding that underscores the need for a more comprehensive approach that incorporates additional morphological and molecular data. Consequently, a nuanced understanding of the diversity and relationships among siphonariid species requires a broader consideration of multiple traits beyond shell morphology. This approach is crucial for refining species boundaries, enhancing accuracy in taxonomic classifications, and facilitating a more nuanced exploration of the ecological and evolutionary aspects of siphonariid biodiversity.

To date, students of Indo-West Pacific (IWP) siphonariids have encountered challenges in reliably identifying many species due to the absence of anatomical descriptions and molecular data. Moreover, the considerable variation in shell characters has often led to misidentifications or has led to uncertainties in the assignment of taxonomic names to identified biological units (e.g., Dayrat *et al.* 2014). In this study, we aimed to address these limitations by examining freshly collected topotypic material and geographical series of specimens. Our approach involved two steps. In a first step, we matched original type specimens with newly collected topotypes ensuring they exhibited consistent morphological features. This matching process is critical as frequently more than one *Siphonaria* species could be found at any given locality. We then used this topotypic material to complete the description of species with previously unavailable or unvalidated information about the anatomical characteristics of species. Of course, this step incorporated the validation or revision of information that was available from previous revisions. Finally, we assigned specimens from further apart to named species based on comparative morphology and mitochondrial genetics. Genetic data has been particularly valuable in this process as it provided an estimate of relatedness independent from our assessments of observed similarity in morphological characteristics. Mitochondrial phylogenetics enhanced our ability to discern intra- and interspecific morphological variation. Molecular analyses allowed us to evaluate the systematic significance of morpho-anatomical features. We usually found that species that have initially been delineated by analysing the amounts of genetic variation could also be distinguished by means of comparative morphology. However, Giribet & Kawauchi's (2015) investigation of *S. pectinata* in the Atlantic has revealed that this may not always be the case. They identified three distinct mitochondrial lineages in *S. pectinata* with allopatric distributions (each one in the Gulf of Mexico and Florida, the eastern Atlantic and Mediterranean as well as Cape Verde). Subsequently, the neotropical populations were recognised as *S. naufragum* Stearns, 1872 and the Cape Verde populations as *S. placentula* Menke, 1853 by Giribet & Kawauchi (2016) in absence of documented morphological differences. Clearly, Giribet & Kawauchi's (2015, 2016) have underscored the crucial role of mitochondrial genetics in elucidating cryptic species within the Siphonariidae.

In the present study, we have encountered some instances when our assessments of the morphological differentiation were at odds with the observed genetic variation. Usually, we found that distinguishable morphs were genetically insufficiently distinct. In these cases, we opted for a conservative approach and refrained from formally recognising a morph in a taxonomic framework.

Our study builds upon and extends the pioneering work of Dayrat *et al*. (2014), who utilized mitochondrial phylogenetics and comparative shell morphology to address the taxonomic diversity of *Siphonaria* in the Indo-West Pacific (IWP) and revealing patterns of cryptic diversity on the way. Dayrat *et al.* (2014) sampled a considerable number of specimens across a broad geographic range, identifying 41 sequence clusters that were hypothesized to represent individual species. However, the authors faced challenges in unequivocally associating these units with taxonomic names due to the conchological resemblance of many so identified species-groups. Notably, 29 of the 41 units recovered by Dayrat *et al.* (2014) remained unnamed because they could not definitely be linked with available species names.

Recognizing these limitations, our study expands on Dayrat *et al.*'s (2014) work in two crucial ways. First, we address the need to complement available shell data with detailed information on anatomy, especially reproductive features. Second, to correctly connect available taxonomic names with biological species, we extensively studied topotypical material, examined type specimens, and delved into the associated taxonomic literature. This dual approach, incorporating anatomical insights and taxonomic history, contributed to a more comprehensive and objective systematic classification.

To achieve a stable and evidence-based taxonomic classification of the Siphonariidae in the IWP and beyond, we meticulously re-evaluated characters of the shell, reproductive, and alimentary anatomy. Our focus on wide geographical sampling, including critical topotypic material, enhanced the robustness of our findings.

We have employed analyses of mitochondrial sequences to formulate species hypotheses, which we then tested in a framework of comparative morphology with emphasis on shell, reproductive and radular characteristics.

We have analysed the largest sequence dataset to date and found that sequences formed readily identifiable genetic clusters that have generally been separated well by means of comparatively long basal branches and have also been statistically well-supported by bootstrapping. We have found that there has been a statistically significant separation between the amounts of genetic divergence within these genetic units and between them (Fig. 5). Except for few outliers, genetic distances between any two units have always been above 6.6% (in 75% of all cases above 20%) while the distances within any genetic unit have generally been below 6.9% (in 75% of cases below 3.4%).

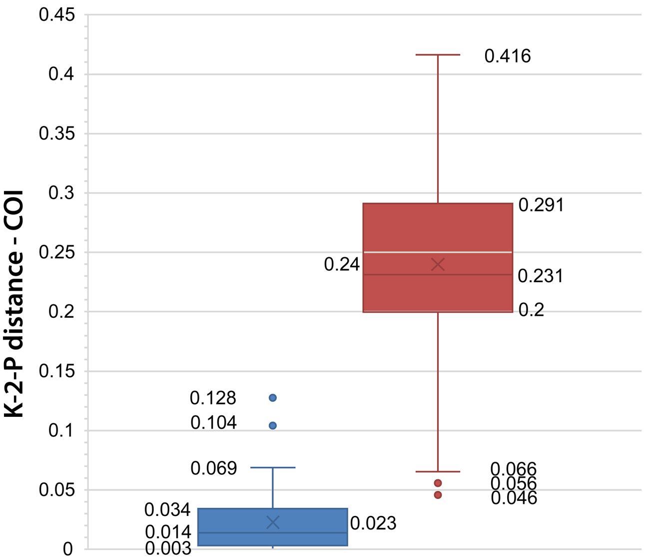

FIGURE 5. Boxplot diagram showing frequencies (mean, median, mode, minimum, maximum and outliers) of pairwise K-2-P distances in COI between sequences of the same genetic unit (= interspecific distances, left) and between sequences from different genetic units within the same major clades (= interspecific distances, right).

Our morphological examinations have revealed that genetic units recognised herein can consistently be morphologically distinguished from one another (except for the few outliers mentioned above). Therefore, we conclude that the intraspecific genetic divergence in *Siphonaria* does generally not exceed ~7% and is frequently much lower than that.

This conclusion is consistent with the findings of other studies. Colgan & da Costa (2013) documented corresponding amounts of intraspecific divergence in COI in the Australian species *S. denticulata* (~ 5%), *S. diemenensis* (~ 7.2%), *S. funiculata* (~ 6.8%), *S. tasmanica* (~ 7.2%) and *S. zelandica* (~ 5.7%).

We have analysed the DNA sequences used by Giribet & Kawauchi (2016) and found that *S. pectinata* and *S. naufragum* differed by COI distances of ≥ 5.3%. In South America, Güller *et al.* (2016) observed pairwise genetic (K2P) distances of ≥ 7.3% between *S. lateralis* and *S. fuegiensis* and much larger distances between any other South American species.

Equipped with a large genetic dataset that encompassed a substantial number of topotypic specimens, we tested the prevailing systematic classification of the IWP species. Traditionally, certain shell morphs have been associated with certain species names, such as *S. laciniosa*, *S. atra*, *S. normalis*, *S. plicata,* and *S. lateralis*. Yet, Dayrat *et al.* (2014) demonstrated that these morphospecies are likely poorly resolved complexes of several more closely related, conchologically similar species. Indeed, there are two issues at work confounding the taxonomy of this group. First, there is morphological plasticity within species in shell characters; second, there are morphologically cryptic species that share highly similar suites of shell characteristics. In the past, these cryptic species were often lumped together under a single species name. Based on previously available information, it has been impossible to unambiguously connect available taxonomic names with biological species for the inability to examine the anatomy and genetics of topotypic samples. A complicating factor in the taxonomic classification of the Siphonariidae is that similar shell morphologies have historically led to misidentifications plaguing the taxonomic record. Furthermore, many publications lack images altogether or provide insufficient documentations of diagnostic characters. Unfortunately, in several cases, Hubendick (1945, 1946) misidentified specimens, which provoked incorrect taxonomic assessments. To give just one example, he misidentified *S. diemenensis* from Tasmania and South Australia as *S. denticulata* (Hubendick 1946: 38). He also frequently synonymised nominal species apparently without examining type specimens or topotypes (e.g., *S. exulum* (NI), *S. javanica* (Java), *S. macaulayensis* (Kermadecs), and *S. scabra* (Port Jackson, Sydney) as synonyms of *S. diemenensis* (SE Australia; Hubendick 1946: 38); *S. sipho* (Philippines), *S. plicata* (Tonga), *S. punctata* (Mauritius), and *S. incerta* (Réunion) as synonyms of *S. laciniosa* (Hubendick 1946: 47); *S. luzonica, S. corrugata*, *S. siquijorensis* (all Philippines), and *S. depressa* (Kiribati) as synonyms of *S. kurracheensis* (Karachi, Pakistan) (Hubendick 1946: 54). These decisions, revoked herein, have caused considerable taxonomic confusion.

Expanding on the phylogenetic analysis of Dayrat *et al.* (2014), we found that the traditionally used shell characters are frequently suitable to delineate species groups. However, among these, individual species can only be delineated by using additional information derived from reproductive anatomy, especially in combination with mitochondrial phylogenetics.

Useful diagnostic shell characters are length, height, apical position, ribbing, colour (external) as well as shell lip/margin (internal). External morphology was only rarely diagnostic. Characters of reproductive anatomy (shape and relative size of parts of the RS, morphology of the SPM) have been suitable to distinguish species. Several species with narrow distributions were found to exhibit comparatively low variability in shell and can readily be distinguished based solely on their distinctive adult shell morphology, such as *S. japonica*, *S. oblia*, S. *obliquata*, *S. sirius*, *S. stowae*, and *S. tasmanica*. Several species with previously unknown type localities have been connected to current populations and localities aiding their unambiguous identification, such as *S. belcheri*, *S. blainvillei*, *S. crenata*, *S. exigua*, *S. fuliginata*, *S. incerta*, *S. lirata*, *S. parcicostata*, *S. radiata*, *S. savignyi*, and *S. sipho*.

Examining geographical series of specimens allowed us to discriminate species that have shown overlapping ranges of morphological variation and/or overlapping distributions. For example, we have been able to distinguish *S. sipho* and *S. viridis* of the so-called *laciniosa* group, which are both widely distributed exhibiting a high variability in shell characters including forms that are strongly and less prominently ribbed. Moreover, we have been able to distinguish *S. javanica* and *S. jiigurruensis* **sp. nov.** from the same species group that have ranges which overlap with *S. viridis*. While the identity of *S. laciniosa* is uncertain, we continue to refer to '*laciniosa* group' for the widespread use of this name in taxonomic literature. The *laciniosa* group has radiated into flocks of genetically well-differentiated, yet morphologically rather similar, locally endemic species in NC (*S. namukaensis* **sp. nov.**, *S. poindimiensis* **sp. nov.**, *S. caledonica* **sp. nov.**), Fiji (*S. tagaqaensis* **sp. nov.**, *S. yagasaensis* **sp. nov.**), and Vanuatu (*S. maloensis*).

The situation with the *atra* group is more complex than that in the *laciniosa* group as it contains three distinct clades. Clade G (see Fig.1) contains four comparatively widely distributed species (*S. atra, S. alba, S. opposita*, *S. subatra*) with high variability in shell characters throughout including strong and weak ribbing, varying degrees of rib extension from the shell edge, and variable edge sculpture and colour. Within the distribution of *S. atra*, we distinguished the genetically highly distinct yet morphologically similar species *S. opposita* **sp. nov.** Throughout the literature these species have usually been identified simply as '*S. atra*'. Several new species, some co-occurring with the previous ones, exhibiting *atra* group characters, are described (*S. cacao* **sp. nov.**, *S. forticosta* **sp. nov.**, *S. hienghenensis* **sp. nov.**, *S. incerta* **sp. nov.**, *S. plana* **sp. nov.**, *S. recurva* **sp. nov.**, *S. tenebrae* **sp. nov.**, *S. vudaensis* **sp. nov.**). Clade H encompasses species that differ somewhat from the typical shell morphology associated with the *atra* group. By contrast, Clade I encompasses species that correspond well with typical *atra* shell features. However, these species are from the western part of the Indian and even the Atlantic Ocean, geographically apart from the western Indian to eastern Pacific distribution of the other species in the *atra* group.

Within the *plicata* and *normalis* groups species exhibit rather similar shells. The *plicata* group encompasses species from three island groups with comparatively restricted distribution. These island groups are Hawaii (with *S. nuttallii*, *S. mauiensis* **sp. nov.**, *S. undans* **sp. nov.**, *S. waikoloaensis* **sp. nov.**), Tonga (with *S. plicata* and *S. tongatapuensis* **sp. nov.**), and Guam (with *S. guamensis*, *S. lirata* and *S. tanguissonensis* **sp. nov.**). The *plicata* group also contains a clade from the Indian Ocean with species occurring on CI (*S. christmasensis* **sp. nov.**, *S. delicata* **sp. nov.**) and Mauritius (*S. griffithsorum*). The species of the *plicata* group have frequently been subsumed under the name *S. nuttallii* in previous taxonomic literature.

The species of the *normalis* group, previously often just identified as *S. normalis*, also exhibit rather low variability in shell characters. They frequently have rather wide distributions in either the northern or southern Pacific. Several genetically well-differentiated species in this group have been found in partial or complete sympatry with other members of this group exhibiting similar shell characters yet maintaining their genetic distinctiveness.

Species of the *lateralis* group have been studied extensively previously resulting in well-established species limits. These species exhibit a combination of diagnostic shell and anatomical characteristics with comparatively low intra-specific variability.

Generally, with respect to shell characters, we found examples of morphologically highly similar species that were genetically distinct. For example, within the laciniosa group, we found that *S. sipho* (unit **24**), *S. viridis* (unit **25**), *S. javanica* (unit **65**), and *S. tanchaensis* **sp. nov.** (unit **20**) resembled each other closely while being differentiated by considerable genetic distances of usually above 20% in COI (Table S6).

Several species displayed wide intraspecific variation in shell characters. Such elevated variability was frequently associated with wide distributions (e.g., *S. gemina* **sp. nov.**, *S. incerta* **sp. nov.**, *S. radiata*, *S. sipho*, *S. viridis*) while others were far less variable and typically narrowly endemic (e.g., *S. camura* **sp. nov.**, *S. oblia*, *S. thersites*).

Particularly noticeable, especially in '*atra* group', is the thickening of the shell interior to form a whitish or transparent shell lip (e.g., *S. atra*, *S. alba*, *S. belcheri*, *S. normalis*, and *S. opposita*). Similarly, shell height showed wide intra-specific variability in several species (e.g., *S. tasmanica*, *S. funiculata*, *S. monticulus*, *S. plicata*, *S. viridis*).

Species are readily discriminated on morphological shape and size differences in RS (predominantly epiphallic parts) and SPM (i.e., with or without barbs, short and bulbous to long and thread-like, corresponding to possession of no, a short or a long flagellum, respectively). The size and to a lesser extent shape of RS parts, not the position in the body cavity, show a degree of inter- and intraspecific variability. For example, the organ size varied markedly in most species. Yet, it was consistent in others (e.g., *S. funiculata* and *S. radiata*). Wide intraspecific variation with the BD distal loop looping around the ED of the RS existed for some species; either in front (most common, e.g., *S. namukaensis* **sp. nov.**), looping behind the ED (e.g., *S. sipho*, *S. radians*) or multiple coils around the ED (e.g., *S. atra*). The path of the BD coupled in parallel with the CD also varied between species while being consistent within species; either both ducts are jointly outside RAM (e.g., *S. sipho, S. viridis*), go jointly through RAM (most common, e.g., *S. japonica, S. crenata, S. atra*), or the ducts have separate paths (BD around anterior of RAM and around ED, and CD through RAM) (only in *S. camura* **sp. nov.**). A further specific variation with the path of the BD occurs in *S. thersites* where the BD is very narrow and enclosed in ventral side tissue of wider whitish CD, with hidden connection to a small flat BC in folds of MG. This finding is inconsistent with the reported 'spermatheca [i.e., BC] missing' as a determinant for the genus *Liriola* and *S. thersites* as its type species (Hubendick 1946: 8, fig. 3).

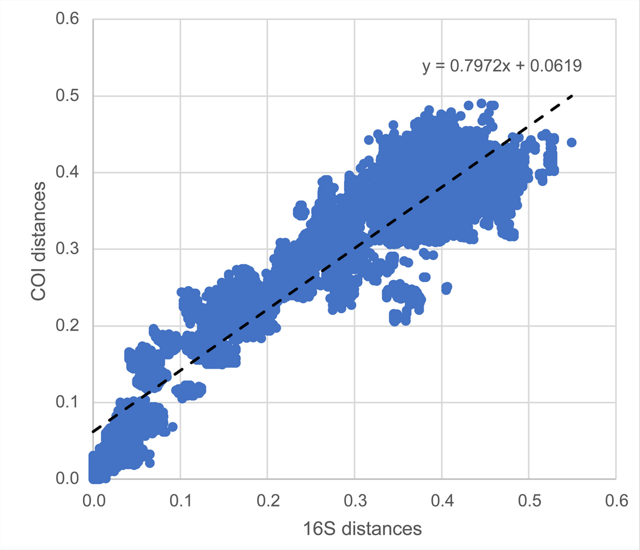

FIGURE 6. Relationships of genetic K-2-P distances in COI and 16S for sequences form the same individuals.

Only few species were found to have barbed SPM (e.g., *S. japonica, S. camura* **sp. nov.**). We found barbed SPM also in some specimens of *S. restis* from WA while other individuals of the same species lacked barbs. A keeled SPM was found in *S. griffithsorum* **sp. nov.** SPM length to AL revealed considerable inter- and intraspecific variability (median length to AL = 49.4 %, n = 149 complete of 168 SPM measured from 73 species) while general SPM morphology remained consistent within each species. *Siphonaria madagascariensis* exhibited the largest SPM length relative to AL and the greatest overall variability (mean length to AL = 161%, SD = 66%, max 254%; n = 4), while S. capensis had the smallest SPM length to AL ratio and the smallest overall intraspecific variability (mean length to AL = 3%, SD = 0.2%, min 2.7%; n = 3).

Radula and jaw morphologies have been insufficient to distinguish species in *Siphonaria* or *Williamia*. As far as known, all *Siphonaria* species exhibit relatively uniform teeth and a largely consistent dentition arrangement (i.e. a single cusped central tooth, flanked by rows of variably cusped lateral teeth, tapering in size from the inside out, with unclear demarcation between median and lateral teeth, mesocones of inner and mid laterals overlapping back of corresponding tooth in preceding row, and each with basal plates possessing broad blunt anterior forks and a posterior notches providing interlocking articulation between rows (e.g., Jenkins 1983, Simone & Seabra 2017). However, the numbers of median and lateral teeth and transverse rows vary widely within species. While *Williamia* generally reveals some typical features that differ from *Siphonaria* (i.e., central tooth small, unicuspid, demarcation of inner and outer lateral teeth more prominent, inner laterals strongly bicuspid, outer laterals single plates) different species cannot be distinguished by using radular characteristics (Marshall 1981, Ruthensteiner 2006).

Jaw structures are largely generic in *Siphonaria*; found to be arch shaped with shingle-arranged, variable layers and rows of similarly shaped cones/rods (Güller 2015, Jenkins 2018). Cone length appears to be loosely related to AL. The jaw of *Williamia* has not been documented.

Distribution. High degrees of endemism in more isolated places, such as Oceanic islands, on one hand and widespread species whose distributions stretch over considerable geographic distances on the other hand, emerge as key results of our study. The phenomenon that some species are widespread while others are not has been noticed for South African species before and correlated with differences in larval development (Chambers & McQuaid 1994a, b). Accordingly, species producing planktonic veliger larvae, such as *S. capensis*, *S. concinna* and *S. oculus*, have wider distributions than species with direct development, such as *S. anneae*, *S. compressa*, *S. dayi*, *S. nigerrima*, *S. serrata* and *S. tenuicostulata*. Unfortunately, we have no data on larval development in the species studied here but we hypothesize that similar differences in reproductive strategy may ultimately be responsible for the observed patterns of distribution throughout the IWP. In other words, our finding may well fit the general paradigm that the duration of the larval stage is a determinant of geographic range size in many marine species (Brown *et al.* 1996). Species inhabiting isolated Oceanic islands are particularly prone to become single island endemics if the duration of their planktonic larval stage is too short to facilitate genetic exchange with other landmasses. Based on these considerations, it is plausible that more widespread species often inhabit island archipelagos while more isolated islands harbour endemic species.

Because Australia was in the focus of the present study, we have sampled the coastline of this continent extensively. Based on these samples, we recognise 21 species from Australian shores, including five new species and one unidentified species (resolving its taxonomic status requires further study). Out of these, eleven species are endemic to the continent. These endemics are usually restricted to certain regions along the Australian coasts. Our study highlights the Indo-West Pacific region as a hotspot of diversity for *Siphonaria* with 86 species recognized herein throughout this region (an area delimited by Mozambique in the southwest, the Persian Gulf in the northwest, Hawaii in the northeast and New Zealand in the southeast; Fig 7). In stark contrast to the diversity uncovered here, only a single species of *Siphonaria* is known from the subarctic and subantarctic regions, respectively (i.e., *S. thersites* in the north Pacific Ocean and *S. lateralis* in the south Pacific; see Gonzàlez-Wevar *et al.* 2018).

During our own field work, we collected between one and six species at a single site. Places with particularly diverse *Siphonaria* faunas were Christmas Island (Site CI01-1) with six sympatric species; Karachi, Pakistan

(Site PA01-1), Tasmania (Site T03-4), Dili, Timor-Leste (Site TL01-1) each with five sympatric species; as well as Okinawa (Site JP01-5), New Caledonia (Sites NC03-2, NC06-3), Biliau Island, PNG (Site PM38), Queensland, Cape Kimberley (Site Q35-1) each with four sympatric species (Table S1). In addition, there have been many sites across the entire region that supported two or three sympatric species.

Based on the material available to us, we found that up to nine species inhabit the same region. The documented hotspots of diversity beyond Australia are New Caledonia (nine species, five of which are endemic), Papua New Guinea (seven species, one endemic), Timor-Leste (seven species, three endemic), Christmas Island (five species, three endemic), Fiji (five species, three endemic), and Hawaii (five species, four endemic) (Fig 7).

The diversity depicted in Fig. 7 may inform future sampling efforts that aim to complete the documentation of the IWP Siphonariidae. Significant sampling gaps persist particularly in large parts of the Indo-Malay Archipelago, continental Southeast Asia, the Indian subcontinent, the Arabian Peninsula, and in West Africa.

Systematics

Family Siphonariidae Gray, 1827

Siphonaria Sowerby I, 1823

Siphonaria Sowerby I 1823 (in 1821–34): 126, pl. 122. Type species: *Siphonaria sipho* Sowerby I 1823, by subsequent designation of Gray (1847: 181).—Numerous subsequent references.

Mouretus Blainville 1824b: 161–162. Type species: *Mouretus adansonii* Blainville, 1824, by monotypy.—Iredale 1921: 207; Morrison 1963: 8; 1972: 52–53; Christiaens 1980a: 78 (all as subgenus of *Siphonaria*).

Liria Gray 1824: 275. Unavailable (introduced in synonymy of *Siphonaria*, and not treated as available before 1961; Art. 11.6 of the Code).

Liriola Dall 1870: 32. Type species: *Siphonaria thersites* Carpenter, 1864, by original designation; as subgenus of *Siphonaria*.—Dall 1870: 32–33; Suter 1909a: 33, 1913: 601; Dall 1926: 26; Thiele 1931: 472; Hubendick 1945: 60; 1946: 8–9, 18–19; Tomlin 1948: 229; Powell 1951: 65; Morrison 1963: 7; Abbott 1974: 335; Christiaens 1980a: 80; Trew 1983: 3; Redfern 2001: 759.

Liphonaria Brazier 1878: 135. Invalid; incorrect subsequent spelling of *Siphonaria*.

Patellopsis Nobre 1886: 32. Type species: *Siphonaria algesirae* Quoy & Gaimard, 1833, by monotypy; as subgenus of *Siphonaria*.—Hubendick 1945: 60, 70; 1946: 9, 12–13, 30–35 (as section of subgenus *Liriola*); Abbott 1974: 335.

Kerguelenia Mabille & Rochebrune in Rochebrune & Mabille 1889: H.27–H.28. Invalid; junior homonym of *Kerguelenia* Stebbing, 1888 [Crustacea], *Kerguelenella* is a replacement name.—Suter 1909a: 34; Iredale 1915: 478; Hedley 1916a: 61, 62; 1917b: 96; Dall 1921: 67; May 1921: 89; Gatliff & Gabriel 1922: 56; May 1923: 87; Odhner 1924: 55; Finlay 1927: 442; Powell 1937: 68; 1939: 217 238; Hubendick 1945: 66–67, 70; 1946: 9, 11–12, 18–19, 24, 26–30, 35 (as a section of *Liriola*); Powell 1955: 122; Marcus & Marcus 1960: 114 (as subgenus of *Siphonaria*); Dell 1964: 290; Abbott 1974: 335 (as subgenus of *Siphonaria*); Powell 1979: 293; White & Dayrat 2012: 64–65, 68.

Pugillaria Iredale 1924: 277. Type species: *Siphonaria stowae* Verco, 1906, by original designation.—Thiele 1931: 472 (as subgenus of *Siphonaria*); Cotton & Godfrey 1932: 155; Macpherson & Chapple 1951: 142; Cotton 1959: 411; Zilch 1959: 85; Iredale & McMichael 1962: 82; Macpherson & Gabriel 1962: 264; Morrison 1963: 7–8 (as section of *Liriola)*; Shikama 1964: 6 (as subgenus of *Siphonaria*); Macpherson 1966: 256; Trew 1983: 3; White & Dayrat 2012: 61; Jenkins 2018: 276, 279, 281.

Benhamina Finlay 1927: 442, 478. Type species: *Siphonaria obliquata* Sowerby I, 1825, by original designation.—Thiele 1931: 472 (as subgenus of *Siphonaria*); Powell 1937: 86; 1939: 217; Hubendick 1945: 60, 66; 1946: 9, 11, 18, 22, 25, 64 (as section of *Liriola*); Powell 1946: 91; Borland 1950: 385–393; Knox 1954: 872; 1955: 86; Powell 1955: 120; 1956: 120; 1957a: 114; Marcus & Marcus 1960: 108; Shikama 1964: unnumbered (as subgenus of *Siphonaria*); Morton & Miller 1968: 302, 336, 338, 354, 378, figs 121–122, pl. 19, figs 10–10a; Berry 1977: 204, 211; Powell 1979: 293, pl. 54, figs 12–13, Trew 1983: 2; Morley 2004: 130; Russell & Phillips 2009: 579.

Mestosiphon Iredale 1940: 437, 439. Type species: *Mestosiphon eumelas* Iredale, 1940, by original designation.—Habe & Kikuchi 1960: 64; Habe & Kosuge 1966: 113 (as *Mestasiphon*, incorrect subsequent spelling of *Mestosiphon*); Yoo 1967: 89 (as *Mastosiphon*, incorrect subsequent spelling of *Mestosiphon*) (all as subgenus of *Siphonaria*); Morrison 1972: 54, 56 (as section of *Siphonaria* s. str.); Habe & Kohno 1980: 23; Jenkins 1983: 29; White & Dayrat 2012: 63, 64, 66.

Mallorisiphon Iredale 1940: 437, 440. Type species: *Mallorisiphon oppositus* Iredale, 1940, by monotypy.—Morrison 1972: 57 (as synonym of *Mestosiphon*); White & Dayrat 2012: 66, 70.

Ellsiphon Iredale 1940: 437, 438. Type species: *Ellsiphon marza* Iredale, 1940, by original designation.—McAlpine 1952: 40, 42.

Triellsiphon Iredale 1940: 437, 439. Type species: *Triellsiphon acervus* Iredale, 1940, by monotypy.—Hubendick 1945: 29; White & Dayrat 2012: 60.

Parellsiphon Iredale 1940: 437, 438. Type species: *Parellsiphon zanda* Iredale, 1940, by original designation.—Hubendick 1945: 29; 1946: 30–31, 41, 61; Morrison 1972: 57; Jenkins 1983: 29; White & Dayrat 2012: 61, 64, 67, 69.

Legosiphon Iredale 1940: 437, 440. Type species: *Legosiphon optivus* Iredale, 1940, by original designation.—Hubendick 1955: 7, 132; White & Dayrat 2012: 62, 65–66.

Hebesiphon Iredale 1940: 437, 441. Type species: *Hebesiphon monticulus* Iredale, 1940, by monotypy.—Morrison 1972: 51, 61; White & Dayrat 2012: 65.

Torquisiphon Iredale 1940: 437. Type species: *Torquisiphon percea* Iredale, 1940, by monotypy.—Hubendick 1946: 63; White & Dayrat 2012: 66.

Talisiphon Iredale 1940: 441, 442. Type species: *Siphonaria virgulata* Hedley, 1915, by original designation.—Cotton 1959: 411; Iredale & McMichael 1962: 82; Morrison 1963:

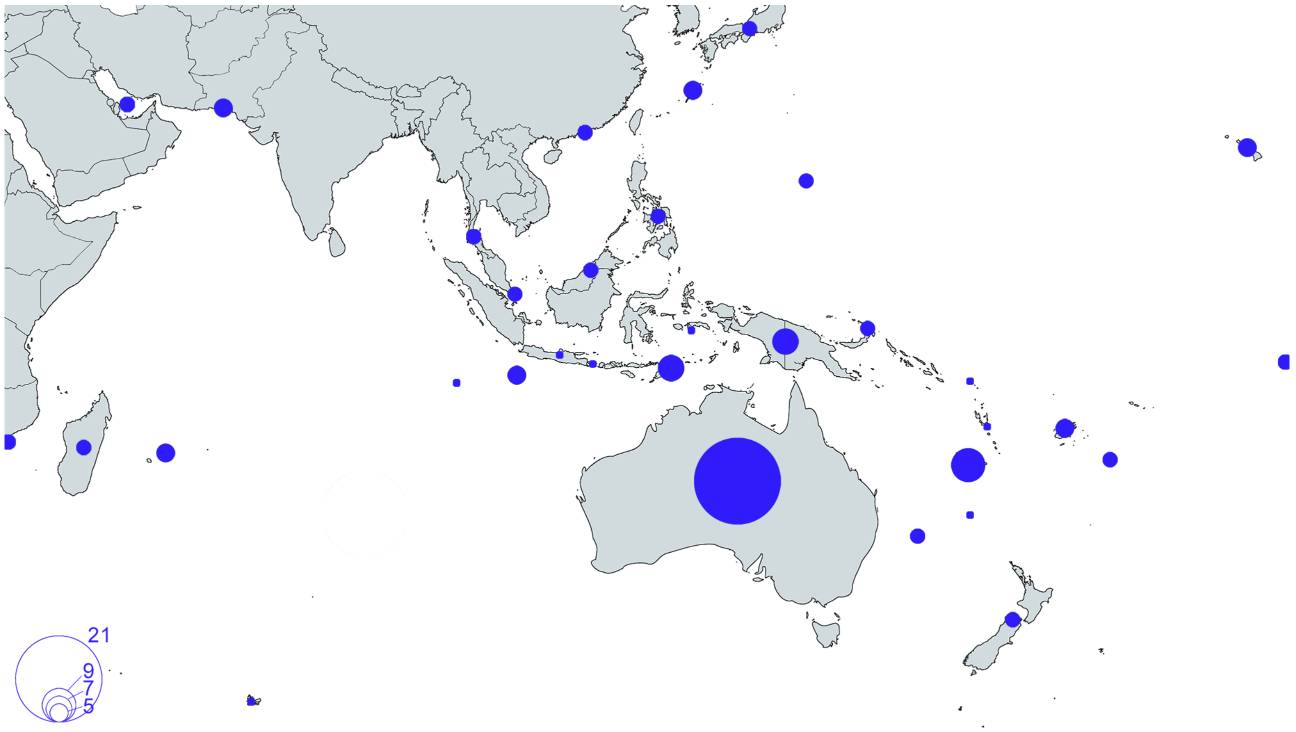

FIGURE 7. Geographic coverage and material sampling of this study. Circle size indicates the number of accepted species in different geographical areas

7 (as section of *Liriola*); Marincovich 1973: 42; White & Dayrat 2012: 66, 69.

Sacculosiphonaria Hubendick 1945: 61, 72. Type species: *Patella japonica* Donovan, 1834, by original designation; as section of *Siphonaria*.—Hubendick 1946: 41–43 (as subgenus of *Siphonaria*); Knox 1955: 88; Kira 1962: 201; Habe & Kikuchi 1960: 64; Marcus & Burch 1965: 256; Habe 1971: 15; Kuroda *et al.* 1971: 302; Christiaens 1980b: 466; Inaba 1983: 145; Fukuda *et al.* 1992: 76; Trew 1983: 9.

Simplisiphonaria Hubendick 1945: 61, 72. Type species: *Siphonaria cookiana* Suter, 1909, by original designation; as section of *Siphonaria*.—Hubendick 1946: 36; Trew 1983: 8 (as subgenus of *Siphonaria*).

Pachysiphonaria Hubendick 1945: 12, 15, 16, 60, 64, 72. Type species: *Siphonaria lessonii* Blainville, 1827, by original designation; as section of *Liriola*.—Hubendick 1946: 20–22, 24; Powell 1951: 65, 1960: 163; Shikama 1964: 7; Rios 1970: 140; Dell 1971: 214; Trew 1983: 2, 5 (as genus); Ludbrook & Gowlett-Holmes 1989: 612.

Ductosiphonaria Hubendick 1945: 61, 70. Type species: *Siphonaria bifurcata* Reeve, 1856, by original designation; as section of subgenus *Siphonaria*.—McAlpine 1952: 42; Hubendick 1955: 4–6; Cotton 1959: 411.

Heterosiphonaria Hubendick 1945: 61. Type species: *Siphonaria gigas* Sowerby I, 1825, by original designation; as section of *Siphonaria*.—Hubendick 1945: 61, 70, 72; 1946: 13, 15, 39–41, 65, 66, 1955: 6; Morrison 1963: 8; Shikama 1964: 6; Keen 1971: 850, 852; Trew 1983: 8–9.

Kerguelenella Powell 1946: 91 (nom. nov. pro *Kerguelenia* Mabille & Rochebrune, 1889, non Stebbing, 1888 [Crustacea]). Type species: *Siphonaria redimiculum* Reeve, 1856, by original designation.—Powell 1951, 55; Carcelles 1953: 206; Knox 1955: 85; Powell 1955: 120–122; 1957a: 114; 1957b: 137; Boreham 1959: 72; Powell 1960: 163; Dell 1963: 227; 1964: 290; Morton & Miller 1968: 313, 379, 380; Dell 1971: 215; Gaillard 1971: 278; Arnaud 1974: 542; Burn & Bell 1976: 234; Simpson 1977: 126, 132; Powell 1979: 293; Christiaens 1980a: 80 (as subgenus of *Siphonaria*); Branch *et al.* 1991: 55; Forcelli 2000: 132; Griffiths & Waller 2016: 1147.

Anthosiphonaria Kuroda & Habe 1952: 302. Type species: *Siphonaria sirius* Pilsbry, 1894, by original designation.—Christiaens 1980a: 79; Inaba 1983: 145; Habe *et al.* 1986: 23; Je 1989: 29; Fukuda *et al.* 1992: 76.

Hubendickula McAlpine 1952: 42. Type species: *Siphonaria diemenensis* Quoy & Gaimard, 1833, by original designation.—Cotton 1959: 411; Ludbrook & Gowlett-Holmes 1989: 610, fig. 11 (as subgenus of *Siphonaria*).

Hubendicula Hubendick 1955: 5–6. Invalid; incorrect subsequent spelling of *Hubendickula*.

Hubendiculata Iredale & McMichael 1962: 82. Invalid; incorrect subsequent spelling of *Hubendickula*.

Siphonacmea Habe 1958b: 35. Type species: *Acmaea oblongata* Yokoyama, 1926, by original designation.—Habe 1962: 96, pl. 44, fig. 15; 1964: 144, pl. 44, fig. 14; Toyohara *et al.* 2001: 27–35.

Planesiphon Zilch 1959: 86. Type species: *Planesiphon elegans* Iredale, 1940, by original designation (as subgenus of *Siphonaria*).—Hubendick 1946: 23; Marcus & Marcus 1960: 122; Iredale & McMichael 1962: 82; Kuroda *et al.* 1971: 303; Jenkins 1983: 5, 12; Inaba 1983: 145; Habe *et al.* 1986: 23; Je 1989: 29; White & Dayrat 2012: 63, 67.

Sacculosiphon Je 1989: 29. Invalid; incorrect subsequent spelling of *Sacculosiphonaria*.

Perellsiphon Fukuda 1994: 50, 809. Invalid; incorrect subsequent spelling of *Parellsiphon*.

Taxonomic remarks. The genus *Siphonaria* was originally described to contain four species, *S. sipho, S. concinna, S. tristensis* and *S. exigua,* without an original type species designation. Sowerby referred to two species as 'typical species of the genus' ("Adanson's Mouret" (Le. *Lepas mouret* Adanson, 1757; unfigured) and "*Patella Sipho*"). However, none of these were available names. Gray (1847: 181) subsequently designated *S. sipho* as the type species. Anton (1838: 26) designated *Siphonaria sowerbyi* Michelin, 1832 and Hubendick (1946: 19) designated *Siphonaria laciniosa* (Linnè, 1758) as type species, but none of these taxa were originally included species rendering these subsequent type designations invalid (Art. 74.1 of the Code).

Several subsequent authors incorrectly attributed the genus name *Siphonaria* to Blainville, 1824, but Blainville (1824a: 268) explicitly attributed *Siphonaria* to Sowerby. Consequently, Blainville did not establish a junior homonym of Sowerby's name. Hubendick (1946: 18) treated Iredale's taxa *Ellsiphon, Legosiphon, Hebesiphon, Mallorisiphon, Mestosiphon, Planesiphon* (although not valid), *Parellsiphon*, *Torquisiphon, Triellsiphon,* and *Pugillaria* as junior synonyms of *Siphonaria* as these were essentially based on conchological attributes. Several authors treated *Liriola* as a subgenus of *Siphonaria* (e.g., Suter 1913: 601; Hubendick 1945: 60, 1946: 8–9, 18–19; Morrison 1963: 7; Abbott 1974: 335). By contrast, Fischer and Crosse (1900: 108) treated *Liriola* as a distinct genus. Contrary to Hubendick (1945: 15, fig. 1, 1946: 8, fig. 3), two determinant anatomical characters specified for the subgenus *Liriola* appear not to be diagnostic: The 'epiphallus and spermoviduct' (i.e. ED and CD) do not open separately (i.e., the genital pore is monaulic) in several species and a 'spermatheca' (i.e., BC) is present in the type species *S. thersites* as well as other species occasionally associated with this taxon (*S. obliquata*, *S. tasmanica*, *S. funiculata*, *S. virgulata* and *S. obvirgulata*, *S. stowae*, *S. lateralis*, *S. acmaeoides*, *S. capensis*, *S. belcheri*, and *S. carbo*). Indeed, all species studied herein possess a monoaulic genital opening and a BC as part of the RS. Hubendick (1946: 30) assigned *Patellopsis* Nobre, 1886 as a section to *Liriola*; however, incorrectly stated the type species to be *S. pectinata* (Linnè, 1758). However, the type species is *S. algesirae* Quoy & Gaimard, 1833 by original designation (Nobre, 1886: 32) although subsequently treated as a synonym of *S. pectinata* by Hubendick (1946: 43), Morrison (1972: 53), and Giribet & Kawauchi (2015: 5). The subsequent designation of *S. lateralis* Gould, 1848 as the type species for *Kerguelenia* Mabille & Rochebrune, 1889 by Hubendick (1945: 60) is invalid because *S. lateralis* was not originally included in *Kerguelenia* (Art. 67.2, 69.1 of the Code). *Siphonaria redimiculum* Reeve, 1856 and *S. macgillivrayi* Reeve, 1856 are the only originally included species. Powell (1946: 91) subsequently designated *S. redimiculum* Reeve, 1856 as the type species of *Kerguelenia*. However, *Kerguelenia* Mabille & Rochebrune, 1889 is preoccupied by *Kerguelenia* Stebbing, 1888 (Crustacea: Amphipoda). Finlay (1927: 442) noted the similarity of *S. obliquata* with *Kerguenella*, but for being conchologically "quite aberrant" placed it in a new genus, *Benhamina*. *Torquisiphon* has been treated as a junior synonym of *Hebesiphon* by Morrison (1972: 60). Hubendick (1946: 22) mentioned *Talisiphon tasmanicus* as a synonym of *Siphonaria tasmanica* implying that he likely considered *Talisiphon* as a junior synonym of *Siphonaria*. By contrast, Morrison (1963: 7) treated *Talisiphon* as a section of the subgenus *Liriola*. Hubendick (1946: 18) treated *Mouretus* as a synonym of *Siphonaria.* The type species of *Mouretus* is *S. adansonii* Blainville, 1824 by original designation of Blainville (1824b: 162), not '*M. mouretus* Blainville' (Morrison, 1972: 53; a nomen nudum). *Hubendickula* was ranked as section in *Siphonaria* s. str. by Hubendick (1955: 5–6). The name *Planesiphon* is unavailable from Iredale (1940: 437, 441) as no type species was designated (Art. 13.1 of the Code). However, Zilch (1959: 86), subsequently made the name available referring to Iredale's (1940) description while designating *Planesiphon elegans* as the type species. He treated the taxon as a subgenus of *Siphonaria*. The prior type species designation of *S. elegans* Iredale, 1940 by McAlpine (1952: 42) is not valid because *Planesiphon* was not treated as an accepted name (Art. 69.1 of the Code).

Hubendick (1945, 1946, 1955) and Morrison (1963) treated *Heterosiphonaria* as a valid section of *Siphonaria* s. str. *Benhamina* has been ranked as a valid genus by Powell (1939: 217; 1946: 91; 1955: 120; 1979: 293, pl. 54, figs 12–13), Borland (1950: 385–393), Morton and Miller (1968: 302, 336, 338, 354, 378), and Morley (2004: 130), but as a section in *Liriola* by Hubendick (1945: 55; 1946: 9, 11, 18, 24–26, 64). Our results indicate that the monotypic genus *Benhamina* is unwarranted because its general morphological and molecular characteristics fall within the range of *Siphonaria*. Moreover, we synonymize *Talisiphon* Iredale, 1940 with *Siphonaria*, and its type species, *S. virgulata*, with *S. funiculata*. The type species of *Simplisiphonaria* Hubendick, 1945 is *Siphonaria cookiana* Suter, 1909 by original designation. This species is a junior objective synonym of *Siphonaria australis* Quoy & Gaimard, 1833 because of Boreham's (1959) subsequent lectotype designation (a juvenile shell of *S. australis* from a mixed syntype lot; Jenkins, 1983: 1, 21, figs 3e–g). The type species of the following genus-group taxa are herein considered as junior synonyms of *Siphonaria* species: *Mestosiphon* Iredale, 1940 (type species *M. eumelas* = *S. atra*); *Ellsiphon* Iredale, 1940 (type species *E. marza* = *S. denticulata*); *Triellsiphon* Iredale, 1940 (type species *Triellsiphon acervus* = *S. atra*); *Legosiphon* Iredale, 1940 (type species *L. optivus* = *S. viridis*); *Ductosiphonaria* Hubendick, 1945 (type species '*S. bifurcata'* [non Reeve, 1856] = *S. zelandica*); *Planesiphon* Zilch, 1959 (type species *P. elegans* Reeve, 1856 = *S. zelandica*).

Siphonaria as delineated herein reveals considerable phylogenetic structure (Fig. 1). However, none of the principal clades retrieved herein is found to exhibit a consistent morphological feature that allows us to consistently distinguish its members from those of any other clade. Therefore, we treat all previously introduced genus-group names listed above as junior synonyms of *Siphonaria*. Given the lack of clearly identifiable diagnostic characteristics, we do not find it useful or even justifiable to maintain subgenera within *Siphonaria* for any of the species examined herein. The sole exception is *Siphonaria thersites* (type species of *Liriola*). This species is the sister group of all remaining *Siphonaria* species (Figs 1–4) and is distinguished by the combination of a very low-level occurrence intertidally, the animal not being fully enclosed by a reduced and often flattened shell, the BD in the RS totally enclosed within the CD and a relatively small and short SPM. Should these characters be revealed as synapomorphies of a distinct taxonomic lineage that incorporates additional extralimital species, then the name *Liriola* was available for such a natural group. However, none of the species from the IWP examined herein is member of this potential lineage.

Siphonaria sipho **Sowerby I, 1823**

(Figs 8–10, 12A–F, L–M)

Patella sipho Sowerby I 1823 (in 1821–34): [126] (*nomen nudum*).

Siphonaria sipho Sowerby I 1823 (in 1821–34): [126], pl. 143, fig. 1 (type locality unknown).—Sowerby I 1825: 32; Blainville 1827: 294; Deshayes 1832: 954; Lamarck 1836: 557; Anton 1838: 26; Lamarck 1839: 205; Catlow & Reeve 1845: 100; Gray 1847a: 181; Sowerby I 1852: 277, 323, fig. 231*; Menke 1844: 55; Gray 1850: 181; Sherborn 1922: 5992; H. Adams & A. Adams 1855 (in 1853–58): 271, pl. 84, fig. 10b; Reeve 1856: pl. 2, species 9; Hanley 1858b: 152; H. Adams & A. Adams 1863: 271; Schrenck 1867: 306; Dall 1870: 31; Fischer 1883 (in 1880–1887): 513, pl. 11, fig. 25); Paetel 1883: 178; 1889: 429; Stearns 1891: 13; Boettger 1892: 168; Tillier & Bavay 1905: 176; Thiele 1931: 472; Abe 1940: 59; Hirase 1941: 94, pl. 121, fig. 11; Kuroda 1941: 137; Kuroda & Habe 1952: 86; Azuma 1960: 62; Berry 1977: 197–198, fig. 15 RS; Galindo 1977: 416; Jenkins 1983: 28; Poppe 2010: 442, pl. 912, figs 1–2; White & Dayrat 2012: 58.

Siphonaria exigua Sowerby I 1823 (in 1821–34): [126], pl. 143, fig. 4 (type locality unknown).—Sowerby I 1820–1825: 126 [1823], pl. 122, fig. 4, 32 [1825]; Blainville 1827: 295; Lamarck 1836: 557; Anton 1838: 26; Lamarck 1839: 205; Catlow & Reeve 1845: 100; H. Adams & A. Adams 1855 (in 1853–58): 271; Hanley 1858a: 25; 1858b: 151; 1863: 271; H. Adams & A. Adams 1863: 271; Schrenck 1867: 306; Paetel 1873: 117; 1875: 92; 1883: 178; 1889: 428; Schepman 1913: 460; Faustino 1928: 352; Morrison 1972: 52; Berry 1977: 190; Galindo 1977 : 416; Trew 1983: 5; White & Dayrat 2012: 63.

Siphonaria radiata Gray 1824: 276 (invalid; unnecessary replacement name; refer to Taxonomic remarks).—Gray 1826: 491; 1827: pl. 4 (6), figs 20–21; White & Dayrat 2012: 67.

Siphonaria cornuta Gould 1846: 11 (type locality: Mangsi [Mangsee Islands, Philippines]).—Gould 1848: 153; 1852: 357; H. Adams & A. Adams 1855 (in 1853–58): 271; Gould 1856: 13, figs 467, 467a, b; Hanley 1858b: 151; H. Adams & A. Adams 1863: 271; Paetel 1889: 428; Faustino 1928: 352; Johnson 1964: 60; White & Dayrat 2012: 62.

Siphonaria siquijorensis Reeve 1856: species 27, pl. 6, fig. 27a, b (type locality: Island of Siquijor, Philippines).—Hanley 1858b: 152; Paetel 1873: 117; 1883: 178; 1889: 420; Galindo 1977: 416; Trew 1983: 7; Higo *et al.* 2001: 142, fig. G4974; Poppe 2010: 444, pl. 913, figs 1, 2; White & Dayrat 2012: 67.

Siphonaria luzonica Reeve 1856: species 29, pl. 6, fig. 29 (type locality: Puteao, Luzon, Philippines).—Hanley 1858b: 152; Paetel 1889: 429; Faustino 1928: 352; Galindo 1977: 416; Trew 1983: 6; White & Dayrat 2012: 65.

Siphonaria corrugata Reeve 1856: species 31, pl. 6, fig. 31 (type locality: Puteao, Luzon, Philippines).—Hanley 1858b: 151; Paetel 1883: 178; 1889: 428; Faustino 1928: 352; Galindo 1977: 416; Trew 1983: 5; Poppe 2010: 440, pl. 911, figs 1a, b, 2a–c, 3a–c; White & Dayrat 2012: 62.

Siphonaria crebricostata—Schrenck 1867: 306 (not *S. crebricostata* Jay, 1839).

Siphonaria albicans Schrenck 1867: 306 (invalid; incorrect subsequent spelling of *albicante* Quoy & Gaimard, 1833; not *S. albicante* Quoy & Gaimard, 1833).

Siphonaria zelandica—Schrenck 1867: 306 (not *S. zelandica* Quoy & Gaimard, 1833).

Siphonaria punctata—Schrenck 1867: 306 (not *S. punctata* Quoy & Gaimard, 1833).

Siphonaria plicata—Schrenck 1867: 306 (not *S. plicata* Quoy & Gaimard, 1833).

Siphonaria sipho elatior Schrenck 1867: 306 (type locality: Philippinen [Philippines]). White & Dayrat 2012: 59, 63, 70.

Siphonaria sipho intermedia Schrenck 1867: 307 (type locality: Philippinen [Philippines]). White & Dayrat 2012: 59, 64, 70.

Siphonaria sipho depressior Schrenck 1867: 307 (type locality: Bai von Hakodate auf Jesso [Hakodate Bay, Hokkaido, Japan]). White & Dayrat 2012: 62, 70.

Siphonaria (*Mestasiphon*) *atra*—Habe & Kosuge 1966: 113, pl. 42, fig. 26 (incorrect subsequent spelling of *Mestosiphon*) (not *S. atra* Quoy & Gaimard, 1833).

Siphonaria sipho var. *sipho*—Hubendick 1945: 29.

Siphonaria sipho var. *exigua*—Hubendick 1945: 29.

Siphonaria (*Siphonaria*) *laciniosa*—Hubendick 1946: 47 (not *S. laciniosa* (Linnaeus, 1758)).

Siphonaria (*Siphonaria*) *laciniosa* var. *exigua*—Hubendick 1946: 47 (in part), pl. 3, fig. 16.

Siphonaria (*Siphonaria*) *laciniosa* var. *sipho*—Hubendick 1946: 47 (in part), pl. 3, fig. 17.

Siphonaria laciniosa elatior—Hubendick 1946: 48.

Siphonaria laciniosa intermedia—Hubendick 1946: 48.

Siphonaria laciniosa depressior—Hubendick 1946: 48.

Siphonaria kurracheensis var. *siquijorensis*—Hubendick 1946: 54.

Siphonaria laciniosa—Kuroda 1960: 43; Okutani 1982: 32; Fukuda 1994: 50, 805 (not *S. laciniosa* (Linneaus, 1758)).

Siphonaria javanica forma *sipho*—Springsteen & Leobrera 1986: 286, pl. 81, figs 21–22.

Siphonaria (*Perellsiphon*) *siquijorensis*—Fukuda 1994: 50, 809 (incorrect subsequent spelling of *Parellsiphon*).

Siphonaria kurracheensis—Hylleberg & Kilburn 2003: 113 (not *S. kurracheensis* Reeve, 1856).

Siphonaria guamensis—Tan & Kastoro 2004: 50 (not *S. guamensis* Quoy & Gaimard, 1833).

S. laciniosa group 'unit 24' (in part)—Dayrat *et al.* 2014: 261, 266, fig. 4F–I.

Material examined. *Type material.* Neotype of *Siphonaria sipho* Sowerby I, 1823, present designation, from Calalinan, Siquijor, Philippines, 9°12.834'N, 123°30.043'E; coll. B.W. Jenkins, 3 April 2019, PHS02-5 (NHMUK 20210025 [M412, SK095], Fig. 8A).

Holotype of *Siphonaria cornuta* Gould, 1846 from 'Mangsi' [= Mangsee] Islands (USNM 5850, Fig. 12E).

Four syntypes of *S. siquijorensis* Reeve, 1856 from Siquijor (NHMUK 1969166, Figs 8K–M).

Three syntypes of *Siphonaria luzonica* Reeve, 1856 from Puteao, Luzon, Philippines (NHMUK 1979163, Figs 8B–D).

Syntype of *Siphonaria corrugata* Reeve, 1856 from Luzon, Philippines (NHMUK 1979165, Fig. 8E).

Other, non-type material. **Philippines, Siquijor:** Sawang, 09°08.249'N, 123°31.113'E, PHS02-3 (AM C.585532 20+p, C.585108 p [M404, SK078], C.585109 p [M406, SK074], C.585110 p [M415, SK098], C.585111 p [M477, SK284], C.585112 p [M479, SK286], C.585116 p [SK277], C.585117 p [SK278]); Calalinan, 09°12.834'N, 123°30.043'E, PHS02-5 (AM C.585908 20+p)); Lazy, 09°07.544'N, 123°38.407'E, PHS03-1 (AM C.595952 1p). **Cebu:** Mactan Point, 10°20.014'N, 124°02.723'E, PHS04-2 (AM C.585946, 20+p, C.585119 p [M413, SK096], C.585120 p [SK094], AM C.585946 10p). **Bohol:** Caubian Is, 10°17.117'N, 124°10.306'E, PHS04-3 (AM C.595936 p [SK561]). **Luzon:** San Agapito, E side Isla Verde, 13°31.782'N, 121°05.499'E, PHV02-1 (AM C.585862 p [M407, SK076]), NW Polillo Is, Bolunga District, nr Panukalan, E Quezon, 14°59'N, 121°49'E (WAM S72342, 10+p). **Japan, Okinawa**: Sun Marina Beach, Onna, 26°27.842'N, 127°48.755'E, JP01-1 (AM C.585618 9 p); Cape Maeda, 26°26.573'N, 127°46.113'E, JP01-2 (AM C.585619 9p, C.595925 p [M597, SK541], C.595927 p [M598, SK542], C.595928 p [M599, SK543]); Onna, 26°26.113'N, 127°46.085'E, JP01-3 (AM C.585620, 2 p); Moon Bay, Onna, 26°26.653'N, 127°48.230'E, JP01-4 (AM C.585625 4p, C.584909 p [M506, SK327], C.584910 p [M508, SK323]); Tancha Bay, rocky point, 26°27.941'N, 127°49.194'E, JP01-6 (AM C.584922 p [M494, SK313], C.584923 p [M497, SK316], C.584924 p [M503, SK324], C.584925 p [M507, SK322]). **Honshu:** Boso Peninsula, Tateyama, Arai Bch, seawall, 34°59.838'N, 139°51.378'E, JP01-2 (AM C.584934 1p [M488, SK307], Fig. 12A, L). **Indonesia**: Riau Islands, NE coast of Pulau Panjang, 04°15.9'N, 108°12.27'E (ZRC.MOL.24910 [M520], Fig. 8P), 24911 p [M521], Fig. 8Q), 24907 p [M517, SK433], 24908 p [M518, SK434]); Anambas, SW Pulau Mubur, Teluk Air Bandung, eastern shore of Pulau Kecik, ZRC EA-ZJ07 (ZRC.MOL.24909 p [M522]).

Taxonomic remarks. *Siphonaria sipho* is the type species of *Siphonaria* by subsequent designation. The name has widely been used through the taxonomic literature, but it has been treated inconsistently in the past resulting in a confused taxonomic history. Sowerby (1823) referred to '*Patella sipho*' as a 'common name', which, to our knowledge, was not described previously and therefore is considered as a *nomen nudum*. The original type material of *S. sipho* is considered lost; we found no references to types in previous systematic literature and no type material was located at the NHMUK after an exhaustive search (K. Way & J. Ablett, pers. com.; Art. 75.3.4 of the Code). The neotype of *S. sipho* (Fig 8A), is herein designated to clarify the taxonomic status of this taxon and its type locality in accordance with Art. 75.3 of the Code. This neotype designation aims to remove prevailing uncertainty about the identity of this species and to clarify the taxonomic status of *Siphonaria*. By designating the neotype, we restrict the type locality of *S. sipho* to Calalinan, Siquijor, Philippines. Altogether four hand-drawn figures of *S. sipho* were published in earlier treatments. The original description of this species was published in 1823 while the original black and white drawings were published in 1824 (Sowerby I 1824: pl. 122, fig. 1; Fig. 8O). Subsequently, the species was depicted by H. Adams & A. Adams (1856: pl. 84, fig. 10b) and Reeve (1856: pl. 2, figs 9a–d) based on specimens from the Philippines. While these figures differ in some respects, they provide a limited number of shell characteristics that aid the identification of this species. Although Sowerby's (1823) figures of *S. sipho* are generalized, the proportions, evenness and nature of shell ribbing, and shape/shading of the interior shown in these figures, closely match the characteristics of topotypic specimens of *S. luzonica* Reeve, 1856 rather than any other Indo West-Pacific species. Based on this close similarity in shell features, we treat *S. luzonic*a as a junior synonym of *S. sipho*. Figures of *S. sipho* in Reeve (1856: pl. 2, fig. 9a–b, [specimen 1] from Philippines) and H. Adams & A. Adams (1856: pl. 84, fig. 10b; no location) closely match Sowerby's figure of *S. sipho*. Reeve's second figure of *S. sipho* (1856: pl. 2, fig. 9c–d [specimen 2] from Philippines), however, differs from the first specimen. It is closely similar with Reeve's (1856: pl. 6, fig. 29a–b) coloured figures of *S. luzonica* and with Reeve's (1856: pl. 6, fig. 31a–b) coloured figures of *S. corrugata*.

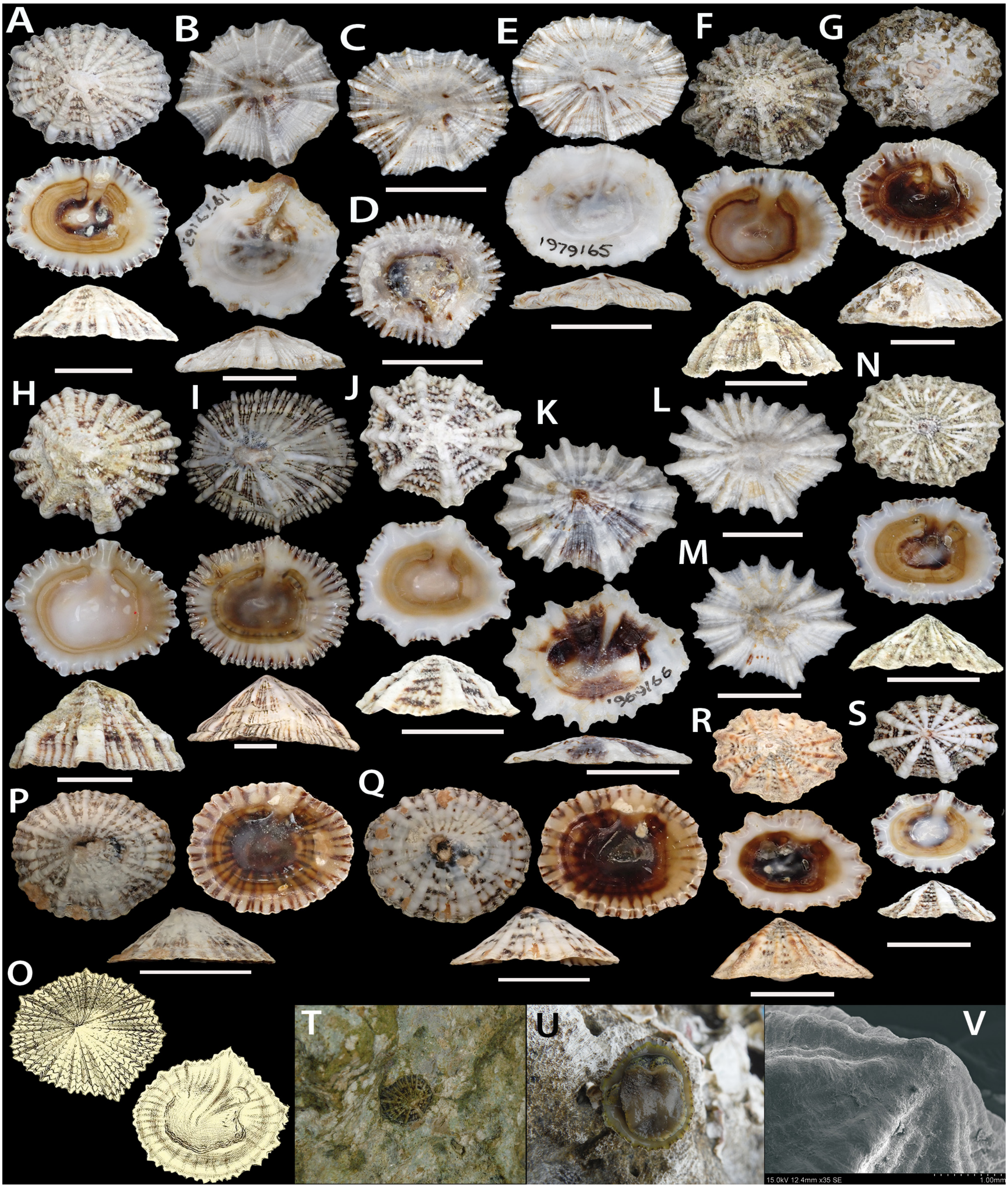

FIGURE 8. Shell morphology of *Siphonaria sipho***. A.** Neotype of *S. sipho* NHMUK 20210025, Siquijor [M412, SK095]. **B–D.** Syntypes of *S. luzonica* NHMUK 1979163, **E.** Syntype of *S. corrugata* NHMUK 1979165. **F.** TS of *S. siquijorensis*, Siquijor, AM C.585108 [M404, SK078]. **G.** Polillo Is, WAM S113803 [SK101]. **H.** Siquijor, AM C.585110 [M415, SK098]. **I.** Okinawa, Tancha Bay, AM C.584923 [M497, SK316]. **J.** *S. exigua* morph, Siquijor, AM C.585111 [M477, SK284]. **K–M.** Syntypes of *S. siquijorensis* NHMUK 1979166. **N.** Cebu, AM C.585119 [M413, SK096]. **O.** Sowerby's original figure of *S. sipho*. **P.** Indonesia, Riau Islands, ZRC.MOL.24910 [M520]. **Q.** Riau Islands, ZRC MOL.24911 [M521, SK437]. **R.** Philippines, Isla Verde, AM C.585862 [M407]. **S.** Cebu, AM C.585120 [SK094]. **T–U.** Animal in situ, Siquijor, PHS02-5. **V.** Protoconch, Siquijor, AM C.585116 [SK277]. Unlabelled scale bars = 10 mm.

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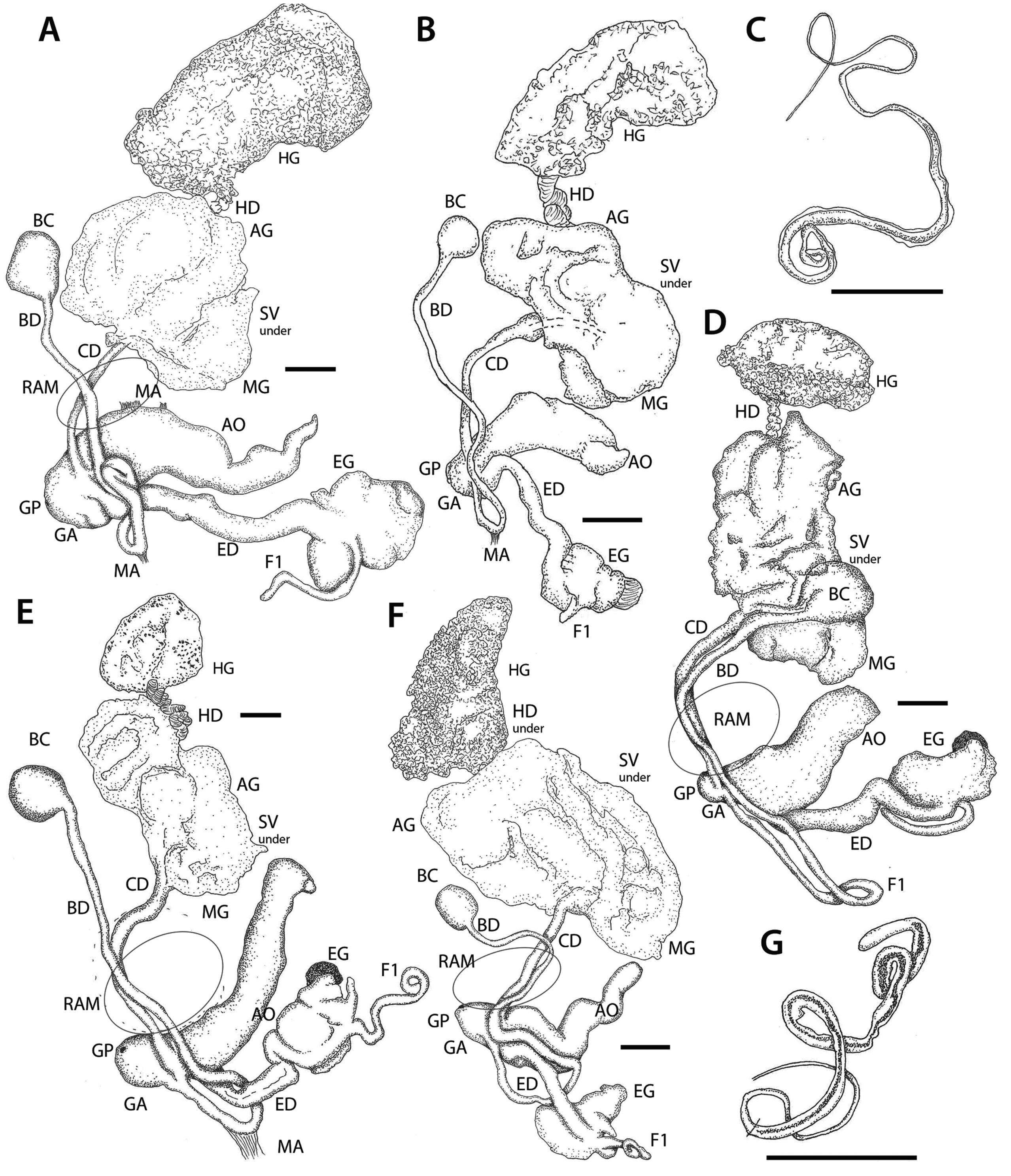

FIGURE 9. Reproductive morphology of *Siphonaria sipho*. **A.** Neotype of *S. sipho* NHMUK 20210025 [M412, SK095], Siquijor. **B–C.** TS of *S. luzonica* and *S. siquijorensis*, Siquijor, AM C.585108 [M404, SK078]. **D.** TS of *S. corrugata*, Polillo Is, WAM S113803 [SK101]. **E.** Okinawa, Tancha Bay, AM C.584923 [M497]. **F–G.** *S. exigua* morph, Siquijor, AM C.585111 [M477, SK284]. Scale bars = 1 mm.

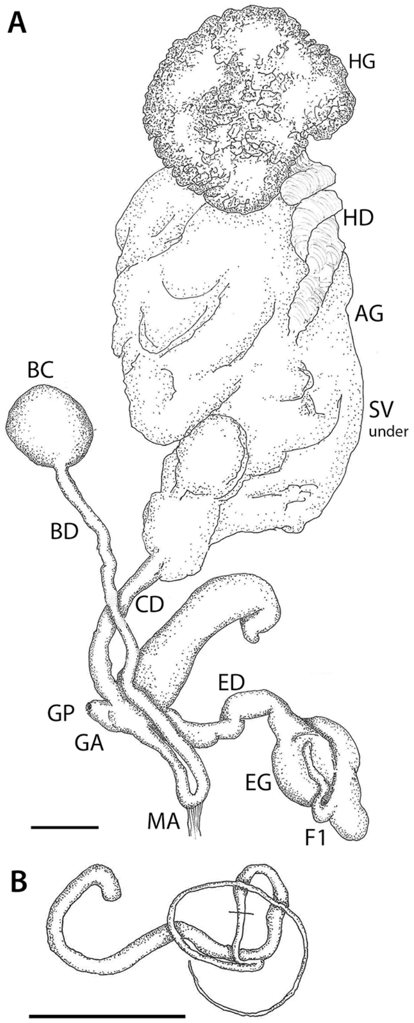

FIGURE 10. Reproductive morphology of *Siphonaria sipho*, continued. **A.** RS, Indonesia, Riau Is, ZRC.MOL.24910 [M520, SK436]. **B.** SPM (same individual). Scale bars = 1 mm.

Our delineation of *S. sipho* is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of the neotype and freshly collected topotypes of *S. sipho depressior* (Figs 8 I) and a geographic series of additional specimens (Tables S1–2), including topotypes of *S. exigua* (Figs 8J), and specimens closely matching the types of *S. luzonica* and *S. corrugata*, respectively (Figs 8B–D, E).

Sowerby I (1823) described *Siphonaria exigua* by reference to the unavailable name *Lepas exigua* published in Martini & Chemnitz (1769: 92, figs 88–89) (work on the Official Index of rejected and invalid works in zoological nomenclature). The original figure of "*Lepas exigua*" is similar to the shell depicted in Sowerby I (1823: pl. 143, fig.4) by absence of a prominent siphonal ridge and the configuration of ribs. Therefore, we treat *S. exigua* Sowerby I, 1823 as a junior synonym of *S. sipho*.

Gray (1824: 276) introduced *S. radiata* as a substitute name for all species figured by Sowerby's (1823) (i.e. *S. sipho*, *S. concinna*, *S. exigua* and *S. tristensis*) instead of using one of these names stating that "he [Sowerby] has … fallen into the common error of modern conchologists, of making too many species; for I have good reason to believe that all the specimens that he has figured, except *S. tristensis*, …. belong to one species". *Siphonaria radiata* Gray (1824: 276) therefore is an unnecessary replacement name and permanently invalid. Gray (1847a: 181) subsequently reverted to using the name *S. sipho* as the type species of the genus. *Siphonaria cornuta* Gould, 1846 was described for shells collected at Mangsee Islands, Sulu Sea during the 'United States Exploring Expedition'. The shells were figured subsequently by Gould (1856). Gould (1846b: 11) indicated that *S. cornuta* was allied to *S. atra*. Johnson (1964: 60) listed Gould's (1856) figured specimen as the 'holotype' and mentioned additional paratypes (3 paratypes MCZ 88100 ex BSNH 3763, original no. 792; 3 paratypes MCZ 216757 ex Smithsonian Inst.). As the original description does not contain an original type designation, Johnson's (1964: 60) subsequent reference to the holotype qualifies as a lectotype designation (Art. 74.6 of the Code). The shell sculpture and geometry of the holotype of *S. cornuta* (i.e., elongate shell, low profile primary ribs, strong protruding shell edge ribbing, interior shell edge colouration and interstice secondary ribbing, Fig. 12E) closely matches diagnostic features of *S. sipho*. For this reason, we treat *S. cornuta* as a junior synonym of *S. sipho*. Pilsbry (1895: 5) considered *S. cornuta* as a synonym of *S. atra*. However, the holotype of *S. cornuta* differs from the more circular geometry and less protruding edge ribbing of *S. atra*. Therefore, we reject Pilsbry's synonymization.

Siphonaria siquijorensis Reeve, 1856 was described from the Island of Siquijor, Philippines. One syntype is figured in Higo, Callomon & Gotō (2001: 142, fig. G4974, "BMNH 1969166"). While topotypic specimens matching the shell form of syntypes were not found in this study, the shell morphology of specimens of *S. sipho* from Okinawa, Japan (Fig. 12B–C) match the shell sculpture and geometry of syntypes of *S. siquijorensis* (Figs 8K–M). For this reason, we treat *S. siquijorensis* as a junior synonym of *S. sipho*. The record of *S. siquijorensis* in Hedley (1909: 369, Qld) is outside of the known distribution of *S. sipho*; likely a misidentification of either *S. atra* or *S. opposita*.

Schrenck (1867: 306) described three infraspecific taxa (*elatior*, *depressior* and *intermedia*), all intended to describe the extent of intraspecific variation within this species, stating 'former and the latter of these forms are available to us from the Philippines, the second, ... from the fauna area in question, the North Japan Sea'. The subspecies *depressior* was recorded from 'Bai von Hakodate auf Jesso' [Hakodate Bay, Hokkaido, Japan]. Hubendick (1946: 48) treated all three taxa as junior synonyms of *S. sipho*. Mitochondrial and comparative anatomical data presented here reveal that specimens matching these nominal taxa are well contained within the range of intraspecific morphological variation of *S. sipho*. Therefore, we maintain their treatment as synonyms of *S. sipho*.

Reeve (1856) incorrectly listed several species as synonyms of *S. sipho* (i.e., *S. crebricostata* [*nomen nudum*; refer below], *S. albicans* [sic *albicante* = *S. atra*], *S. zelandica* [Australia], *S. punctata* [Mauritius], and *S. plicata* [Tonga]). Schrenck (1867: 306) and Hutton (1880: 36, adding *S. inculta* Gould) appear to have accepted Reeve's synonymy. The listing of *S. exigua* in Adcock (1893: 11) as synonym of *S. luzonica* (from SA; misidentified *S. zelandica*) is erroneous. The identity of '*S. sipho* Sow.' in Vernhout (1913: 252, from Ceram) is implausible for being well outside the known distribution of *S. sipho*. It possibly refers to *S. costellata* **sp. nov.** described herein.

The identity of *S. sipho* in Hutton (1880: 36, 1883: 143, from New Zealand) is unclear and most likely a misidentification of *S. australis* (Jenkins, 1983: 11). The synonymy given by Hutton (1880) is incorrect and includes distinct species. Therefore, the stated distribution of *S. sipho* ('Philippine Islands, Indian Archipelago, Mauritius, Tonga, Chatham Islands, Auckland to Dunedin [NZ]') is also incorrect.

Hubendick (1946: 47) treated *S. sipho* and *S. exigua* as intraspecific taxa within *S. laciniosa*, most likely based on the type specimen of *Patella laciniosa* Linneaus, 1758: 781, held at UUZM. Examination of type specimens and morpho-anatomy in this study reveal that Hubendick's interpretation of *S. sipho* is based on misidentifications of *S. javanica, S. viridis* and *S. sipho*. His synonymization of *S. sipho* with *S. laciniosa* is rejected. Kuroda (1960: 43) also incorrectly synonymized *S. sipho* Sowerby with *S. laciniosa*. He listed '*S. laciniosa*' from Okinawa (unfigured). We consider this record to be identical either with *S. sipho* or *S. tanchaensis* **sp. nov.**, both found in Okinawa and exhibiting shells very similar to *S. laciniosa*. Morrison (1972) treated *S. sipho* as a junior synonym of *S. laciniosa* 'Lamarck, 1819' along with 26 other nominal species based on similarity to a '*laciniosa*' shells figured throughout the literature and a 'common reproductive development'. These synonymies are not supported by examination of type specimens and comparative morpho-anatomy and are therefore rejected.

External morphology (Figs 8T–U, 12L–M). Foot sole dark grey, foot edge pale yellow, unpigmented; foot wall, pneumostome and cephalic lobes pale greyish yellow, covered in irregular blotches of black pigmentation; mantle thin, translucent, pale yellowish grey, edge thickened, lobed, with black pigmentation edge bands aligning with underside of rib interstices.

Shell (Figs 8, 12A–F; Table S9). Highly variable, medium sized (max sl mean = 16.8 mm, SD = 2.9 mm, n = 9), circular ovate, low to commonly tall; thick, apex offset central sightly to posterior and left, apical sides straight to convex, sometimes strongly convex (Figs 8G–H, J); protoconch homostrophic (n = 2; Figs 8V), shell whorl dextral; shell exterior and edge usually uneven; growth striae prominent in bands; rib count (mean = 37, SD = 5; n = 9), 10–12 fairly evenly spread primary ribs, pale white, raised rounded ridges, widen to shell edge, protrude beyond shell lip to unevenly scallop and corrugate the edge, ends of primary ribs may be flared creating uneven roughness on rib ridges, between primary ribs brown flecks/bands with two to six finer whitish secondary ribs (sometimes none), rib interstices narrow, darker; paired primary ribs on siphonal ridge, no more prominent than other primary ribs. Interior shell margin white to cream, dark brown markings on shell edge align under rib interstices may extend over shell margin (as in Sowerby's original figure), white rays align on shell margin under primary/secondary ribs, ADM distinct, varies from tan to dark brown; siphonal groove distinct, same colour as shell edge; spatula golden tan with central white to dark chocolate brown; ADM scar distinct, brown to white as spatula; cephalic muscle weakly convex; thickening and whitening of shell lip common, translucent, infills and reduces lip scalloping, spatula becomes whitened.

Neotype (Fig. 8A). Shell (sl = 18.7, sw = 14.4, sh = 6.3 mm) circular ovate, medium; thick, apex offset weakly to posterior and left, ~14 primary ribs, with 1–3 in between finer secondary ribs; siphonal ridge formed by adjacent dual primary ribs. Interior shell lip and margin white under ribs, dark brown rays on shell lip aligning under rib interstices; taller and slightly darker interior shell form of *S. sipho*. RS (Fig. 9A).

Reproductive system (Figs 9–10; n = 15). Positioned to the right side of coelom, against foot wall, on foot muscle and under the respiratory cavity; epiphallic parts positioned over BM and between RAM; GA very small, with singular GP through foot wall; AO large, base wide, elongated, tip bluntly pointed and solidly embedded in MG, joined to lower ED and upper GA; ED as long as AO, narrow, centrally bent, joins to outer side of GA; GA, AO, ED all white muscular fibrous tissue; EG soft whitish tissue, slightly folded, medium in size, joins end of ED; single flagellum (F1), short, often looped, appears as an extension of broader ED; BD and CD connect closely but in opposing directions into GA between ED join and GP, BD narrower and longer, both smooth, whitish, featureless, pass closely together through outer side of RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex may be large; CD connecting to ducts; BD with large distal loop often looping behind ED, MA often present; BC small, embedded in top of AG, spherical, thin whitish translucent test; HD short, small, folded, links ducts in soft white folded tissues of AG to yellowish granulated HG; AG similar size to HG, sides match curvature of inner foot wall.

Spermatophore (Figs 9C, G, 10B). Thread-like (mean total length = 3.63mm, SD = 1.06mm, n = 2), translucent, test thin; head section, tip bluntly rounded, evenly cylindrical, elongate, containing a white gelatinous mass; taper region into the filamentous transparent flagellum is short; both sections smooth, featureless. Head shorter and thicker than flagellum (mean head length = 1.46 mm, SD = 0.11 mm, n = 2; mean of SPM length ~ 41%, SD = 9%; mean head width = 120 µm, SD = 20 µm, n = 2; mean flagellum width = 13 µm, n = 2, SD = 15 µm). Seven SPM tightly coiled in one bursa found in [SK078].

Radula and jaw. Dentition formula 40:1:40 (Hubendick 1946: 47, misidentified as *S. laciniosa*).

Comparative remarks. *Siphonaria sipho* (*laciniosa* group, unit 24) is genetically well-differentiated from other species by COI distances of ≥ 14.9% (Table S6).

The sister species of *S. sipho* is *S. rodrigoensis* **sp. nov.** (Fig. 3). The nominal taxa *S. luzonica*, S. *exigua*, and *S. corrugata* are synonymized herein based on examination of topotypic samples. *Siphonaria siquijorensis*, *S. exigua*, and *S. corrugata* are treated as conspecific based on examination of specimens corresponding closely to the types. Shells matching Sowerby's original figure (Fig. 8O), Reeve's figures of *S. sipho* and specimens matching Sowerby's original figure of *S. exigua* are all conspecific.

Anatomically the RS and SPM of all forms reveal some variation in RS structure (i.e., AO may be very wide and blunt (Fig. 9D); and F1 short and (un)looped (Figs 9B, D–F). This variation is considered as infraspecific. *Siphonaria sipho* exhibits a wide range of shell variation, particularly in shell thickness and height, primary and secondary ribbing as well as internal and exterior colouration. This variation appears uncorrelated with shell size or geographical distribution. Shell variability ranges from a heavily ribbed, tall shape (resembling *S. exigua*; Fig. 8J) to a low, finer ribbed shape with ribs aligning closely to the shell edge (i.e., not strongly protruding; resembling *S. cornuta*, *S. luzonica* and *S. corrugata* shell forms). Populations on Riau Island, Indonesia, represent a geographical outlier that is morphologically somewhat distinct but genetically not well-differentiated from other representatives of this species. The Riau Island specimens differ by having a smaller, lower shell, less raised ribbing, weaker edge scalloping, a smaller AO, shorter, narrower ED, and shorter F1.

Throughout the range of *S. sipho* we found seven congeners occurring in partial sympatry. Four of these are sympatric in the Philippines: The shell of *S. bifurcata* resembles finer ribbed forms of *S. sipho* but is distinguished by narrower primary ribs, fewer intervening secondary ribs, a weakly flared siphonal ridge edge, and paler interior colouration as well as by having a smaller AO, GA and a shorter ED. *Siphonaria sirius* has a lower shell height, a siphonal ridge formed by single rib, a darker exterior and interior, broader and white primary ribs as well as a smaller AO and bursal loop. *Siphonaria caubianensis* **sp. nov.** has a lower height, darker exterior and interior, strongly and unevenly scalloped edge, broader and white primary ribs, a larger AO, bursal loop, and smaller BC. *Siphonaria alba* has broader primary ribs, a shorter, wider ED, and a smaller AO. Four species occur in sympatry with *S. sipho* in Okinawa: *Siphonaria camura* **sp. nov.** and *S. rucuana* are smaller in shell size, the former having a fragile, evenly brown shell; the latter a combination of less raised shell, even ribbing, and darker interior colouration. Both have a smaller AO, shorter wider unlooped BD, and *S. camura* **sp. nov.** has a barbed SPM. *Siphonaria subatra* has a darker exterior and interior colouration, narrower ribbing, lower shell, a smaller BC, a slightly smaller AO. *Siphonaria tanchaensis* **sp. nov.** closely resembles *S. sipho* anatomically and morphologically; it has a similar shell geometry, colouration and ribbing, and internal colouration (i.e., spatula, shell lip including a thickened white lip form). However, has a taller shell, narrower ribs, and a paler, less banded inner shell lip, a smaller BC, ED and AO, and a shorter SPM. *Siphonaria sipho* co-occurs with *S. japonica* in Honshu, and has a lower, thinner, and more fragile shell, dark brown exterior and interior colouration, narrower ribbing, a smaller AO, larger BC, and a barbed SPM. *Siphonaria radians*, sympatric on Riau Islands, has a lower shell with a more posteriorly offset apex and a multi-ribbed siphonal ridge without a flared edge, a larger AO, longer wider twisted ED and a smaller BC.

Specimens identified as *S. sipho* from Java, Bali, and PNG by Adam & Leloup (1939) are here attributed to *S. viridis*. The figure of *S. sipho* in Hirase (1941: 94, pl. 121, fig. 11) is probably a specimen of *S. tanchaensis* **sp. nov.** The RS figured in Hubendick (1945: 31, fig. 48) matches the RS of *S. sipho*. The RS figure in Hubendick (1945: 31, fig. 52) attributed to '*S. kurracheensis*' differs from RS of *S. kurracheensis* and is probably of *S. sipho*.

Specimens from Palawan figured as '*Siphonaria javanica*' in Springsteen & Leobrera (1986: pl. 81, figs 21–22) are specimens of *S. sipho*. The record of '*S. sipho* var. *exigua*' in Subba Rao & Dey (2000: 190) from Andaman and Nicobar Islands is based on a misidentification.

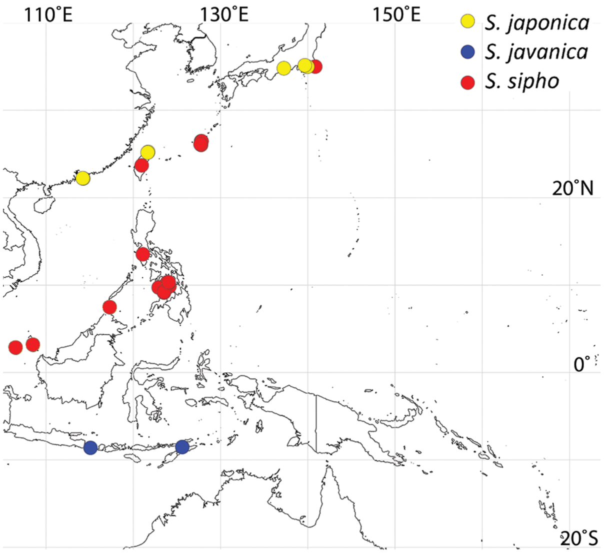

FIGURE 11. Occurrence records of *S. sipho*, *S. javanica* and *S. japonica*.

Figured specimens of '*S. sirius*' in Poppe (2010: pl. 913, figs 3–4) are here attributed to *S. sipho*. Instead, *S. sirius* typically possesses a single rib forming the siphonal ridge. Specimens figured as 'unit 25, *laciniosa* group' in Dayrat *et al*. (2014: fig. 4F, H, I) from Okinawa, Taiwan, and the Philippines are all consistent with characters typical of *S. sipho*.

Distribution and habitat. Philippines (Bohol, Balicasag, Bandian, Negros, Olango, Siquijor, Mactan, Isla Verde, Cebu, Mangsee Is), Taiwan, Japan (Okinawa, Boso Peninsula, Honshu), Indonesia (Riau and Anambas Islands) (Fig. 11). Commonly found in sheltered locations, such as hollows and crevices, across upper and mid littoral levels, on bare, exposed rocks. Home scars prominent.

Siphonaria javanica (Lamarck, 1819)
(Figs 12G–H, K, N–O, 15A)

Patella javanica Lamarck 1819: 333 (type locality: Java).—Delessert 1841: unpaginated text, pl. 23, figs 3a–c; Hanley 1858b: 152; Mermod 1950: 696; Trew 1983: 5.

Siphonaria javanica—Blainville 1827: 294.—Anton 1838: 26; H. Adams & A. Adams 1855 (in 1853–58): 271, 1863: 271; Paetel 1873: 117; 1883: 178; 1889: 428; Morrison 1972: 52; Tan & Kastoro 2004: 50; Pinchuck & Hodgson 2009: 371; White & Dayrat 2012: 59, 64, 70.

Siphonaria (*Siphonaria*) *stellata*—Hubendick 1945: 29, 31, 72, figs 42, 53; 1946: 48 (in part), pl. 3, fig. 23 (not *S. stellata* (Helbling, 1779)).

Siphonaria (*Siphonaria*) *siquijorensis*—Hubendick 1946: 47, pl. 2, fig. 38 (not *S. siquijorensis* Reeve, 1856).

Siphonaria (*Siphonaria*) *laciniosa* var. *exigua*—Hubendick 1946: 47 (in part), pl. 3, fig. 19 (not *S. exigua* Sowerby I, 1823).

Siphonaria laciniosa forma *exigua*—Hubendick 1947b: 3 (not *S. exigua* Sowerby I, 1823).

Siphonaria laciniosa forma *sipho*—Hubendick 1947b: 3 (not *S. sipho* Sowerby I, 1823).

Material examined. *Type material*. Lectotype of *Patella javanica* Lamarck, 1819, present designation, from 'les côtes de Java' [coasts of Java, Indonesia]) (MHNG MOLL-50923, syntype number '2', Fig. 12G). Paralectotypes, same data as lectotype (MHNG MOLL-50923, syntype number '1', d, Fig. 12H; syntype number '3', d, Fig. 12I).

Other, non-type material. **Timor-Leste:** N of Dili: Dolokoan Beach, 8°31.424'S, 125°37.091'E, TL01-1 (AM C.584795 p [M434, SK145]; Fig. 12J).

Taxonomic remarks. The type series for *Patella javanica* Lamarck, 1819 comprises three syntypes labelled 1 to 3. Syntypes #1 and #2 are siphonariids (Figs 12G–H); however, syntype #3 is a liotiid (Fig. 12I). In the original description Lamarck (1819) stated that the shell had 'small white sides … fine and longitudinal streaks between its ribs' while the interior was 'blackish, bordered with yellow and a white edging'. This description closely matches syntype 2 (Fig. 12G), which is herein designated as the lectotype of *Patella javanica* for stabilisation of the name (Art. 74.1 of the Code). The figure of *Patella javanica* in Delessert (1841: pl. 23, fig. 3a–c), matches syntype #1 (Fig 12H).

Hubendick (1946: 38) treated *S. javanica* Lamarck, 1819 as variety of *S. laciniosa*. This treatment is rejected herein. Specimens figured in Hubendick (1946: 47) as *S. laciniosa* var. *sipho* (pl. 3, fig. 19, 'Java') and *S. stellata* (pl. 3, fig. 23, 'Sunda Islands'), respectively, are of *S. javanica*. The 'very minute barbs' on the SPM mentioned by Hubendick (1946: 48) have not been observed. Such barbs on SPM have been observed only in *S. japonica*, *S. camura* **sp. nov.** The RS figured as *S. kurracheensis siquiorensis* (sic!) in Hubendick (1945: 31, fig 52; from 'Edam Java') matches the RS of *S. alba* as described herein, not *S. kurracheensis* nor *S. javanica* (Fig. 15A).

No type specimen of *P. javanica* was figured in Memod (1950). Morrison (1972: 51) in redefining selected species groups, incorrectly considered *S. sipho* as a synonym of *S. javanica* and incorrectly stated this taxon to be the type species of the genus. Further, Morrison (1972: 52) incorrectly treated *S. exigua* and *S. sipho* as synonyms of *S. javanica* based on similarity of the shell and a 'common reproductive development'. These synonymies are not supported by examination of type specimens and comparative morpho-anatomy. The figured specimen in Morrison (1972: 55, fig. 1, 'North Borneo') matches the lectotype (Fig. 12G). Reversing taxonomic precedence, Rehder (1980: 97) incorrectly stated *'Patella javanica* Lamarck, 1819*'* (= *S. javanica*) to be a synonym of *S. sipho*. Records of '*S. javanica*' in Tan & Chou (2000: fig. 116) and Tan & Woo (2010: 61) are misidentifications of *S. viridis* (refer Comparative remarks, *S. viridis*). The record of '*S. javanica'* in Tan & Kastro (2004: 50) from Anambas and Natuna Islands, Indonesia is incorrect and attributable to *S. sipho*.

External morphology (Figs 12N). Foot sole centrally pale grey to dark yellow at foot edge, unpigmented; foot wall and cephalic folds dark yellow with irregular black flecks; mantle translucent dark grey to join of foot wall, yellow markings aligning with underside of ribs, black bands between on edge align under rib interstices, edge lobed and thickened to shell lip.

Shell (Fig. 12G–I, K; Table S9). Medium sized (max sl mean = 19.3 mm, SD = 9.7 mm, n = 2), ovate; height tall; apex offset central, apical sides convex, posterior straight to concave, protoconch area dark brown; protoconch direction central to weakly heterostrophic (n = 1), shell whorl dextral; growth striae prominent, shell thick; rib count (mean = 54, SD = 1, n = 2), ~ 11 primary ribs pale white, fairly straight, rounded ridges, increasingly raised/broaden and protrude beyond shell lip (~1 mm) to unevenly scallop and corrugate the edge; 3 or more interspersed finer secondary ribs pale white with irregular black/brown flecks, rib interstices white, uneven axial brown streaks; paired fused primary ribs form siphonal ridge. Interior shell margin intensely white with fine dark brown rays on edge aligning under rib interstices, siphonal groove distinct; spatula dark chocolate brown; ADM scar indistinct and paler brown with some darker rays to shell margin, CMS convex, paler than shell lip; thickening of shell lip not observed.

Reproductive system (Fig. 15A; n = 1). Positioned to right side of coelom, against foot wall on foot muscle, under respiratory cavity; epiphallic parts positioned between RAM and BM; GA small, with singular GP through foot wall; AO large, very wide, elongated, bluntly pointed, joined to lower ED and upper GA; ED relatively long, wide, unfolded, joins to outer side of GA; GA, AO, ED all white muscular fibrous tissue; EG medium, joins end of much longer ED, soft whitish tissue, slightly folded; single, coiled end flagellum (F1), appears as an extension of wider ED, lays over back of BM; BD and CD junctions into GA close between ED join and GP, both ducts narrow, very long, smooth, whitish, featureless, pass closely together through outer side of RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex large; CD connecting to ducts; BD with large

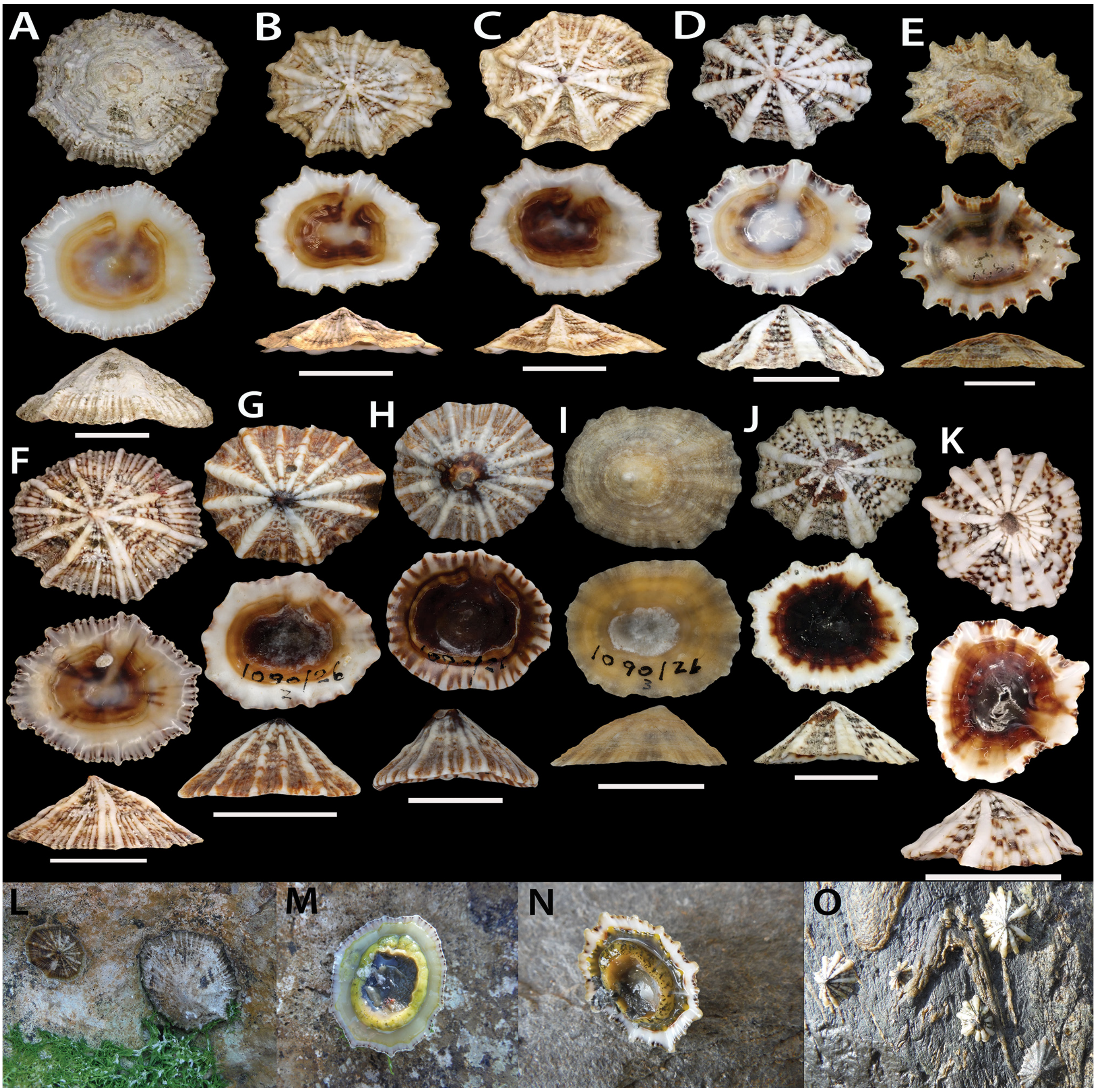

FIGURE 12. Shells of *S. sipho* and *S. javanica*. **A–F.** *S. sipho*. **A.** Honshu, Boso Peninsula, AM C.584934 [M488]. **B–C.** Okinawa, AM C.584910 [M508]. **D.** Philippines, Cebu AM C.585120 [SK094]. **E.** Holotype of *S. cornuta* USNM5850. **F.** Okinawa, Tancha Bay, AM C.584925. **G–H, J–K.** *S. javanica*. **G.** Lectotype of *P. javanica* MHNG-MOLL-50923 (specimen #2). **H.** Paralectotype MHNG-MOLL-50923 (specimen #1). **I.** Paralectotype MHNG-MOLL-50917 (specimen #3, not a siphonariid). **J.** Timor-Leste, Dili, AM C.584795 [M434]. **K.** Dili, AM C.585948 [SK563]. **L–O.** Animals in situ. **L.** *S. sipho*, Okinawa. **M.** *S. sipho*, Okinawa [M488]. **N**. *S. javanica*, Dili, [M434]. **O.** *S. javanica*, Dili. Scale bars =10 mm.

distal loop without MA, BC very small, embedded in top of AG, spherical, thin whitish translucent test; HD short, small, folded, links ducts in soft white folded tissues of AG to yellowish granulated HG; AG similar size to HG, sides match curvature of inner foot wall.

Comparative remarks. In the molecular phylogeny (Figs 1, 3), *S. javanica* (*laciniosa* group, unit 65) is represented by a single individual only. The species is genetically well-differentiated from other species by COI distances of ≥ 27.6% (Table S6). Throughout the range of *S. javanica*, we found eight congeners occurring in partial sympatry. *Siphonaria viridis* (sympatric in northern PNG and Timor-Leste) has a smaller shell with less raised ribs and less scalloped edge, a shorter and broader ED and slightly larger BC. *Siphonaria atra* (sympatric in northern PNG) has a lower, darker, unpatterned shell with less raised darker and narrower ribs and a shorter ED. *Siphonaria normalis* has a smaller shell with less raised ribs, a less to unscalloped edge, and a shorter ED and larger BC. *Siphonaria opposita* (sympatric on Timor-Leste) has a lower, paler, unpatterned shell with narrower ribs, less scalloped edge, flared siphonal ridge, a shorter ED, a more pointed AO, and a bursal loop on BD. *Siphonaria alba* has a lower darker, unpatterned shell, a twisted ED, and a larger BC. *Siphonaria forticosta* **sp. nov.** has a lower, darker shell with less raised ribs, weaker edge scalloping, a smaller AO and ED, a larger BC, and a longer F1. *Siphonaria planucosta* **sp. nov.** has a smaller, lower, darker shell with less raised and even ribbing, a less scalloped edge, a shorter ED and AO, and a larger BC. *Siphonaria campestra* **sp. nov.** has a lower shell with less raised ribs, less scalloped edge, darker interior, and shorter ED, F1, and AO. *Siphonaria javanica* is conchologically resembles several species of the *laciniosa* group but differs anatomically (i.e., RS structure mainly size of BC; epiphallus parts of ED, F1). Hubendick (1945: fig. 53) figured the distal parts of the reproductive system of what he considered to be *S. kurracheensis* var. *siquiorjensis* from Java. However, this figure matches closely the anatomy of *S. javanica* (Fig. 15A) and therefore we consider this treatment as a misidentification. Shells from Indonesia depicted as *S. javanica* by Dharma (1992: pl. 17, fig. 1) closely resemble *S. sipho*, while those depicted by Dharma (2005: pl. 79, figs 19a–b) from East Java and Bali are correctly attributed to *S. javanica*. Specimens from Palawan identified as '*S. javanica*' by Springsteen & Leobrera (1986: pl. 81, figs 21–22) are misidentified specimens of *S. sipho*. A specimen from Singapore figured by Tan & Chou (2000: fig. 116) as '*S. javanica*' closely resembles *S. viridis* with respect to shell colouration, number and prominence of primary ribs, interior margin, size rather than *S. javanica*. There are currently no confirmed records of *S. javanica* from Singapore. A record of '*Siphonaria javanica*' from Hainan (Hasegawa *et al*. 2001: 28) is likely a misidentification from outside of the known distribution of this species (Fig. 11). The correct identity of these specimens is unknown.

Distribution and habitat. Recorded from throughout Indonesia and Timor-Leste (Fig. 11). In this study collected on exposed to moderately exposed rocky boulder shores at upper littoral levels.

Siphonaria japonica (Donovan, 1824)

(Figs 13A–L, Q–S, 15B–E)

Patella japonica Donovan 1824: unpaginated, pl. 76 (type locality: Japan).—Kuroda *et al.* 1971: 483, pl. 64, fig. 7; White & Dayrat 2012: 64.

Siphonaria cochleariformis Reeve, 1856: species 28, pl. 6 (type locality: Hainan).

Siphonaria japonica—Hanley 1858b: 152; Paetel 1889: 428; Pilsbry 1920: 141; Abe 1940: 59; Hirase 1941: 94, pl. 121, fig. 12; Kuroda 1941: 137; Hubendick 1945: 27, fig. 34, 36, 39, 41; Kuroda & Habe 1952: 86; Kuroda 1960: 43; Habe & Kikughi 1960: 64; Shikama 1964: 6; Cook 1969: 697; Berry 1977: 197, fig. 19; Galindo 1977: 416; Chambers 1980: 141, 143; Hirano & Inaba 1980: 323; Hirano 1980: 335; Morton & Morton 1983: 298; Zhongyan 2004: 197, fig. 30, 198, pl. 108, fig. E; Chim & Tan 2009: 269; Murty *et al.* 2013: 104; Dayrat *et al.* 2014: 266, 'unit 2', fig. 3B; Gonzàlez-Wevar *et al.* 2018: 5, fig. 1.

Siphonaria alterniplicata Grabau & King 1928: 62 (type locality: 'Peitaiho').—Hubendick 1946: 62; Galindo 1977: 416; White & Dayrat 2012: 60; Coan *et al.* 2015: 221, pl. 38 A, B (as "*S. alterniplata*").

Siphonaria (*Sacculosiphonaria*) *japonica*—Hubendick 1946: 42, pl. 2, figs 29–32; Knox 1955: 46; Kira 1962: 201, pl. 69, figs 8a–b; Habe 1971: 15, pl. 4, fig. 16; Yoo 1976: 89, pl. 19, figs 1, 3; Inaba 1983: 145; Christiaens 1980b: 466; Fukuda *et al.* 1992: 76, pl. 23, figs 360a–b; Chambers *et al.* 1998: 51; Noseworthy *et al.* 2007: 90.

Siphonaria (*Siphonaria*) *kurracheensis*—Hubendick 1945: 72, 31 fig. 51 (not *S. kurracheensis* Reeve, 1856).

Sacculosiphonaria japonica—Kuroda *et al.* 1971: 483, pl. 64, fig. 7; Trew 1983: 9.

Siphonaria (*Kerguelenella*) *corallina* Christiaens 1980a: 80, fig. 18.—Christiaens 1980b: 467.

Siphonaria (*Sacculosiphon*) *japonica*—Je 1989: 89 (incorrect subsequent spelling of *Sacculosiphonaria*).

Material examined. *Type material.* Neotype of *Patella japonica* Donovan, 1824, present designation, from Headland S of Chitose Bch, Boso Peninsula, Japan, 34°59.240'N, 139°58.304'E; coll. B.W. Jenkins, 15 March 2020, JP02-2 (AM C.584938 [M489, SK308]; Figs 13A, 15D–E).

Syntypes of *Siphonaria cochleariformis* Reeve, 1856 (NHMUK 1981015, Fig. 13H–K).

Syntypes of *Siphonaria alterniplicata* Grabau & King, 1928 (MBM 280642, 72 shells, Peitaino, July 1925; Fig. 13F).

Holotype of *Siphonaria* (*Kerguelenella*) *corallina* Christiaens, 1980 from Channel Rock, Hong Kong, China; on corals at 10m depth (NHMUK 1977170, Fig. 13G).

Other, non-type material. **Japan, Honshu:** Boso Peninsula, Point S of Chitose Beach, 34°59.240'N, 139°58.304'E, JP02-2 (AM C.585394 9p, AM C.585113 p [SK423], AM C.585934 p [SK425], AM C.585935 p [SK339], AM C.584983 p [SK338], AM C.595953 p [SK566]); seawall Arai Bch, Tateyama 34°59.838'N, 139°51.378'E, JP02-1 (AM C.585389 10p, AM C.585235 p [SK340]). **China:** Hong Kong, Cape D'Aguilar 22°12.28'N, 114°15.38'E (ZRC.MOL.2001-1768 21p, ZRC.MOL.24905 p [M476, SK283], ZRC.MOL.24903 p [SK403], ZRC.MOL.24904 p [SK404], ZRC.MOL.24906 p [SK405]).

Taxonomic remarks. Type species of *Sacculosiphonaria* Hubendick, 1945 by original designation. This name became first available with publication of the original plate 79 (June 1, 1824) not the bound volume (3, 1825). Plates and texts were 'published monthly, bound yearly' (Molluscabase Eds. 2022). The original description does not contain an original type designation. The original type material is considered lost as it could not be found at the NHMUK in 2022 (J. Ablett, pers. comm.). The neotype is designated herein to clarify the identity of this nominal species and to designate the type locality (Art. 75.3 of the Code).

Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Figs 13B–D) and geographic series of additional specimens (Tables S1–2).

Pilsbry (1920a: 141) treated *S. cochleariformis* Reeve, 1856 as a junior synonym of *S. japonica* (Donovan, 1824). This was followed by Hubendick (1946: 43), Kuroda & Habe (1952), Kuroda (1960), and Dayrat *et al.* (2014). We maintain this synonymy but note that it requires corroboration through examination of topotypic material, which is currently unavailable. The types of *S. cochleariformis* (NHMUK 1981015, Figs13H–K) closely resemble the figures in the original description of Reeve (1856). These shells also match the original description and figures of *P. japonica* in Donovan (1824). Moreover, Reeve (1856) appeared to be unaware of the description of *S. japonica*. Hedley (1915: 752) correctly stated that the record of *S. cochleariformis* from NSW (Angas, 1867: 232) is by mistake.

The type locality of *S. alterniplicata* can be inferred from the title of the work to be 'Peitaiho' [China, Beidaihe District, 39°50′N, 119°29′E] (Grabau & King, 1928: 62)'. The syntype of *S. alterniplicata* figured in Coan *et al.* (2015: 221, fig. 38). The proposed synonymy of *S. alterniplicata* (Fig. 13F) remains to be tested by examination of topotypes.

Siphonaria (*Kerguelenella*) *corallina* was described by Christiaens (1980a: 80) based on five specimens collected from corals and barnacles at 10m depth off Channel Rock, Hong Kong, with the largest specimen lodged as holotype in NHMUK (Fig. 13G). Christiaens figured the shell and half radula row for the holotype (Christiaens, 1980a: 80, fig. 18A, C) indicating the radula dentition formula of 19.1.19. No other material is recorded. Unfortunately, no animals are available to confirm anatomical (mainly radula) or assess molecular characteristics. However, examination of the holotype indicates the specimen is a juvenile. It is brownish transparent and has wide and glassy growth lines on the shell consistent with early growth stages in siphonariids. The holotype can be aligned well with the early growth stages of adult specimens of *S. japonica* (Fig. 13N), revealing that shell profile, apex, prominent ribs, and formation of dual siphonal ridge ribs match. By contrast, the holotype cannot be aligned with early growth stages in shells of other co-occurring species, such as *S. alba* (Fig. 13M), *S. subatra* (Fig. 13O) and *S. rucuana* (Fig. 13P). While molecular sequences are required for validation, we postulate that the holotype of *S. corallina* is a juvenile of *S. japonica*. Regarding collected depth, it is not uncommon for *Siphonaria* to occur subtidally (e.g., *S. lateralis* has been recorded from 'bottom of a 6 m deep tide pool' at the Snares Islands (AM C.586004; coll. D. Horning) and at '3 to 4.5m' at Aerial Cove, MI, Australia (coll. J. Lowry). However, most specimens have been recorded intertidally.

External morphology (Fig. 13Q). Foot sole, foot wall, mantle, cephalic folds and pneumostomal lobe all evenly orange in colour; mantle thin, narrower than foot wall, edge thickened lobed with black bands aligning with rib interstices; dark irregular black blotches of pigmentation on foot wall and cephalic lobes, fading to join with mantle, concentrated over centre of cephalic folds; pneumostome long between right adductor muscles and within mantle.

Shell (Figs 13A–L; Table S9). Medium sized (max sl mean = 19.4 mm, SD = 1.7 mm, n = 9), circular ovate, height medium, shell thin; apex offset strongly posterior and weakly left, apical sides strongly convex, protoconch direction homostrophic (n = 1), shell whorl dextral; growth striae prominent uneven, radial colour banding faint, exterior pale brown; rib count (mean = 46, SD = 6, n = 5), wavy and bent, pale red brown/grey, ridges narrow, rounded, golden tan, variably raised, uneven, slightly broaden to align with unscalloped shell edge; ~ 20 primary ribs, 2–3 finer secondary ribs between primary ribs, interstices narrow with regular red brown and irregular dark grey/white markings; paired primary ribs form siphonal ridge, protrudes slightly beyond shell edge. Interior: shell lip with white rays aligning under primary/secondary ribs, fade over pale tan shell margin; ADM scar and spatula evenly dark brown, siphonal groove distinct; ADM not prominent, CMS straight; thickening/whitening of shell lip not apparent.

The neotype (Fig. 13A). Shell (sl = 20.5, sw = 16.8, sh = 7.5 mm) elongate ovate, medium; thin, apex offset weakly to posterior and left, exterior uneven, mottled brown with radial banding, interstices with dark grey and reddish flecks, ~ 42 ribs, siphonal ridge clear, formed by adjacent dual ribs. Interior shell lip dark brown strongly corrugated with pale rays aligning under ribs, margin whitish tan, RS (Fig. 15D) and SPM (Fig. 15E).

Reproductive system (Figs 15B, D; n = 4). Positioned to the right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts positioned between RAM and BM; GA small, with singular GP through foot wall; AO small, elongated, narrow, centrally bent, bluntly pointed, joined to lower ED and upper GA; ED long, wide, centrally coiled / folded, joins to outer side of GA; GA, AO, ED all white muscular fibrous tissue; EG large elongated, slightly shorter than ED, soft whitish tissue, slightly folded, joins ED; single, long, narrow, coiled flagellum (F1), appears as an extension of wider ED, lays over back of BM; BD and CD junctions into GA close between ED join and GP but in opposing directions, both ducts narrow, long, smooth, whitish, featureless, pass closely together through RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex medium; CD connecting to AG/MG ducts, BD with folded distal loop and MA, BC very large, embedded in top of MG against AG, elongated spherical, thin whitish translucent test; HD short, large, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; AG smaller than HG, sides match curvature of inner foot wall.

Spermatophore (Figs 15C, E). Cylindrical, thread-like (length = 13.9 ± 1.5 mm, n = 3), test thin, translucent; head tip tapered bluntly rounded, section containing a white gelatinous core, tapers to a thin flagellum and tip; both sections smooth, 8–12 short barbs on upper flagellum pointing towards head (n = 3); head section smooth, longer thicker than flagellum (head length = 8.3 ± 0.2 mm, n = 3; 60% of SPM length, SD = 6%; flagellum length = 5 ± 1.5; head section width = 195 ± 12 µm; flagellum width = 33 ± 12 µm), 10 SPM tightly coiled in white gelatinous

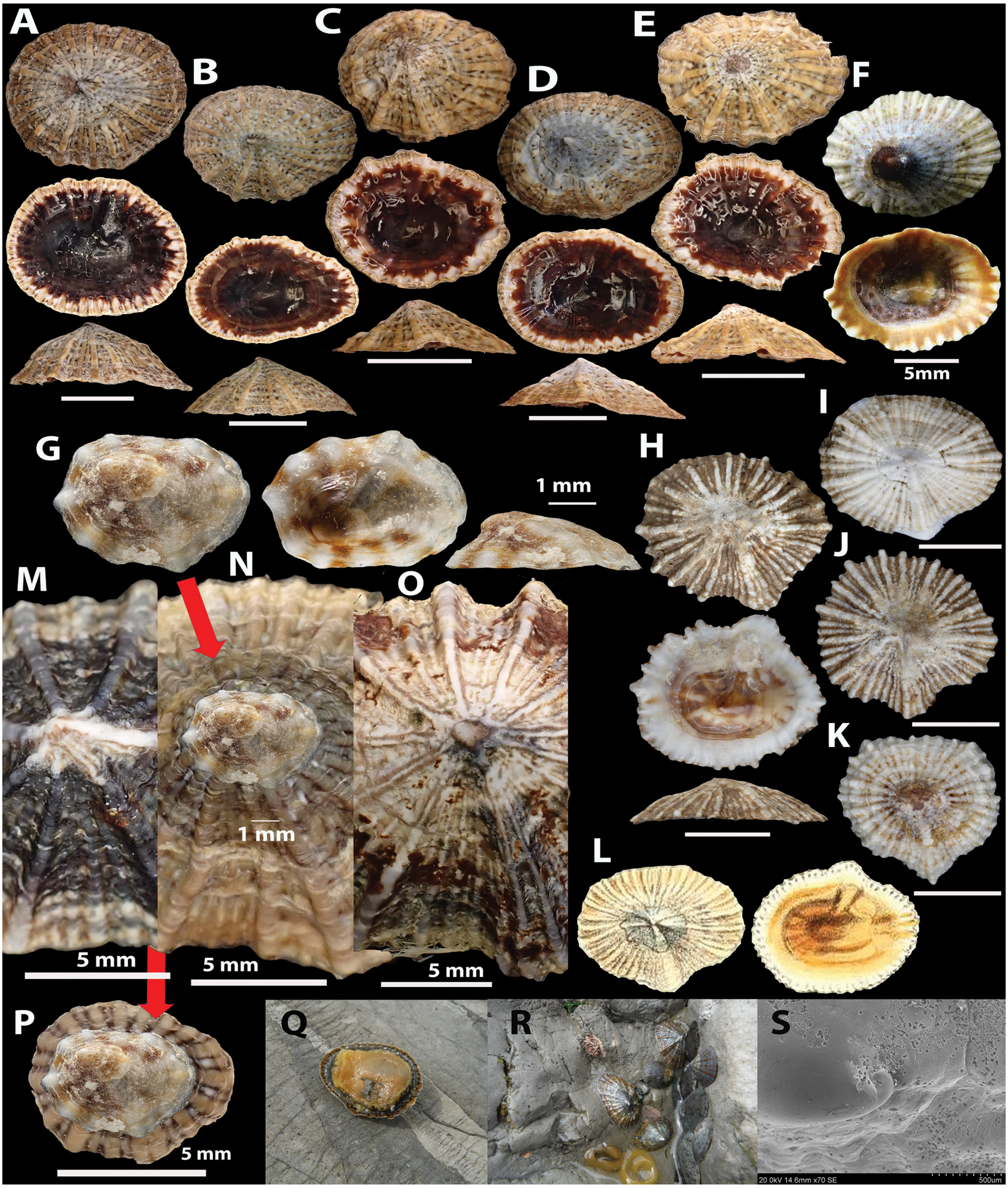

FIGURE 13. Shells of *S. japonica* . **A.** Neotype of *Patella japonica*, Boso Peninsula, AM C.584938 [M489, SK308]. **B.** AM C.595953 [SK566]. **C.** AM C.585389 [SK340]. **D.** AM C.584939 [SK338]. **E.** AM C. 585935 [SK425]. **F.** Syntype of *S. alterniplicata* MBM 280642. **G.** Holotype of *S. corallina* NHMUK 1977170. **H–K.** Syntypes of *S. cochleariformis* NHMUK 1981015. **L.** Reeve's original figure for species 28. **M–P.** Comparisons of apical sculptures. **M.** Shell apex of *S. alba* shown for comparative reasons [M523]. **N.** Apex of *S. corallina* superimposed on *S. japonica*, Hong Kong, ZRC MOL 24904 [M404]. **O.** Shell apex of *S. subatra* AM C.584930 [SK349]. **P.** Apex of *S. corallina* superimposed on *S. rucuana*, Hong Kong ZRC 1999-20333 [M523]. **Q.** Animal of *S. japonica*. **R.** *In situ* **S.** Protoconch, AM C.585983 [SK339]. Unlabelled scale bars = 10 mm.

mass in BC of one specimen (ZRC.MOL.24905 [M476, SK283]).

Radula and jaw. Dentition formula "varies at any rate between 32:1:32 and 40:1:40" (Hubendick 1946: 43).

Comparative remarks. *Siphonaria japonica* (*normalis* group, unit 2) forms a distinct mitochondrial clade together with its sister species, *S. camura* **sp. nov.** (Figs 1, 4). The minimum distance between *S. japonica* and *S. camura* n. sp. is 11.1% in COI (Table S8).

Throughout the range of *S. japonica* we found four congeners occurring in partial sympatry. Three are sympatric with *S. japonica* on Honshu: *Siphonaria acmaeoides* has a more solid, whitish, smoother shell with a more central apex, a smaller AO and BC, and a shorter F1 and short drop-like SPM. *Siphonaria sirius* has more prominent and raised ribbing with stronger edge scalloping, a larger AO, and SPM without barbs. For comparison with *S. sipho* refer to that species. *Siphonaria camura* **sp. nov.** has a smaller, paler shell with less raised ribbing, strongly offset and hooked apex with weaker edge scalloping, smaller AO and F1, and a larger BC.

Shell, RS, and SPM of '*S. cochleariformis'* depicted by Hubendick (1945: 26, fig. 34–36, 28, fig. 43; 1946: 14, fig. 20) from Japan, subsequently reproduced by Berry (1977: 210, fig. 19), correspond well with *S. japonica* (both taxa are synonyms). However, we found that type specimens of *S. cochleariformis* (Fig. 13H–K) differ from typical *S. japonica* in being more solid, whitish, unpatterned, and having a thickened margin and raised ribs. However, no topotypic material of *S. cochleariformis* is available to study and we cannot address its taxonomic status. Figures of the SPM of '*S. kurracheensis*' in Hubendick (1945: 31, fig. 51) are attributed to *S. japonica*; the number of barbs corresponds well with features typical of this species whereas flagellum barbs are absent in *S. kurracheensis*. Figured specimens of *S. japonica* in Yoo (1976: pl. 19, figs 1, 4) from Korea are misidentifications; fig. 2 and possibly fig. 3 are correctly identified. A record of '*S. japonica*' from Hainan Island (Hasegawa *et al.* 2001: 29) is plausible but requires confirmation by dissection and/or DNA sequencing.

Distribution and habitat. Recorded from Hong Kong, Honshu, Taiwan (Fig. 11). In this study, commonly found on exposed rocky shores at various locations on Honshu, in crevices and hollows across the upper littoral level.

Siphonaria obliquata Sowerby I, 1825
(Figs 14A–D, N, Q–R, 15F–H)

Siphonaria obliquata Sowerby I 1825: 32 ("Van Diemen's Land" [Tasmania; in error]).—Reeve 1842: pl. 138, figs 4–5; Catlow & Reeve 1845: 100; Jay 1850: 104; Reeve 1856: species 12; Hanley 1858b: 152; Hutton 1873: 56; Paetel 1873: 117; 1875: 92; Hutton 1878a: 41; 1880: 36; 1883 : 141, pl. 17, figs A–D; Paetel 1883: 178; 1889: 429; Suter 1904: 68; Iredale 1908: 408; Suter 1909a: 33; Moss 1908: 41, pl. 9, fig. 24; Cottrell 1911: 582; 1912: 374; Suter 1913: 599; Iredale 1915: 478; Oliver 1923: 498; Odhner 1924: 55; Bucknill 1924: 83, fig. 3, 15–15a; Finlay 1927: 442, 478; Hubendick 1943: 4; Galindo 1977: 416; Powell 1979: 293, pl. 54, figs 12–13; Jenkins 1983: 28; Raven & Bracegirdle 2010: 46; White & Dayrat 2012: 66.

Siphonaria scutellum Deshayes, 1841: 1, pl. 35.—Catlow & Reeve 1845: 100; Jay 1850: 104; Dall 1870: 39 (non Blainville); Hutton 1873: 55; 1880: 36; 1883: 114; Stearns 1894: 405, 430; Suter 1909a: 33; Hubendick 1946: 24; Galindo 1977: 416; White & Dayrat 2012: 68.

Kerguelenia obliquata—Mestayer 1920: 117, figs 1, 2.

Benhamina obliquata—Finlay 1927: 442, 478. Powell 1937: 86, 1939: 217; Hubendick 1945: 60, 66, figs 11, 14; Powell 1946: 91, pl. 13 fig. 16; Borland 1950: 385; Knox 1954: 874, 1955: 86; Powell 1955: 120; 1957a: 114, pl. 20, fig. 16; Marcus & Marcus 1960: 108; Morton & Miller 1968: 302, fig. 109; pl. 19, fig. 10, 10a; Powell 1979: 293, pl. 54, figs 12, 13; Trew 1983: 3; Russell & Phillips 2009: 579.

Siphonaria (*Benhamina*) *obliquata*—Thiele 1931: 472; Hubendick 1946: 24, pl.6, fig.1–3; Shikama 1964: pl. 2, fig. 10; Berry 1977: 204, 210, fig. 19.

Siphonaria scutella—Burch 1945: 16 (invalid; incorrect subsequent spelling of *scutellum*).

Siphonaria obiliquata Murty *et al.* 2013: 104 (invalid; incorrect subsequent spelling *obliquata*).

Material examined. *Type material.* Neotype of *Siphonaria obliquata* Sowerby I, 1825, present designation, from near quarry, NZ, Dunedin, W side Blackhead, 41°30.34′S, 171°56.76′E; coll. K. Walton, 6 Dec. 2020 (NMNZ M.331450 [M515, SK421], Fig. 14A).

Five syntypes of *S. scutellum* Deshayes, 1841 from Chatham Islands (MNHN IM-2000-5117, Fig. 14C).

Other, non-type material. **NZ, South Island:** same data as neotype (NMNZ M.331114 p); Gentle Annie Point, N of Mokihinui River Mouth, West Coast 45°55.78′S, 170°25.72′E KW20-103 (NMNZ M.331115 6p, p [M516, SK422]; Fig. 14B); between Buttler and Gray Rivers, W Coast, 41°43.8'S, 171°29.31'E, NZS01 (AM C.585927 p [SK394], C.585928 p [SK401]). Point Elizabeth, 42°24'S, 171°13'E (AM C265378) (Fig. 14D).

Taxonomic remarks. *Siphonaria obliquata* is the type species of *Benhamina* Finlay, 1926 by original designation. The original type material is considered lost as it could not be found at the NHMUK in 2020 (J. Ablett, pers. comm.). The neotype is designated herein to ensure an unambiguous identification of this species, to stabilize its nomenclature, and to designate a correct type locality (Art. 75.3 and 76.1 of the Code). Sowerby (1825: Appendix 7), originally stated the origin of this species to be "Van Diemen's Land [Tasmania]". However, this probably incorrect since *Siphonaria obliquata* has never been found in Tasmania or elsewhere in Australia. The type locality is corrected to South Island, NZ (see above for details). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes of *S. obliquata* and of *S. sculellum* and geographic series of additional specimens (Tables S1–2).

Reeve (1856) correctly stated that *S. obliquata* occurs in NZ and that *S. scutellum* is its junior synonym. Stearns (1894: 405, 430) reversed the priority of both species when treating them as synonyms referencing "Carpenter's Reeve-Cuming List' (Stearns (1894: 405). He also incorrectly states the distribution to be Galapagos. This was subsequently followed by Dall (1870: 39), who incorrectly added occurrence on the "W coast [of S America] N of Panama". Hubendick (1946: 24) correctly treated *S. scutellum* as a synonym of *S. obliquata,* but incorrectly listed it as a synonym of *S. australis* (Hubendick 1946: 49). Burch (1945: 16) listed '*S. scutella* Deshayes' as a valid species from Galapagos, which is rejected herein.

External morphology (Fig. 14N). Animal extends beyond shell coverage; foot sole swollen smooth, foot wall, mantle, cephalic folds and pneumostomal lobe evenly pale grey/cream, paler at edge foot/wall; blotches of black pigmentation on centre of cephalic folds, faintly on foot wall; mantle narrower than width of foot wall, non-translucent, covers exposed inner shell lip, edge thickened, lobed, vertical bands of black pigmentation aligned with shell rib interstices; single genital pore distinct, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two centrally touching cephalic folds; pneumostomal lobe long under the mantle between the right ADMs.

Shell (Fig. 14A–D, R; Table S9). Large sized (max sl mean = 48.1 mm, SD = 8.9 mm, n = 24), elongate ovate; height low to medium, often with lateral profile of shell edge arched profile; apex offset weakly posterior and central (usually eroded), apical sides anteriorly strongly convex, posteriorly straight to concave; protoconch direction heterostrophic (n=2; Fig. 14R), shell whorl dextral; exterior uneven, growth striae prominent, concentric brown tonal bands prominent, shell thick (often > 2mm); apical rib count (mean = 57, SD = 10.2, n = 24), ribs pale white, ridges rounded, interstices darker brown; 20–25 primary ribs, adapical, slightly more prominent than interspersed finer secondary ribs, often bifurcate, curved, increasingly raised and broaden to shell lip, shell edge weakly corrugated; siphonal ridge often indistinct, formed by paired primary ribs, wide at shell edge. Interior smooth, shell lip brown to black with white rays corresponding under ribs, margin white to tan, ADM scar paler, siphonal groove apparent, shallow, same colour as shell edge; spatula tan to fawn, often with irregular brown to grey markings; ADM scar distinct, CMS straight to convex, paler than shell lip; thickening of shell lip translucent, infills and reduces lip scalloping, spatula becomes whitened. Shell lip tends to thicken in adult specimens.

The neotype (Fig. 14A). Shell (sl = 35.5, sw = 22.6, sh = 11.2 mm) elongate ovate, medium; thick, apex offset weakly to posterior and left, exterior uneven, mottled brown with radial banding, ~ 45 ribs, siphonal ridge not prominent, formed by non-adjacent dual ribs. Interior shell lip dark brown weakly corrugated with pale rays aligning under ribs, margin whitish tan, RS (Fig. 15F) and SPM (Fig. 15G). Neotype specimen [M515] grouped within unit **96** (*S. obliquata*).

Reproductive system (Figs 15F–H; n = 3). RS positioned within right side of coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned between sides of BM and RAM; AO, GA and ED merged, very large rounded, tapered to ED; ED wide, short, bent at join to distinct EG, large rounded fold, with orange striated prostate, curved continuation at top of ED, flagellum (F1) indistinct, twisted; epiphallic parts all muscular tissue; CD and BD both wide, short, featureless, jointly connect into AO on under side, BD over CD (in RS of neotype, BD appears absent but is enclosed within side tissue of CD (Fig. 15F), pass between outer side of RAM and inner foot wall; BD significantly wider, slightly curved; CD twisted immediately prior to entering MG/AG complex close to BD; BC large rounded, positioned between footwall and AG, test thick, opaque, filled with orange-brown gelatinous mass; curved elongated SV embedded in AG close to top of BC; single large GP with lobes at end of GA; HD prominent, brownish, folded and heavily lobed, links AG to yellow-tan, finely granulated HG; MG and larger AG small folded soft white tissue, MG at anterior of AG, sides moulded to curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 15G). Short elongate, test thin, featureless, translucent (length = 4.38 mm, n = 1), head bluntly pointed; flagellum short; both sections smooth, featureless, short clear webbing spans the bend at taper between head and flagellum; head much larger than flagellum (head length = 3.0 mm, n = 1, ~ 76 % length of SPM; head width = 790 µm; flagellum width = 96 µm); three SPM found in neotype BC ([M515]), 2 appear to be the white core remnants of larger SPM's decomposing; while the shape / size is consistent, no test or flagellum present.

Radula and jaw. Dentition formula 68:1:68 (258 rows) and description of jaw in Hutton (1883: 141, as '*scutellum*'); see Cottrel (1911: 586, fig. 6) for a description, dentition formula "about 64:1:64" (Hubendick 1946: 25).

Comparative remarks. *Siphonaria obliquata* (*lateralis* group, unit 96) represents the sister group of a clade formed by three species, *S. tasmanica*, *S. lessonii*, and *S. funiculata* (Figs 1, 4). From these species it differs by 16S distances of ≥ 7.6% (*S. funiculata*), ≥ 7.9% (*S. lessonii*), and ≥ 8.9% (*S. tasmanica*) (no COI sequences available).

Within the distributional range of *S. obliquata*, we found three sympatric congeners: *Siphonaria australis* and *S. propria* are sympatric on the South Island of NZ, and have smaller, more circular ovate shells, with more scalloped shell edges, prominent raised ribbing, wider HDs, smaller ephiphallic parts and BCs, and threadlike SPM. *Siphonaria lateralis* is sympatric on Auckland Island, NZ, and differs by having a much smaller, evenly brown, and fragile shell, a smaller BC, a larger, wider BD, and more bulbous SPM. Anatomically, the structure of RS resembles that of *S. lateralis* and *S. tasmanica*, *S. funiculata*, *S. lessonii* (Güller *et al.* 2015: 85, fig. 4) and

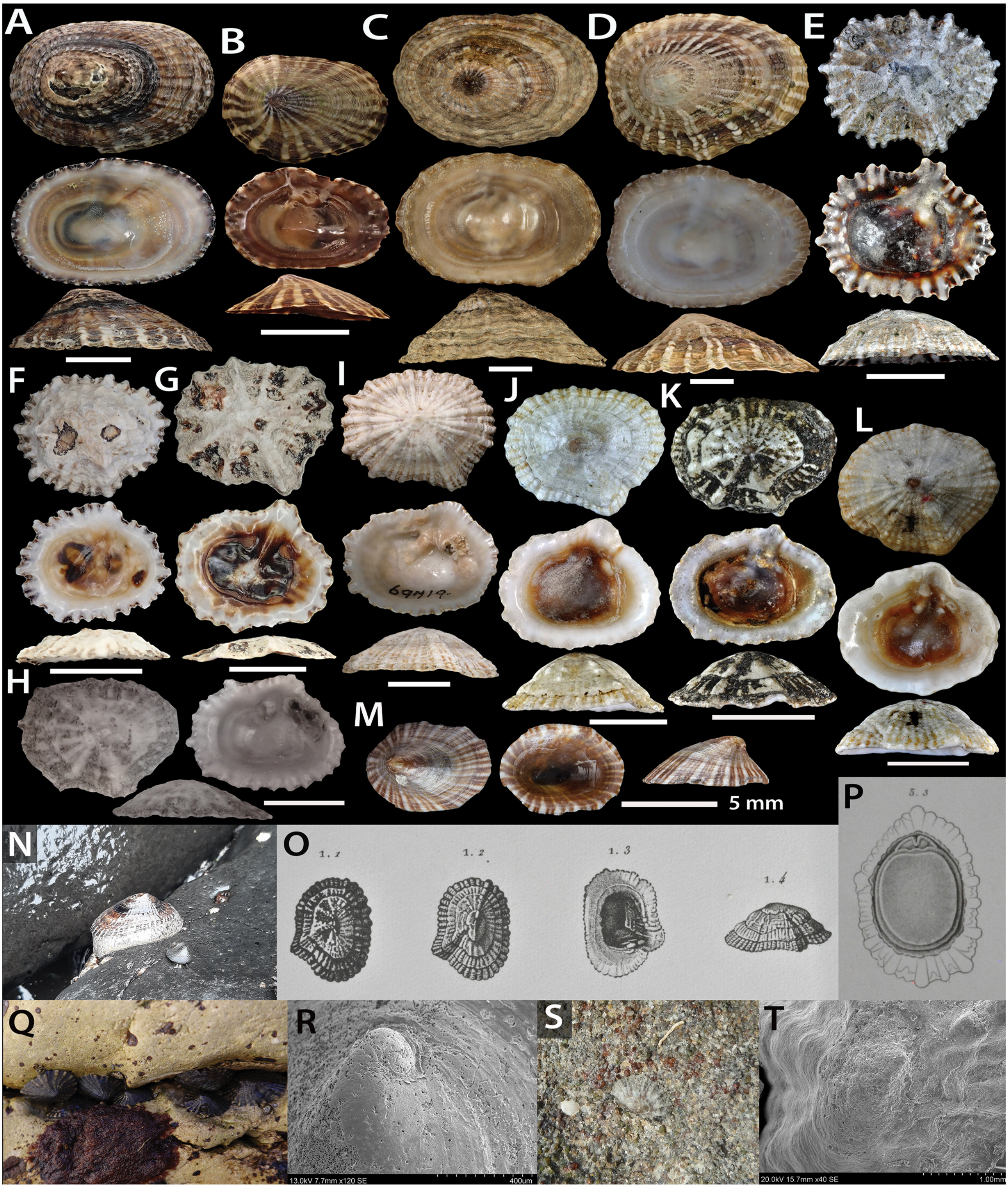

FIGURE 14. Shells of *S. obliquata*, *S. crenata*, and *S. basseinensis*. **A–D, N, Q–R.** *S. obliquata*, **A.** Neotype of *S. obliquata* NMNZ M.331450 [M515]. **B.** South Island, TS, NMNZ M.331115 [M516]. **C.** Largest syntype of *S. scutellum* MNHN IM-2000-5117. **D.** Port Elisabeth, AM C.265378. **N, Q.** Animal and *in situ* NMNZ M.331115. **R.** South Island, TS, NMNZ M.331115 [M516]. **E–I, P, S–T.** *S. crenata*. **E.** Probable holotype MNHN IM 2000-35937. **F.** Pakistan, Karachi, AM C.585338 [SK153]. **G.** Karachi, AM C.585851 [M242]. **H.** Holotype of *S. rosea* UUZM 1577. **I.** Saudi Arabia, Persian Gulf, AM C.69719. **P.** Original figure in Savigny (1817: pl. 3, fig. 3.5). **S.** *In situ*; **T.** Protoconch AM C.585853 [SK302]. **J–L, O.** *S. savignyi*, **J.** Lectotype of *S. savignyi* IM 2000-35936. **K.** Paralectotype MNHN IM 2000-35935. **L.** Paralectotype MNHN IM 2000-35934. **O.** Original figures in Savigny (1817: pl. 1, fig. 1.1–1.4). **M.** Syntype of *S. basseinensis* NHMUK 1893.2.16.29. Unlabelled scale bars = 10mm.

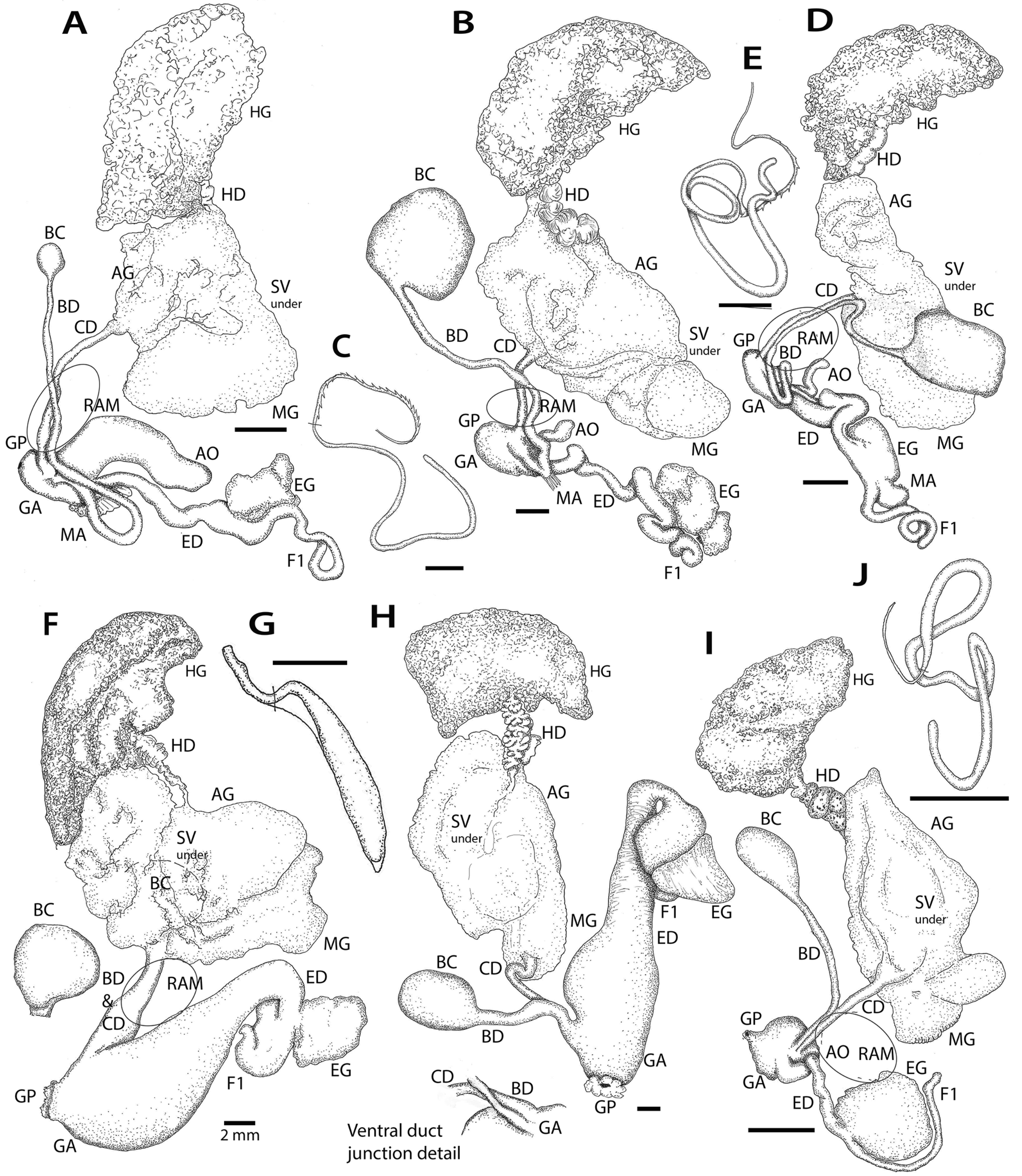

FIGURE 15. Reproductive anatomy of *S. javanica*, *S. obliquata*, and *S. australis*. **A.** *S. javanica.* Timor-Leste, Dili, AM C.584795 [M434]. **B–E.** *S. japonica*. **B–C.** Hong Kong, ZRC.MOL.24905 [M476, SK283]. **D–E.** Honshu, Boso Peninsula, Neotype AM C.584938 [M489, SK308]. **F–H.** *S. obliquata*. **F–G.** NZ, Dunedin, Neotype NMNZ M.331450 [M515, SK421]. **H.** South Island, West Coast, TS, NMNZ M.331115 [M516, SK422]. **I–J.** *S. australis* **I–J.** NZ, Stewart Is, AM C.585247 [M480, SK284]. Unlabelled scale bars 1 mm.

S. fuegiensis (Güller *et al.* 2015: 92, fig. 9), all of which are relatively closely related.

Hutton (1883: 141, pl. 17, figs B–D) and Cottrel (1911: 587–590, figs 2–4, 6–7, pl. 29, fig. 3) described the anatomy of *S. obliquata*; radula and jaw, RS. The RS depicted herein corresponds well with the RS depicted in Hutton (1883: 141), Cottrell (1911: 590), and Hubendick (1945: 18, fig. 14), but also reveals some intraspecific variation (e.g., details of epiphallic parts, of HD and CD in Cottrel and width of CD = "spov" in latter). The SPM shown herein (Fig. 15G) corresponds well with that shown by Hubendick (1945: 14, fig. 11), reproduced by Berry (1977: 210, fig. 19). The egg mass has been described by Mestayer (1920: 171). Borland (1950: 385) described the distribution, behaviour and ecology of *S. obliquata*.

Distribution and habitat. Recorded from North and South Islands as well as Chatham, Stewart and Snares Islands, NZ, between latitudes of 34° S and 48° S (Fig. 16). In this study found to be common on exposed rocky intertidal shores in sheltered positions, such as crevices, vertical faces, mostly shaded from the midday and afternoon sun, across upper and mid littoral levels.

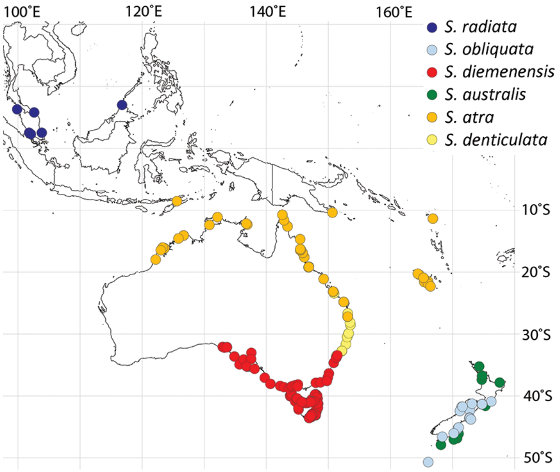

FIGURE 16. Known occurrence records of *S. obliquata*, *S. radiata*, *S. diemenensis*, *S. australis*, *S. atra* and *S. denticulata*

Siphonaria radiata (Blainville, 1826)

(Figs 17A–B, U–V, 18A–B)

Pileopsis radiata Blainville 1826: 462 (type locality unknown).

Siphonaria radiata—Blainville 1827a: pl. 2, figs 4, 4a (as 'radiée'); 1827b: 294 (type locality unknown); Lamarck 1836: 556, 1839: 205; Jay 1839: 39; Catlow & Reeve 1845: 100; Hanley 1858b: 152; H. Adams & A. Adams 1855 (in 1853–58): 271; 1863: 271; Paetel 1889: 429; Morrison 1972: 52; Galindo 1977: 416; Jenkins 1982: 12, White & Dayrat 2012: 67.

Siphonaria '*normalis* group, unit 12', Dayrat *et al.* 2014: 260, fig. 3N.

Material examined. *Type material.* Neotype of *Pileopsis radiata*, present designation, Malaysia, Port Dickson, 02°31.234'N, 101°48.026'E; coll. B.W. Jenkins, 15 Feb 2015, PD01-1 (AM C.585861, Fig. 17A).

Other, non-type material. **Malaysia:** Bak Bak Beach, Kudat, Sabah, 07°00′ N, 116°46′ E (AM C.585236 20p, C.595941 d [SK523]); Bukit Keluang, Terengganu, 5°47.81'N, 102°36.43'E (ZRC 1999-1978 12p; ZRC.MOL.24900 p [M528, SK444], ZRC.MOL.24901 p [M596, SK528]); Port Dickson, 02°31.234'N, 101°48.026'E PD01-1 (AM C.585959 3p, C.585821 7d, C.585921 p [SK337 protoconch H2]); Air Papan, Mersing, Johor, 2°30.98′ N 103°50.1'E (ZRC 1999-1755 20p, ZRC.MOL.24895 p [M527]; ZRC.MOL.24896 p [M526]); Tg. Bidara, Malacca, 02°17.568'N, 102°5.207'E (ZRC 1999-1746 9p; ZRC.MOL.24891 p [SK348], Fig. 17B; ZRC.MOL.24892 p [M525], ZRC.MOL.24893 p [M595], ZRC.MOL.24894 p [M594]); Pulau Langkawi, 6°18′ N, 99°52′ E (AM C.595974 20+p, C.585098 p [SK525], C.585697 p [SK524]).

Taxonomic remarks. Blainville (1826: 462) introduced the new name *Pileopsis radiata*, and subsequently transferred it to *Siphonaria* in Blainville (1827a: pl. 2, figs 4,4a; 1827b: 294). The original type material is considered lost; no types were found in the MNHN (Philippe Bouchet, pers. comm.). The neotype is designated herein in accordance with Art. 75.3 of the Code to clarify the identity of this nominal taxon as well as to restrict its type locality. Blainville's name is not invalidated by *S. radiata* Gray, 1824, which is not an available name (for details see under *S. sipho*). *Siphonaria radiata* (Blainville, 1826) is a senior secondary homonym of *S. radiata* Sowerby I, 1835 (not reviewed herein) and *S. radiata* A. Adams & Reeve, 1850, which has been replaced by *S. radians* H. Adams & A. Adams, 1855. Hubendick (1946: 49) incorrectly considered *S. radiata* (Blainville, 1827) a synonym of *S. australis*.

External morphology. Foot sole grey, paler to foot edge; foot wall bluish to inner, evenly dark cream, with irregular black pigmented blotches, paler to foot, pustules prominent; cephalic folds thick, narrow, irregular black pigmentation darker over centre of cephalic folds; mantle wide thin translucent edge lobed thickened band; eye spots prominent, pneumostome small, under mantle.

Shell (Figs 17A–B, V; Table S9). Small sized (max sl mean = 13.29 mm, SD = 1.55 mm, n = 42), circular ovate, height medium to tall; apex slightly curved, apex offset slightly to posterior and left, apical sides convex, posterior strongly concave, protoconch direction weakly heterostrophic to central (n = 1; Fig. 17V), shell whorl dextral, shell thick; growth striae prominent, even, unraised; radial colour bands indistinct; rib count (mean = 30, SD = 3.1, n = 42), primary ribs distinct from secondary ribs; ~ 16 pale brown to off white primary ribs, ridges raised, rounded; siphonal ridge formed by paired adjacent primary ribs, most primary ribs broaden weakly, project beyond shell lip (especially siphonal ridge) with ends slightly raised to scallop and corrugate shell edge; 0–2 finer secondary ribs between primary ribs, rib interstices darker. Interior shell margin and spatula dark brown to golden tan, often some calcification; off white to cream rays on shell margin align under primary/secondary ribs, extend to spatula; siphonal groove distinct, paler than margin; ADM scar indistinct, similar to margin and

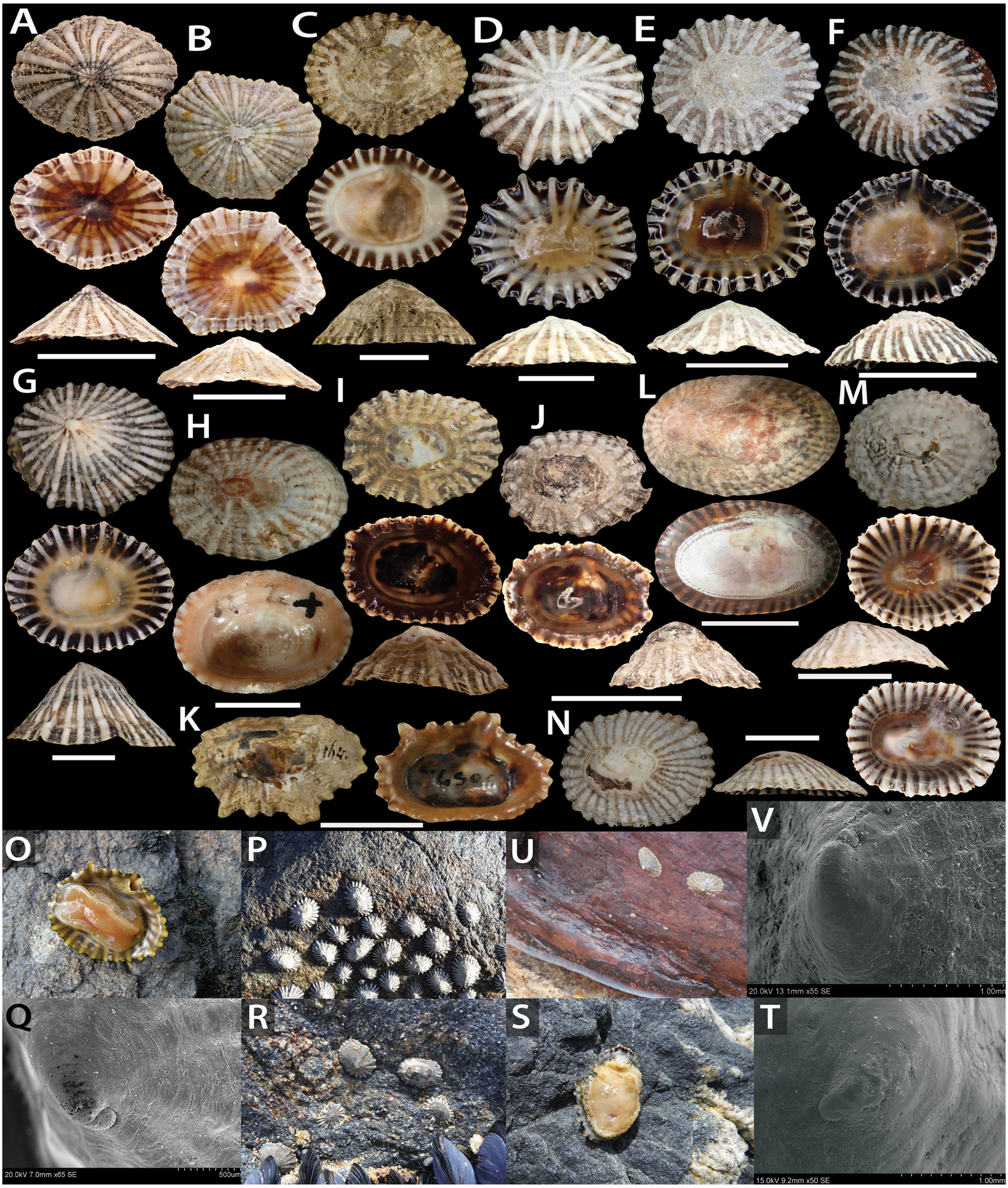

FIGURE 17. Shells of *S. radiata*, *S. diemenensis*, *S. australis* and *S. capensis*. **A–B, U–V.** *S. radiata*. **A.** Malaysia, Port Dickson, neotype AM C.585861 [M408]. **B.** Malacca, ZRC.MOL.24891 [SK348]. **U.** Port Dickson, *in situ.* **V.** Protoconch, AM C.585921 [SK337]. **C–G, O–Q.** *S. diemenensis*. **C.** Lectotype MNHN-IM-2000-35952. **D.** Tas, TS, AM C.584797 [SK047]. **E.** Tas, AM C.585270 [M107]. **F.** Vic, AM C.585286 [M168]. **G.** Tas, AM C.585260 [M170]. **O.** Animal. **P.** Tas, TS, *in situ*. **Q.** Protoconch, Vic, AM C.585357 [SK029]. **H–J, R–T.** *S. australis*. **H.** Lectotype MNHN-IM-2000-5036. **I.** NZ, Stewart Is, AM C.585249 [M481, SK288]. **J.** Stewart Is, AM C.585247 [M480, SK289]. **K.** Holotype of *S. inculta* USNM 5857. **R–S.** *In situ* and animal. **T.** Protoconch, AM C.265856 [SK511]. **L–N.** *S. capensis*. **L.** Lectotype MNHN IM 2000-38235. **M.** South Africa, MNHN-IM-2019-1481 [M585]. **N.** IM-2019-1477 [M584]. Unlabelled scale bars = 10 mm.

spatula; CMS straight; whitening and thickening of shell lip observed.

The neotype (Fig. 17A). Shell (sl = 15.1, sw = 10.8, sh = 5.5 mm) circular ovate; thick, apex offset weakly offset to posterior and left, apical sides straight, 32 ribs, ~17 whitish primary ribs, with 0–2 in between secondary ribs, rib interstices dark, siphonal ridge formed by adjacent dual primary ribs. Interior evenly dark brown, white rays on shell lip under ribs.

Reproductive system (Fig. 18A; n = 4). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts between RAM and extending over BM; ED distinct entry to top of small GA, AO small, short, bent, tip blunt, bulbous, appears part of GA under ED; ED thick, short, centrally bent; AO, GA and ED all muscular white tissue; EG very large, elongated, 2 lobes, folded, soft white tissue; single thick elongated blunt flagellum F1 appears as extension of ED at EG join; BD and CD connect closely together into GA, both ducts smooth, short, broad, slightly bent, pass together through outer edge of RAM (BD over CD) connecting into MG; BC medium to large, bulbous, white opaque test, embedded along with part of BD in soft white folds of MG; HD short, broad, coiled, links soft white folded AG to small yellowish granulated HG; AG larger than HG, both with outer sides curved reflecting the close positioning to curvature of inner foot wall at right posterior quarter of coelom; SV embedded in AG close to BC.

Spermatophore (Fig. 18B). Broad head with short flagellum (length = 4.6 ± 0.57 mm, n = 2); head section cylindrical, bulbous, centrally bent, tip rounded; test thin, smooth, featureless, translucent encasing a white opaque central core; short looped tapering section merges head to filamentous flagellum; head slightly shorter, wider than translucent flagellum (head length = 2.28 ± 0.67 mm, n = 3; flagellum length = 2.38 mm, n = 1; length/head length ~ 52%; head width = 172 ± 17 µm; flagellum width = 26 ± 0 µm, n = 3); 5 SPMs tightly coiled in cream gelatinous mass in BC of one specimen (Fig. 18B).

Comparative remarks. *Siphonaria radiata* (*normalis* group, unit 12) is the sister species of *S. planucosta* **sp. nov.** (Figs 1, 4C). Both species are separated from each other species by distances of at least 11.5% in COI (Table S8). The lowest interspecific genetic distances were observed between *S. radiata* and *S. madangensis* **sp. nov.** (unit 88) = 10.7%, *S. costellata* **sp. nov.** (unit 13) = 11%, and *S. normalis* (unit 14) = 11.4%) (Table S8).

We found a sympatric congener in Sabah: *Siphonaria kudatensis* (for comparison refer to *S. kudatensis*). *Siphonaria radians* has a lower, slightly larger shell with finer ribbing, a less prominent siphonal ridge, weaker edge scalloping, a larger AO, longer twisted ED, longer narrower BD with distal loop and a smaller BC. Shell geometry and sculpture of *S. radiata* resemble that of *S. costellata* **sp. nov.** (unit **13**) and *S. normalis* (unit **14**). However, *S. radiata* possesses slightly fewer and broader primary ribs, fewer secondary ribs, narrower interstices, more prominent siphonal ridge and more scalloped edge than these two species. The interior colouration also differs being generally paler browns to white with prominent red-brown rays extending to spatula in *S. radiata*. The SPM of *S. radiata* resembles that of *S. normalis* and *S. gemina* **sp. nov.** The record of '*S.* cf *kurracheensis'* in Way & Purchon (1981: 321) is a misidentification and likely of *S. radiata*. The specimen figured as '*normalis* group, unit 12' in Dayrat *et al.* (2014: 260, fig. 3N) corresponds well with the present species.

Distribution and habitat. Recorded from W coast of Thailand and Port Dickson, Malacca Strait, Malaysia (Fig. 16). In this study, found on exposed and bare rocky shores, mid littoral level (Fig. 17U).

Siphonaria crenata Blainville, 1827

(Figs 14E–I, P, S–T, 18C–E)

Siphonaria crenata Blainville 1827b: 295.—Hanley 1858b: 151; Paetel 1889: 428; Morrison 1972: 60 (unfigured and without descriptions).

Siphonaria rosea Hubendick 1943: 1, pl. 1, fig. 1 (type locality: Insel Kharg, Persischer Meerbusen [Kharg Island, Persian Gulf, Iran]).—Hubendick 1945: 72; Galindo 1977: 416; Smythe 1979: 69; Christiaens 1980a: 81; White & Dayrat 2012: 67.

Siphonaria (*Siphonaria*) *rosea*—Hubendick 1946: 53, pl. 4, figs 12–15.

Material examined. *Type material.* Probable holotype of *S. crenata* Blainville, 1827 (type locality unknown; Savigny collection) (MNHN IM 2000-35937, Fig. 14E).

Holotype of *Siphonaria rosea* Hubendick, 1943 from "Insel Kharg, Persischer Meerbusen" [Kharg Island, Persian Gulf, Iran]; coll. G. Thorson, 1937 (UUZM 1577, Fig. 14H).

Other, non-type material. **Saudi Arabia:** Persian Gulf, 28°N, 50°E (AM C.69719 d, Fig. 14I); **Pakistan:** Karachi, French Beach, 24°50.367'N, 66°49.387'E PA01-1 (AM C.585851 p [M242, SK233], Fig. 14G, C.585892 p [M239], C.595917 p [SK534]), PA01-2 (AM C.585853 p, C.585338 p [SK153], Fig. 14F; C.585853 p [SK302]).

Taxonomic remarks. Savigny (1817: pl. 1, figs 1–4; pl. 3, figs 1–5) published engravings without captions of two distinct siphonariids (Fig. 14O–P herein) (see Bouchet & Danrigal, 1982 for bibliographic details). The first reference to Savigny's figures appeared in Blainville (1825: 655): Under "et corrections" for the genus *Siphonaria,* he referenced Savigny's figure ("Ègypt. Gastéropod., pl.3, fig. 1–5") [= *S. crenata*] as 'figured the animal of a species of this genus' without assigning a name. Later, Blainville (1827b: 295) introduced the name *S. crenata* with reference to these figures stating "Savigny AEgypt. Zoolog.; Gastropodes, pl. 3, fig. 3–35." without mentioning Savigny's plate 1. Specimen 4 in the Savigny collection (MNHN IM 2000-35937, Fig. 14E) resembles the specimen figured by Savigny (1817: pl. 3, fig. 3.5; Fig. 14P herein) with respect to shell edge and prominence of ribbing rather than any other of the figured shells.

Bouchet & Danrigal (1982: 15) mentioned three syntypes of *S. savignyi* to be held by the MNHN (most likely MNHN IM 2000-35934, Fig. 14L; 2000-35935, Fig. 14K; 2000-35936, Fig. 15J). The last two shells closely match in Savigny's (1817) figures pl. 1, fig. 1 (Fig. 15K) and pl. 1 figs 2–4 (Fig. 14J) respectively. Our delineation of *S. crenata* is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected specimens of *S. crenata* (Fig. 14F) and *S. rosea* (Fig. 14G) and geographic series of additional specimens (Tables S1–2). Hubendick (1946: 50) listed among some 'transitional forms' in an 'Indian-West Pacific form-group', a '*S. zanda* <> *S. rosea*' form (Hubendick 1946: 50, pl. 5, figs 1, 2). This shell is probably a specimen of '*S. rosea'* (= *S. crenata*, Figs 14E–F). Hubendick (1946: 54) proposed *S. crenata* to be a possible synonym of *S. kurracheensis*. However, type specimens of *S. kurracheensis* differ from Hubendick's (1946: 54) interpretation of this taxon, and of the specimens from 'Persian Gulf/Suez' figured as '*S. kurracheensis*' by Hubendick (1946: pl. 2, figs 36–40; except fig. 38 from 'Java Sea'), are consistent with typical characteristics of *S. crenata* but not *S. kurracheensis*. A shell figured as '*Siphonaria savignyi*' from Woody Point, Moreton Bay, Qld, Australia by Hubendick (1955: 2 (MV F13951)) is a misidentification and attributed here to *S. opposita*. Morrison (1972: 61) stated that '*S. basseinensis'* mentioned by Tillier & Bavay (1905: 176) is a record of *S. crenata*; however, this statement is not supported herein following examination of the type specimens of *S. crenata* (Fig. 14E) and of *S. basseinensis* Melvill, 1893 (Fig. 14M). This nominal species is not assessed in the present study. Morrison (1972: 56–58) treated *Siphonaria rosea* and 29 other nominal species as synonyms of *Siphonaria laciniosa* based on similarity in shell shape and "a common reproductive development". These synonymies are not accepted herein following examinations of type specimens and comparative morpho-anatomy. Bouchet & Danrigal (1982: 15) incorrectly considered a shell figured by Reeve (1856: pl. 5, species 20) as *S. kurracheensis* to be identical with *S. savignyi*.

External morphology. Foot wall, pneumostome, cephalic folds and mantle evenly cream, foot edge paler, foot sole darker; faint black pigmentation over upper foot wall and mid centre of cephalic folds; mantle narrower than foot wall, thin translucent, white banded edge thickened strongly lobed, overlaid with black bands aligning to rib interstices; pneumostomal lobe thin and within mantle between the right ADMs, closes the pneumostomal and anal openings at the mantle edge; genital pore inconspicuous, located on foot wall posterior to right cephalic fold; two small black epithelial eye spots centralised on two thick centrally touching cephalic folds.

Shell (Fig. 14E–G, T; Table S9). Medium to large sized (max sl mean = 15.2 mm, SD = 1.1, n = 4), ovate; height medium to low; apex offset sightly posterior and central (usually eroded), apical sides strongly convex, protoconch direction weakly heterostrophic (n = 2; Fig. 14T), shell whorl dextral; growth striae prominent in bands, shell thickness thick; rib count (mean = 32.3, SD = 1.1, n = 4), primary ribs pale white, fairly straight, increasingly raised and protrude beyond shell lip to unevenly scallop and corrugate the edge; 1–2 interspersed pale white finer secondary ribs, rib interstices darker; paired primary ribs on siphonal ridge, no more prominent than other primary ribs. Interior shell margin dark brown to tan, white rays align on shell margin under primary/secondary ribs, siphonal groove distinct, same colour as shell edge, points to right anterior; spatula dark chocolate brown to mottled tan even whitish (Fig. 14F–G); ADM scar distinct, CMS straight, paler than shell lip; thickening of shell lip translucent, infills and reduces lip scalloping, spatula becomes whitened.

Reproductive system (Fig. 18C–E; n = 4). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts positioned between RAM and BM; GA small indistinct with singular GP through foot wall; AO large wide bluntly pointed, joined to upper GA; ED short wide thickened, bent, joins to GA; GA, AO, ED all white muscular fibrous tissue; EG large, soft whitish tissue, folded, joins ED; single short flagellum (F1) shorter narrower than ED, lays over EG, appears as an extension of ED. BD and CD connect closely in opposing directions to GA between AO and GP, both ducts narrow elongated bent smooth whitish, pass together through RAM (BD over CD) into soft white folded tissues of MG, BC partly embedded in folds, small flat bulbous, thin whitish translucent test (0 SPM in brownish gelatinous mass of BC); MG/AG complex relatively small; HD short narrow coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; AG/MG larger than HG, sides match curvature of inner foot wall.

Comparative remarks. *Siphonaria crenata* (*atra* group, unit 43) is member of Clade H in the *atra* group (Figs 1, 2) forming a subclade together with *S. belcheri* and *S. madagascariensis*. It is well-differentiated from other species by COI distances of ≥ 21.4% (Table S5). Within its range, we found four species in partial sympatry with *S. crenata* (e.g., in Karachi, Pakistan): *Siphonaria asghar* has a smaller, taller, paler shell with a less distinct siphonal ridge and weaker edge scalloping, smaller AO, shorter wider BD without distal loop, and a smaller BC. *Siphonaria belcheri* has a smaller, taller shell with less raised ribbing, weaker edge scalloping, darker reddish-brown interior, and slightly longer BD. *Siphonaria kurracheensis* has a smaller shell with less edge-protruding ribbing and weaker edge scalloping, and a smaller AO. *Siphonaria perexigua* **sp. nov.** has a smaller, taller shell with a less prominent siphonal ridge, less raised ribbing, weaker edge scalloping, a paler interior, smaller AO, longer ED, and a relatively larger BC.

Hubendick's (1943: 3, fig. 9) illustration of the RS of *S. rosea* from the Persian Gulf corresponds well with the RS of *S. crenata* shown herein (Figs 18C–E) in terms of having a long thin BD, short CD, large EG, short ED and F1, and a large, twisted AO. Moreover, figured shells of '*S. rosea*' in Hubendick (1943: 1, fig. 1a–b, 1946: 91, pl. 4, fig. 12–15 from the same locality are consistent with typical features of *S. crenata* as herein delimited. Shells of '*S. savignyi'* figured in Hubendick (1946: 92, pl. 4, fig.

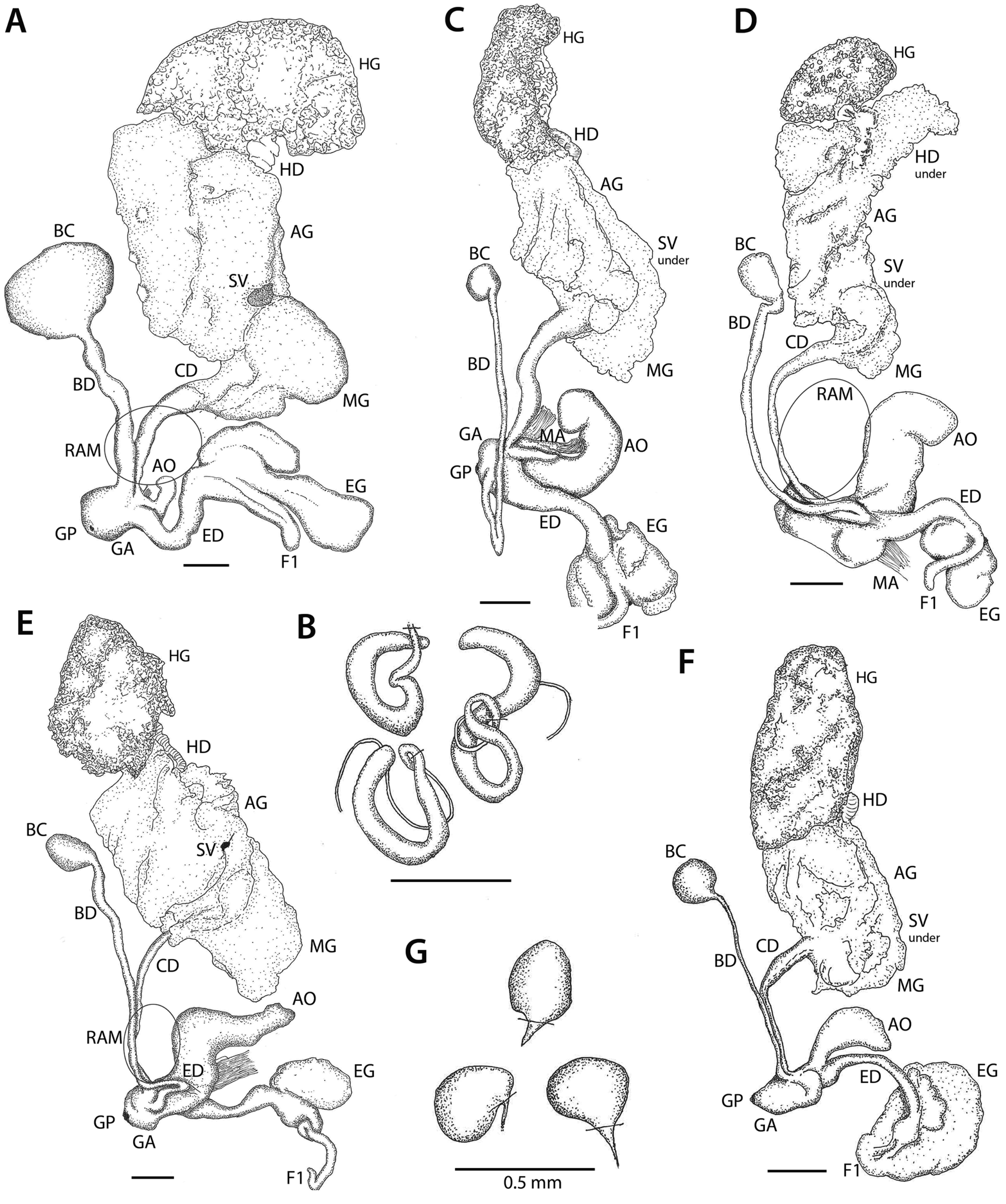

FIGURE 18. Reproductive morphology of *S. radiata*, *S. crenata* and *S. capensis*. **A–B.** *S. radiata*, Malaysia, Malacca, ZRC. MOL.24891 [SK348]. **C–E.** *S. crenata*, Pakistan, Karachi, **C.** AM C.585851 [M242, SK233]. **D.** AM C.585338 [SK153]. **E.** AM C.595917 [M592, SK534]. **F–G.** *S. capensis*, Mozambique, Inhaca. **F.** MNHN IM-2019-1488 [SK507]. **G.** MNHN IM-2019-1481 [M585]. Unlabelled scale bars 1 mm.

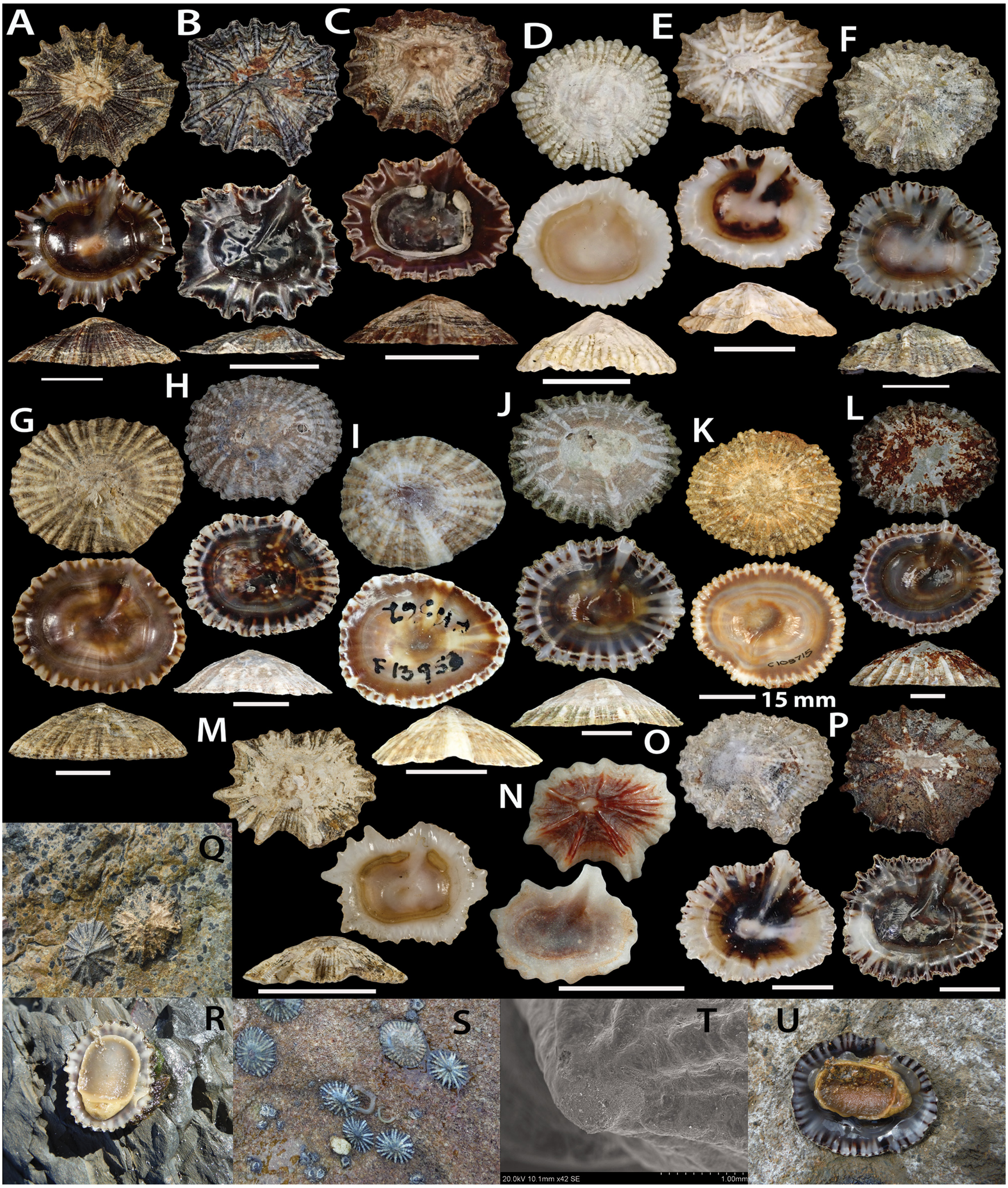

FIGURE 19. Shells of *S. atra* and *S. denticulata*. **A–F, M–Q, T–U.** *S. atra*, **A.** Lectotype MNHN-IM-2000-35950. **B.** NC, Hienghène, NC, AM C.585003 [M391, SK173]. **C.** Probable holotype of *Mestosiphon eumelas* AM C.103711. **D.** Probable holotype of *Triellsiphon acervus* AM C.103716. **E.** NC, Ponerihouen, TS of *T. acervus* AM C.584983 [M405, SK072]. **F.** NC, Port Quenghi, AM C.585018 [M379]. **M.** *S. albicante* lectotype MNHN IM-2000-38234. **N.** Paralectotype IM-2000-5026. **O.** NC, Ouassé, TS of *T. acervus* AM C.584976 [M411, SK061] **P.** Qld, Cape Kimberley, TS of *M. eumelas* AM C.585167 [M454, SK178]. **T.** WA, Catamaran Bay, AM C.585300, protoconch. **Q, U.** *In situ*, animal NC, Port Quenghi, NC07-1. **G–L, R.** *S. denticulata*. **G.** Lectotype MNHN-IM-2000-35951. **H.** NSW, Kiama AM C.585333 [SK043]. **I.** Holotype of *S. currumbinensis* MV F.15562. **J.** NSW, Currumbin, TS of *S. currumbinensis* AM C.585123 [M074, SK033]. **K.** Probable holotype of *Ellsiphon marza* AM C.103715. **L.** Qld, Yeppoon, TS of *E. marza* AM C.584743 [SK030]. **R.** Animal. Unlabelled scale bars = 10 mm.

25–29) from ‘Port Tewfick, Red Sea’ and ‘Gulf of Suez’ are also likely specimens of *S. crenata*. Figured specimens of ‘*S. kurracheensis*’ in Bosch *et al.* (1995: 186, fig. 863) and Ali *et al.* (2011: 1086, fig. 1B) are herein considered to represent *S. crenata* as well for corresponding shell size, ribbing, and extension of siphonal ridge.

Distribution and habitat. This species is recorded from the Red Sea and the Persian Gulf through to Karachi, Pakistan (Fig. 28). In this study found in sheltered positions on exposed rocky intertidal shores, upper littoral level (Fig. 14S).

Siphonaria diemenensis **Quoy & Gaimard, 1833**

(Figs 17C–G, O–Q, 20A–C)

Siphonaria diemenensis Quoy & Gaimard 1833: 327, pl. 25; figs 1–12 (type locality: “le canal d’Entrecasteaux, à Île de van Diémen” [D’Entrecasteaux Channel, Tasmania]).—Lamarck 1836: 562; 1839: 207; Catlow & Reeve 1845: 100; Jay 1850: 104; H. Adams & A. Adams 1855 (in 1853–58): 271; Reeve 1856: pl. 1, species 4; Hanley 1858b: 151; H. Adams & A. Adams 1863: 271; Angas 1865: 189; Dall 1870: 31, 37; Tenison Woods 1877: 56; Hutton 1878: 42; Adcock 1893: 11; Tate & May 1901: 418; Pritchard & Gatliff 1903: 220; Verco 1907: 105; May 1921: 88; 1923: 87, pl. 41, fig. 2; Cotton & Godfrey 1932: 152, pl. 3, fig. 6; Macpherson & Chapple 1951: 142; Cotton 1959: 411; Macpherson & Gabriel 1962: 262, fig. 299; Burn & Bell 1976: 234; Mapstone 1978: 85; Jenkins 1981: 2; 1983: 29; Hochlowski & Faulkner 1983: 1917; Hochlowski *et al.* 1983: 7413; Trew 1983: 5; Capon & Faulkner 1984: 2506; Jenkins 1984: 113; Phillips *et al.* 1984: 78, text-fig; Quinn 1988: 115; Ludbrook & Gowlett-Holmes 1989: 610, fig. 11.29 l, m; Wilson 2002: 172, fig. 172; Grove *et al.* 2006: 60; Chim & Tan 2009: 270; Grove 2011: 62, pl. 29, fig. 13; White & Dayrat 2012: 62; Colgan & da Costa 2013: 74.

Siphonaria diemensis Anton 1838: 26.—Menke 1844: 54; Paetel 1873: 117; 1883: 178; 1889: 428; Galindo 1977: 416 (invalid; incorrect subsequent spelling of *diemenensis*).

Siphonaria diemanensis Tenison Woods 1878a: 46; 1878b: 99 (invalid; incorrect subsequent spelling of *diemenensis*).

Siphonaria scabra—Angas 1867: 232 (not *S. scabra* Reeve, 1856).

Siphonaria atra—Angas 1867: 233 (in part) (not *S. atra* Quoy & Gaimard, 1833).

Siphonaria cochlearformis Whitelegge 1889: 117 (in part) (invalid; incorrect subsequent spelling of *S. cochleariformis* Reeve, 1856, not *S. cochleariformis* Reeve, 1856).

Siphonaria diemenensis var. *denticulata*—Tenison Woods 1878a: 47; 1878b: 99; Tate & May 1901: 418 (not *S. denticulata* Quoy & Gaimard, 1833).

Siphonaria (*Ductosiphonaria*) *diemenensis*—Hubendick 1945: 70, figs 23, 28–29.—Hubendick 1946: 38, pl. 2, fig. 16.

Siphonaria (*Ductosiphonaria*) *diemenensis* var. *diemenensis*—Hubendick 1946: 38, pl. 2, fig. 16.

Siphonaria (*Ductosiphonaria*) *diemenensis* var. *denticulata*—Hubendick 1946: 38, pl. 2, fig. 17 (not *S. denticulata* Quoy & Gaimard, 1833).

Siphonaria (*Ductosiphonaria*) *diemenensis* var. *scabra*—Hubendick 1946: 38, pl. 2, fig. 14, 15 (not *S. scabra* Reeve, 1856).

Siphonaria (*Ductosiphonaria*) *diemenensis* var. *macauleyensis*—Hubendick 1946: 38 (not *S. macauleyensis* Oliver, 1915).

Hubendickula diemenensis—McAlpine 1952: 42; Cotton 1959: 411; Iredale & McMichael 1962: 82.

Siphonaria (*Hubendickula*) *diemenensis*—Ludbrook & Gowlett-Holmes 1989: 610, fig. 11. 29 l, m.

Siphonaria ‘unit 7’—Dayrat *et al.* 2014: 252, 258, 259, fig. 3 H; González-Wevar *et al.* 2018: 5.

Material examined. *Type material.* Lectotype of *Siphonaria diemenensis* Quoy & Gaimard, 1833, present designation, from ‘le canal de d’Entrecasteaux, á l’île de van Diémen’ [d’Entrecasteaux Channel, Tasmania] (MNHN-IM-2000-35952, Fig. 17C). Paralectotype, same data as lectotype (MNHN-IM-2000-5059).

Other, non-type material. **Australia, NSW:** Terrigal, The Skillion, 33°27.008’S, 151°27.122’E, NSW08-2 (AM C.585631 5p); Wy-ar-gine Point Balmoral, 33°49.159’S, 151°15.195’E, NSW06-5 (AM C.585630 6p); Laings Point Sydney Harbour, 33°50.419’S, 151°16.638’E, NSW06-3 (AM C.585404 17p); Bombo Kiama, 34°39.232’S, 150°51.649’E, NSW03-1 (AM C.585682 7p); Murunna Point Camel Head, 36°22.720’S, 150°04.766’E, NSW02-1 (AM C.585402 10p, C.585001 p [SK037]); Oman Point Eden, 37°04.634’S, 149°53.445’E, NSW01-1 (AM C.585527 20+p). **Vic:** Bastion Head Mallacoota, 37°34.429’S, 149°45.927’E, V09-1 (AM C.585611 4p); Cape Conran, 37°48.798’S, 148°43.608’E, V08-2 (AM C.585543 20+p, C.585293 p [M196]); Frankston, 38°09.236’S, 145°06.457’E, V06-1 (AM C.585356 p); Point Lonsdale (nr Queenscliff), 38°17.276’S, 144°36.977’E, V05-1 (AM C.585436 10p); Port Fairy, 38°23.692’S, 142°14.260’E, V01-1 (AM C.585694 7p); Roadknight Point, 38°25.707’S, 144°11.102’E, V04-1 (AM C.585716 8p, C.585286 p [M168], C.585287 p [M169]); West Head Flinders, 38°28.883’S, 145°01.727’E, V06-3 (AM C.585542 20+p, (AM C.585290 p [SK003], C.585291p [M198]); Loutit Bay Lorne, 38°31.190’S, 143°59.429’E, V03-2 (AM C.585541 20+p); San Remo, 38°31.489’S, 145°21.858’E, V07-1 (AM C.585357 p [SK029]); Crofts Bay, 38°35.363’S, 142°50.633’E, V01-3 (AM C.585680 6p); Marengo Rocks Apollo Bay, 38°46.772’S, 143°39.997’E, V03-1 (AM C.585433 10+p). **Tas:** Georges Bay, Burns Bay, 41°16.62’S, 148°28.92’E (TMAG E41975 3p); Beaumaris, Shelly Point, 41°26.136’S, 148°16.638’E (TMAG E41965 4p); Denison Beach, Porch Rocks, 41°47.334’S, 148°16.158’E (TMAG E41963 2p); Bicheno, 41°52.837’S, 148°18.525’E, T02-1 (AM C.585692 7p); Bicheno Courland Bay, 41°55.866’S, 148°18.414’E (TMAG E41960 p); Swansea Spiky Beach, 42°11.142’S, 148°4.104’E (TMAG E41961 7p); Louisville, Alginate Bay, 42°32.4’S, 147°54.6’E (TMAG E24490 p) ; Maria Island, Darlington Bay, 42°34.8’S, 148°3.6’E (TMAG E16769 2p); Maria Island, Hopground Beach, 42°35.4’S, 148°3.6’E (TMAG E08499 3p); Earlham, foreshore, 42°39.6’S, 147°57’E (TMAG E08098 6p); Dodges Ferry, 42°51.083’S, 147°36.981’E, T03-1 (AM C.585428 10+p); Dodges Ferry, Red Ochre

Beach, 42°51.6’S, 147°36.6’E (TMAG E08843 p); Park Beach, Dodges Ferry, 42°51.716’S, 147°36.665’E, T03-4 (AM C.585260 p [M170], C.585261 p [SK016]); Carlton Beach, Spectacle Island, 42°52.044’S, 147°36.024’E (TMAG E41955 4p); Primrose Sands, 42°53.4’S, 147°40.2’E (TMAG E04957 p); Lauderdale, Roches Beach, 42°54.6’S, 147°0.3’E (TMAG E03265 p); Lagoon Bch (near Saltwater River), 42°56.903’S, 147°39.962’E, T03-2 (AM C.585253 p [SK015], C.585254 p [SK185]); Taroona Beach, 42°57.18’S, 147°21’E (TMAG E41969 14p); Kingston Beach, 42°58.8’S, 147°19.2’E (TMAG E02012 p); Eaglehawk Neck, eastern side, 43°0.6’S, 147°0.6’E (TMAG E01661 3p); Blackmans Bay, 43°0.6’S, 147°19.8’E (TMAG E15878 8p); Saltwater River, 43°01.083’S, 147°43.578’E, T03-11 (AM C.585725 7p); Tasman Arch, 43°02.033’S, 147°56.963’E, T03-3 (AM C.585771 5p, C.585256 p [M175], C.585257 p [M176]); Pirates Bay, Fossil Island, 43°1.8’S, 147°57’E (TMAG E01299 p); Tinderbox Beach, 43°3.6’S, 147°19.8’E (TMAG E05223 3p); North Bruny Island, Dennes Point, 43°3.87’S, 147°21.066’E (TMAG E41968 3p); Nubeena, Parsons Bay, 43°6’S, 147°6’E (TMAG E05994 p); Kettering, Oyster Cove, 43°6.6’S, 147°16.2’E (TMAG E05350 3p); Nubeena, White Beach, 43°7.2’S, 147°43.8’E (TMAG E06016 p); North Bruny Island, Simmonds Bay, 43°7.8’S, 147°21.6’E (TMAG E02677 2p); Fortescue Bay, 43°8.4’S, 147°57.6’E (TMAG E05581 2p); Three Hut Point d’Entrecasteaux Channel, 43°16.195’S, 147°14.414’E, T04-3 (AM C.585482 18p, C.584797 p [SK047], C.585269 p [M112]); Huon Point d’Entrecasteaux Channel, 43°17.471’S, 147°05.778’E, T04-1 (AM C.585430 10+p); South Bruny Island Coal Point, 43°19.8’S, 147°19.8’E (TMAG E35239 2p); South Bruny Island, Adventure Bay, Cemetery Bluff, 43°20.388’S, 147°19.44’E (TMAG E41956 2p); Moss Glen, 43°31.910’S, 146°53.641’E, T05-1 (AM C.585270 p [M107],C.585271 p [M115]); Fishers Point, 43°34.260’S, 146°55.244’E, T05-4 (AM C.585570 3p); Flensing Rock, 43°34.291’S, 146°54.856’E, T05-2 (AM C.585714 8p, C.585272 p [SK013]); Pancake Bay, 43°34.673’S, 146°55.293’E, T05-5 (AM C.585273 p [M113]; Cape Portland, Petal Point, 40°46.566’S, 147°56.604’E (TMAG E41972 3p); Herbies Landing 40°50.112’S, 147°38.724’E (TMAG E41966 4p); Bridport—beach 40°59.808’S, 147°23.526’E (TMAG E41957 p); S of Granite Point Bridport, 40°59.739’S, 147°23.468’E, T01-1 (AM C.585550 22p, C.595920 p [SK552]); Tamar River, Kelso, foreshore, 41°6’S, 146°6’E (TMAG E16716 2p); Aikenhead Point, Devonport, 41°09.997’S, 146°21.927’E, T01-2 (AM C.585691 7p); Goat Island, foreshore of island and nearby mainland, 41°8.214’S, 146°8.196’E (TMAG E41962 p); Somerset, foreshore, 41°2.178’S, 145°49.962’E (TMAG E41975 14p); Somerset, 41°01.168’S, 145°47.632’E, T01-3 (AM C.585461 14p, C.585252 p [M117]); Wynyard, Inglis River mouth, 40°58.8’S, 145°43.8’E (TMAG E02094 2p); Boat Harbour, beach, 40°55.8’S, 145°37.2’E (TMAG E07953 p); Rocky Cape, Castle Rock Bay, 40°53.238’S, 145°31.356’E (TMAG E41971 6p); Rocky Cape, Picnic Beach & rocks to S, 40°52.026’S, 145°29.052’E (TMAG E41958 p); Little Peggs Beach 40°51.084’S, 145°21.384’E (TMAG E41970 p); Stanley, Godfreys Beach, 40°45.138’S, 145°17.67’E (TMAG E41959 p); Marrawah, Green Point, 40°54’S, 144°54’E (TMAG E09069 4p); Lucas Point Pilot Bay Macquarie Harbour, 42°12.241’S, 145°12.005’E, T06-1 (AM C.585479 17p); Trial Harbour, 41°55.758’S, 145°10.434’E (TMAG E41964 5p); **King Island:** E coast, 39°54.6’S, 144°6.6’E (TMAG E04045 p); Fitzmaurice Bay, 40°3.708’S, 143°52.896’E (TMAG E41967 p); Lavinia Beach, beach nr Lake Martha Lavinia, 39°39.018’S, 144°4.692’E (TMAG E41973 2p). **SA:** Cape Northumberland, 38°03.503’S, 140°40.378’E, SA15-1 (AM C.585452 12p); Cape Northumberland Port Macdonnell, 38°03.308’S, 140°39.398’E, SA15-2 (AM C.585676 6p, C.595918 p [SK085]); Cape Thomas, 37°04.461’S, 139°44.659’E, SA14-1 (AM C.585426 10+p); Fisheries Bay Lands End, 35°37.999’S, 138°06.921’E, SA13-2 (AM C.585464 15p); Groper Bay nr West Cape, 35°14.108’S, 136°49.883’E, SA10-1 (AM C.585722 9p); Pondalowie Bay, 35°13.989’S, 136°49.892’E, SA10-2 (AM C.585712 8p, C.585215 p [SK014]); Port Neill, 34°07.102’S, 136°21.271’E, SA06-1 (AM C.585423 20+p); Port Moonta, 34°03.273’S, 137°33.592’E, SA09-1 (AM C.585386 10p); Salmon Point, 33°38.547’S, 134°51.916’E, SA04-2 (AM C.585549 22p); Wellesley Point, 33°38.483’S, 134°51.963’E, SA04-1 (AM C.585422 10+p); Whyalla, 33°02.539’S, 137°35.511’E, SA07-1 (AM C.585721 9p); Rocky Point, 32°12.250’S, 133°14.861’E, SA02-4 (AM C.585421 10+p); Cape Thevenard, 32°08.703’S, 133°38.553’E, SA03-3 (AM C.585708 8p); Ceduna, 32°07.438’S, 133°40.260’E, SA03-2 (AM C.585451 12p); Port Le Hunte Point Sinclair, 32°05.554’S, 132°59.476’E, SA02-2 (AM C.585447 11p); Cactus Beach Point Sinclair, 32°05.135’S, 132°58.943’E, SA02-3 (AM C.595959 11p).

Taxonomic remarks. The lectotype (Fig. 17C) is designated herein for the stabilisation of the name and to ensure the unambiguous identity of this taxon (Art. 74.1 of the Code). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes and geographic series of additional specimens (Tables S1–2). We also demonstrate that previous treatments of *S. denticulata* as a synonym or variety of *S. diemenensis* are incorrect and that *S. diemenensis* and *S. denticulata* are distinct species. Menke (1844: 54) regarded *S. diemenensis* (as “*diemensis*”) as ‘closely related and associated’ with *S. javanica* (as “*iavana*” and “*iavanica*”), which is incorrect. The shell of *S. diemenensis* has more numerous and narrower ribs than that of *S. javanica*. Both species also differ in RS structure: AO larger, BD longer, narrower, F1 shorter in *S. diemenensis* than *S. javanica*. Both species have non-overlapping distributions in cool temperate waters of SE Australia (Fig. 16) and in the Tropical Philippines (Fig. 11), respectively.

Tryon & Pilsbry’s (1891: 25) reference to *Patella diemensis* Philippi, 1848 from Hobarttown, Tasmania, as a possible siphonariid is incorrect. This taxon is a junior synonym of *Patella peronii* Blainville, 1825 (Coan &

Kabat, 2017: 110). Hutton (1878: 41) stated that he earlier misidentified specimens of '*Benhamina obliquata*' (= *S. obliquata*) from NZ as *S. diemenensis*. Subsequently, Suter (1909b: 33, 1913: 599) and Hubendick (1946: 24) agreed. Hutton (1878: 10, 42) also incorrectly listed *S. denticulata* as a synonym of *S. diemenensis* and was uncertain whether *S. diemenensis* inhabited NZ. Herein, we establish that *S. diemenensis* is not present in NZ. Verco (1907: 104) incorrectly considered *Trimusculus albida* (Angas, 1878) as a possible white form of *S. diemenensis*. According to Oliver (1915: 546), Suter's (1907) specimens of *S. diemenensis* were a misidentification of *S. raoulensis*.

Hubendick (1946: 38) treated *S. denticulata* Quoy & Gaimard, 1833, *S. scabra* Reeve, 1856, *S. exulum* Hanley, 1858 (including '*Ellsiphon exulorum'* Iredale, 1940) and *S. raoulensis* Oliver, 1915 as synonyms of *S. diemenensis*. Hubendick (1946: 38–39) also treated another five taxa as varieties of the former. We consider that four of these names are incorrectly assigned to *S. diemenensis* (i.e., *denticulata* Quoy & Gaimard, 1833, *scabra* Reeve, 1856, *exulum* Hanley, 1858, and *perplexa* Oliver, 1915). *Siphonaria exulum, S. perplexa* and *S. macauleyensis* are all conspecific with *S. exulum*. Hubendick's (1946: 38) inclusion of *S. javanica* Blainville, 1827 and *S. alternicosta* Potiez & Michaud, 1838 as possible synonyms of *S. diemenensis* are also rejected. McAlpine (1952: 41) erroneously treated *S. scabra* as a junior synonym of *S. diemenensis*. Yet, these are distinct species. Grove *et al.* (2006: 60) incorrectly listed *S. denticulata*, *S. javanica* Blainville 1827 (not Lamarck, 1819), *S. exulum* and *S. scabra* as synonyms of *S. diemenensis*.

External morphology (Fig. 17O). Foot sole smooth, reddish orange, darker at foot edge; foot wall dark yellowish grey with evenly spread white subepithelial pustules becoming more vivid and dense close to the foot sole and around pneumostomal lobe; genital pore inconspicuous, located on foot wall posterior to right cephalic fold; fringing mantle reasonably wide, thin, yellowish, translucent to transparent, extends to shell edge, outer edge lobed, weakly banded yellow and black reflecting corrugations and inner colouration of shell lip and ribs; pneumostomal lobe large and within mantle between the right ADMs, closes the pneumostomal and anal openings at the mantle edge; two small black epithelial eye spots centralised on two thick centrally touching orange grey cephalic folds that darken to their outer edge, covered with white mucous cells similar (but smaller) to those of the foot wall tissue.

Shell (Figs 17C–G, Table S9). Small to medium sized (max sl mean = 17.7 mm, SD = 3.1 mm, n = 8), ovate; height tall; apex central, usually eroded, apical sides strongly convex, protoconch direction homostrophic (n=6; Fig. 17P), shell whorl dextral; growth striae indistinct with weak external colour banding aligning with growth stages; rib count (mean = 29, SD = 5.6, n = 8), primary ribs off white, strongly raised, rounded and straight, extend past a fairly even shell lip to scallop the edge; very few secondary ribs, rib interstices dark, strongly prominent, paired primary ribs over an indistinct siphonal ridge; interior shell margin coloured white aligning under primary ribs, very dark brown to black aligning under rib interstices, colour extends from shell lip to spatula region, spatula yellowish brown; ADM scar indistinct, paler colour than spatula, CMS straight. Shell thickening not displayed.

Reproductive system (Figs 20A–C; n = 2). Positioned within coelom under the respiratory cavity, over foot muscle and against right side of foot wall. GA, EG and ED positioned between BM and RAM; single GP inconspicuous, opening from an extremely small GA through foot wall posterior to right cephalic fold; AO short, wide, bluntly pointed; join of AO, GA and ED distinct, all whitish fibrous muscular tissue; ED very long, thin, bent, twisted; EG wide, lobed, with single curved, indistinct flagellum (F1); BD and CD very thin and long, jointly connect into GA between ED, AO and GP; BD noticeably longer than CD with a prominent central loop over epiphallic parts before joining BC (no distal loop), both ducts smooth, featureless, pass together outside RAM connecting into curved MG, BD ventral to CD; BC bulbous elongated, thin test, internally embedded in folds of MG (0 to 5 SPM in BC); HD long, thick, coiled, links ducts in folds of small AG to elongated narrow yellowish granulated HD; AG larger than HG, MG and AG folded, soft white tissue; SV embedded on left side of AG under BC; outer edge of AG and HG sides match curvature of inner foot wall.

Spermatophore (Fig. 20B). Thread-like (length = 9.35 ± 3.61 mm, n = 2), translucent, test thin; head section, tip bluntly rounded, weakly bulbous, elongate, containing a white gelatinous mass; tapers quickly into consistently filamentous transparent flagellum; both sections smooth, featureless. Head shorter and thicker than flagellum (head length = 4.7 ± 0.7 mm, n = 2; mean ~ 20% of SPM length; head width = 260 ± 42 µm; flagellum width = 45 ± 21 µm, n = 2). Typically, tightly coiled in bursa, embedded in white gelatinous mass. The SPM (Fig. 20B) reasonably matches the SPM of *S. diemenensis* figured in Hubendick (1945: 23, fig, 29) apart from width of head section.

Radula (Figs 83A–D). Dentition formula 35:1:35 with 141 transverse rows, n = 1, AM C.201772); single central rachidian tooth flanked squarely by 35 half row laterals, of which 3 are inner, 7 mid and 25 outer laterals (n = 1); central tooth with narrow pointed mesocone, inner lateral mesocones predominantly bicuspidate but with an irregular few unicuspidate, endo and ectocones absent (Figs 83A–B); mid laterals with pointed mesocone; single ectocone, protrudes at acute angle halfway along the tooth's length; outer laterals with a broad 'chisel' shaped pointed mesocone flanked by small, single, pointed ecto and endocones (Fig. 83C), angle of separation of each cone from the mesocone varies, basal plate of outer laterals typically as broad as the tooth's length.

Comparative remarks. *Siphonaria diemenensis* (*lateralis* group, unit 7) represents the sister group of a clade containing the three species *S. jeanae*, *S. propria*, and *S. australis* (Figs 1, 4). It is well-differentiated from these species by COI distances of ≥ 18.8% (*S. jeanae*), ≥ 19.5% (*S. propria*), and ≥ 19.9% (*S. australis*) (Table S8). From other species it differs by COI distances of ≥ 20% (Table S8).

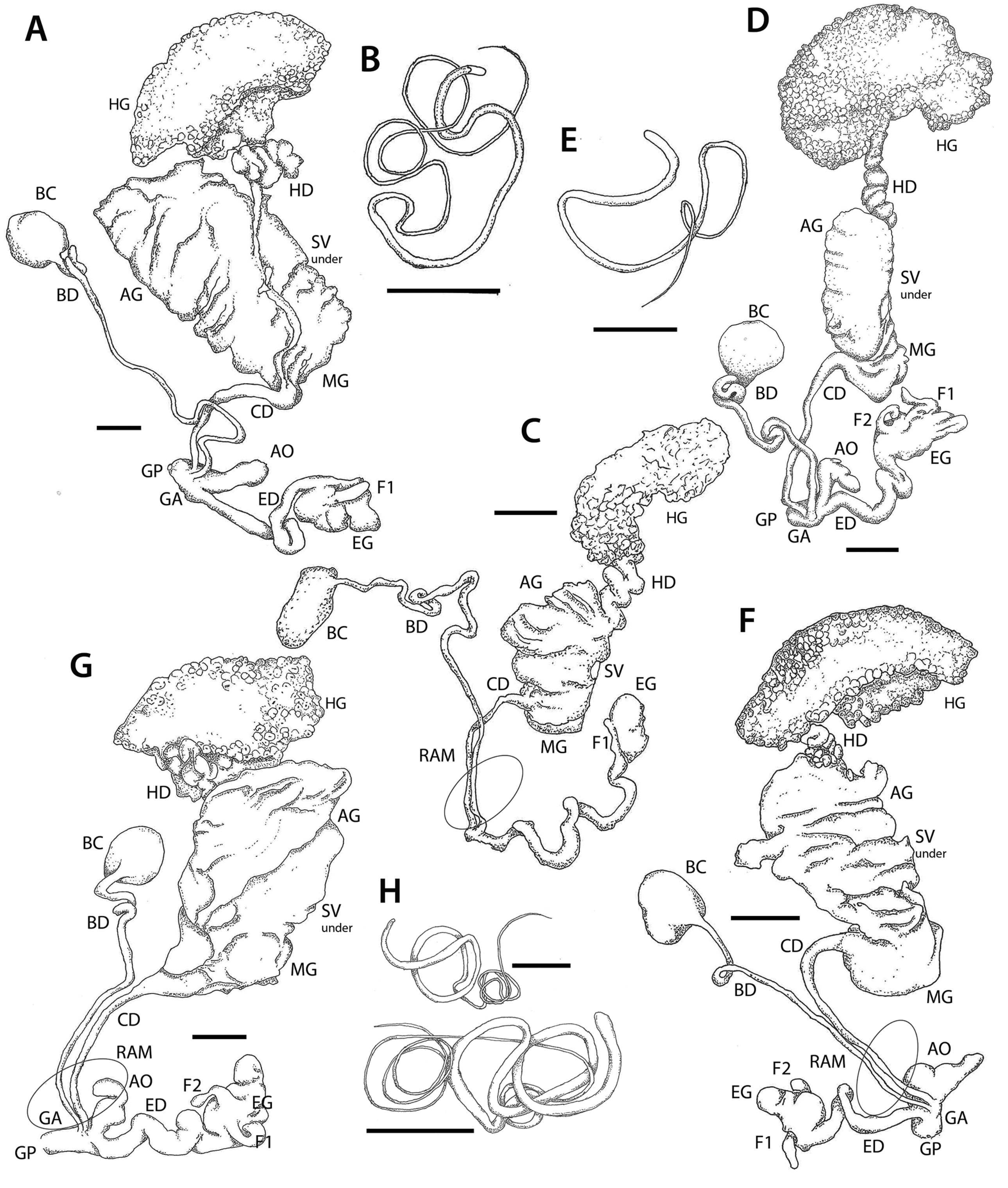

FIGURE 20. Reproductive morphology of *S. diemenensis* and *S. denticulata*. **A–C.** *S. diemenensis*. **A–B.** NSW, Murunna Point, AM C.585001 [SK037]. **C.** Tas, d'Entrecasteaux Channel, TS, AM C.584797 [SK047]. **D–H.** *S. denticulata*. **D**, **E.** SPM, NSW, Kiama, AM C.585333 [SK043]. **F.** Qld, Currumbin Point, TS of *S. currumbinensis* AM C.585123 [SK033]. **G–H.** Qld, Yeppoon, TS of *Ellsiphon marza* AM C.585123 [SK030]. Scale bars = 1 mm.

Within its range we found eight partially sympatric congeners. With four of these species, it co-occurs in Sydney, NSW, Australia: *Siphonaria pravitas* **sp. nov.** has a lower shell with stronger raised ribs and edge scalloping, no BD distal loop, larger BC, wider F1, shorter SPM. *Siphonaria scabra* has a paler shell with finer ribbing and coarser exterior, a longer AO, BC and F1, and a bursal loop. *Siphonaria denticulata* has a larger, lower shell with less prominent ribbing and a more scalloped edge, a smaller, pointed AO, shorter and wider ED, no bursal loop and a larger BC. *Siphonaria emergens* has a smaller, elongate, paler brown shell with a strongly offset apex, less prominent ribbing and edge scalloping.

A further five congeners are sympatric with *S. diemenenesis* in SE Australia: *Siphonaria funiculata* has a paler, taller shell with less raised ribs broadening to a fainter scalloped edge, a larger AO, shorter BD and ED, absent to smaller F1, and a larger, drop-like SPM. *Siphonaria stowae* has a smaller, elongate, and paler shell with a strongly offset apex, less prominent ribbing and edge scalloping, a smaller AO, shorter ED, larger BC, and shorter SPM. *Siphonaria tasmanica* has a lower, bluish coloured shell with a more offset apex, fainter edge scalloping and less raised ribs broadening to edge, a smaller AO and BD, shorter ED, and short, drop-like SPM. *Siphonaria jeanae* has a smaller, has a smaller, lower, bluish coloured shell, a smaller AO, shorter ED, and short, drop-like SPM. *Siphonaria zelandica* has a paler, lower shell with less prominent and finer, narrower ribbing, a shorter ED and BD, and short, drop-like SPM.

Exterior shell characteristics of *S. diemenensis* resemble those of *S. denticulata*. Hubendick's (1946) treatment of *S. scabra* and *S. denticulata* as varieties of *S. diemenensis* is rejected as these are accepted herein as distinct species. A specimen figured as '*S. diemenensis*' by Davey (1998: 113, text-fig.) is identified herein as *S. funiculata*. Our description of the radula matches that of Hutton (1883: 124, pl. 17, figs E–G), but the dentition formula is more than twice the count of 12:1:12 given by Hubendick (1946: 38). The RSs figured herein (Figs 20A, C) closely matches figures by other authors (e.g., Hubendick 1945: fig. 23; McAlpine, 1952: 43, fig. 2). The RS and SPM (Fig. 20B). Hubendick;'s (1946: 14, fig. 19) illustrations of RS and SPM of '*S. bifurcata*' from 'Port Jackson' (= Sydney) are herein attributed to *S. diemenensis* with which the largely correspond apart from a narrower and shorter SPM head section. The specimen figured as 'unit 7' in Dayrat *et al.* (2014: fig. 3H) from Portland, Vic closely resembles *S. diemenensis*. This unit was subsequently referred to as '*Siphonaria* sp. (Australia)' in González-Wevar *et al.* 2018. The record of '*S. diemanensis* Quoy & Gaimard 1835' (sic) in Smythe (1979: 69) from the United Arab Emirates is incorrect and well outside the known distribution of this species.

Distribution and habitat. Endemic to cool-temperate waters of south coast Australia, between just north of Sydney through to west of Cape Northumberland, South Australia, including Tasmania (Fig. 16). In this study found on exposed places on intertidal rocky shores, common across upper and mid littoral, associated with mussel and barnacles, home scars common.

Siphonaria australis Quoy & Gaimard, 1833

(Figs 15I–J, 17H–J, R–T)

Siphonaria australis Quoy & Gaimard 1833: 337, pl. 25, figs 32–34 (type locality: 'détroit de Cook, à la Nouvelle-Zélande' [Cook Strait, New Zealand]).—Anton 1838: 26; Lamarck 1839: 207; Catlow & Reeve 1845: 100; H. Adams & A. Adams 1855 (in 1853–1858): 271, 1863: 271; Paetel 1873: 117; Hutton 1873: 55; 1878a: 42; 1880: 36; 1882: 24; 1883: 142, pl. 17, figs E–G; Filhol 1880: 552; Paetel 1883: 178; 1889: 428; Suter 1904: 68; Iredale 1908: 408; Moss 1908: 41, pl. 9, fig. 25; Suter 1913: 598. 1915: unpaginated text, pl. 24, fig. 6; Iredale 1915: 478; Oliver 1923: 498; Finlay 1927: 442; Powell 1937: 86; 1939: 217; 1946: 91; Knox 1954: 872; 1955: 86; Powell 1957a: 114; Dell 1960: 148; Morton & Miller 1968: 302, fig. 109, pl. 9, fig. 7, 7a; Galindo 1977: 416; Powell 1979: 292, pl. 54, fig. 11; Jenkins 1983: 1, 21, pl. 3a–I, 22, 4a–f; Trew 1983: 4; Paul 1984: 28; Russell & Phillips 2009: 579; Raven & Bracegirdle 2010: 46; White & Dayrat 2012: 61.

Siphonaria sipho—Hutton 1883: 143; Filhol 1880: 552 (not *S. sipho* Sowerby I, 1823).

Siphonaria zelandica—Lamarck 1836: 58; Hutton 1878a: 41; Filhol 1880: 552; Suter 1904: 68; 1913: 600; 1915: unpaginated text, pl. 24, fig. 8O; Odhner 1924: 55; Finlay 1927: 442; Powell 1933: 186; 1937: 86; 1939: 217; 1946: 91; Borland 1950 : 386; Knox 1955: 68; Powell 1955: 120; 1957a: 114; Dell 1960: 147; 1963: 227; Morton & Miller 1968: 83, pl. 19, figs 8,a; Galindo 1977: 416; Powell 1979: 292, pl. 54 fig. 10; Trew 1983: 7; Wells & Wong 1978: 417 (not *S. zelandica* Quoy & Gaimard, 1833).

Siphonaria funiculata—Hutton 1873: 55 (not *S. funiculata* Reeve, 1856).

Siphonaria zealandica Hutton 1873: 55; 1880: 36; 1883: pl. 17, fig. H–M.—Oliver 1915: 547; Oliver 1923: 58 (in part); Bucknill 1924: 82, pl. 3, figs 16–16a (invalid; incorrect subsequent spelling of *zelandica,* not *S. zelandica* Quoy & Gaimard, 1833).

Siphonaria diemenensis—Hutton,1873: 55; Suter 1907: 141; 1909: 33 (not *S. diemenensis* Quoy & Gaimard, 1833).

Siphonaria inculta Gould 1846: 11 (type locality: NZ).—Gould 1848: 153; 1852: 153, fig. 465, a, b; H. Adams & A. Adams 1855 (in 1853–1858): 271; Gould 1856: 12, fig. 465, a, b; H. Adams & A. Adams 1863: 271; Hanley 1858b: 152; Hutton 1878a: 7; 1880: 36; 1883: 143; Paetel 1889: 428; Johnson 1964: 90; Jenkins 1983: 21, pl. 3b; Trew 1983: 5; White & Dayrat 2012: 64.

Siphonaria cancer Reeve 1856: pl. 2, species 7 (type locality: NZ).—Hanley 1858b: 151; Paetel 1873: 117; Hutton 1873: 55; 1878a: 41; Filhol 1880: 552; Paetel 1883: 178; 1889: 428; Jenkins 1983: 2, 21, pl. 3c, d; Trew 1983: 5; White & Dayrat 2012: 61.

Siphonaria cookiana Suter 1909b: 258 (type locality: Lyall Bay, Cook Strait, [NZ]).—Knox 1955: 86; Boreham 1959: 71 (both in part); Jenkins 1983: 1, 21, figs 3e–g.

Siphonaria (*Siphonaria*) *australis*—Hubendick 1946: 49.

Siphonaria canessi Galindo 1977: 416 (invalid; subsequent incorrect spelling of *S. cancer*).

Siphonaria canuicer Galindo 1977: 416 (invalid; subsequent incorrect spelling of *S. cancer*).

Material examined. *Type material.* Lectotype of *Siphonaria australis* Quoy & Gaimard, 1833 from 'détroit de Cook, à la Nouvelle-Zélande' [Cook Strait, New Zealand] MNHN IM 2000-5036 (Fig. 17G); paralectotype (MNHN-IM-2000-5037), same data as lectotype.

Holotype of *Siphonaria inculta* Gould, 1846 USNM

5857, possible paratype MCZ 169190 (Fig. 17K), same data as holotype (figured in Gould, 1852: 358, fig. 465, 465a, 465b and in Jenkins, 1983: 21, pl. 3b).

Lectotype of *Siphonaria cancer* Reeve, 1856, NHMUK 198112 (figured in Jenkins, 1983: 21, pl. 3c), four paralectotypes NHMUK 198112, same data as lectotype (figured in Jenkins, 1983: 21, pl. 3d).

Other, non-type material. **NZ; North Island:** Big Bay, Manakau Harbour, Auckland, 37°02.58'S 174°38.72'E (AM C.265856 p [SK511 protoconch I6], Fig. 17S). **South Island:** N end Seaview Marina, Lower Hutt, 41°14.85'S, 174°54'E (NMNZ M.331451, 2 p). **Stewart Is:** Watercrest Bay, 46°54.223'S, 168°07.195'E STI01-1 (AM C.585953 4 p, C.585247 p [M480, SK289] Fig. 17H); E of Ringaringa Bch, 46°54.544'S, 168°08.646'E STI02-1 (AM C.585952 6p, C.585249 p [M481, SK088], Fig. 17I).

Taxonomic remarks. The lectotypes of *S. australis* and *S. cancer* have been designated by Jenkins (1983). Our delineation of *S. australis* is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes of *S. australis* (Figs 17I–J), *S. inculta, S. cancer* and *S. cookiana* (Tables S1–2). *Siphonaria spinosa* Reeve, 1856 is a junior synonym of *S. aspersa* Krauss, 1848 as based on examination of the types (Jenkins, 1983: 29). Reeve (1856: pl. 7, fig. 32a, b) incorrectly stated this taxon to originate in NZ. *Siphonaria inculta* Gould, 1846b was first figured in Gould (1852: 358, fig. 465a, b) and is considered a junior synonym of *S. australis*. Reference to '*S. cancer* Reeve*'* in Swinhoe (1865: 165) from Formosa [Taiwan] is based on a misidentification. Reference to *S. zelandica,* as a synonym of *S. sipho*, in Schrenck (1867: 306) is erroneous and a probable misidentification of *S. australis*. Hutton (1878a: 41) considered *S. cancer* to be a probable variety of '*S. zelandica*', but is *S. australis*. He also (p. 42) misidentified specimens from 'New Zealand' (probably of *S. australis*) as '*S. diemenensis'*. Hubendick's (1946: 49) interpretation of *S. australis* is partly confused: He incorrectly included *S. zelandica* and *S. lentula* (as *lentulus*) in the synonymy of *S. australis*, which is rejected herein. The nominal species *S. scutellum* (= *S. obliquata*) and *P. innocuus* (= *S. exulum*) are here removed from the synonym of *S. australis*, but the synonymy of *S. inculta* and *S. cancer* is maintained.
Morrison (1972: 56–58) treated *S. cancer* as a synonym of *S. laciniosa* based on conchological similarity and 'common reproductive development'. This is rejected herein based on examinations of types and comparative morpho-anatomy. Raven & Bracegirdle (2010: 46) incorrectly treated *S. zelandica* as a synonym of *S. australis*. The re-description of this species by Jenkins (1983) forms the foundation for the delimitation of this species in the present study.

External morphology (Fig. 17R). Foot sole smooth, pale cream/yellowish, paler to foot edge; foot wall pale grey-cream with irregular dark/black markings along foot wall & concentrated over cephalic lobes; genital pore conspicuous, located on foot wall posterior to right cephalic fold; fringing mantle thick, cream, translucent to transparent, extends to shell edge, outer edge with thick lobes, strong dark bands aligning with shell lip rib-interstices; pneumostomal lobe large and within mantle between the right ADMs, closes the pneumostomal and anal openings at the mantle edge; two small black epithelial eye spots centralised on two thick centrally touching cephalic folds that darken to their outer edge.

Shell (Figs 17G–I; Table S9). medium sized, ovate (max sl mean = 17.99 mm, SD = 1.93 mm, n = 99), asymmetrical, thick, height low to medium, edge often very uneven, exterior grey/light brown, uneven; rib count (mean = 28.5, SD = 4.4, n = 99), raised irregularly spaced radial ribs, broaden to edge, ridges rounded to flat; apex weakly offset to posterior and left, protoconch direction homostrophic (n = 1, Fig. 17S), body whorl dextral; apical sides convex increasingly to shell margin, growth striae indistinct discontinuous, radial ribs project unevenly weakly beyond shell edge, particularly in larger specimens, dual primary ribs form siphonal ridge, project furthest; rib interstices brown, furrowed often fairly deep. Interior glossy, uneven, light brown to tan, margin chocolate brown with white rays aligning under ribs; ADM scar paler, spatula pale blue/yellowish tan, siphonal groove usually mottled dark brown or grey, CMS straight to convex.

Reproductive system (Fig. 15I; n = 3). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall & over foot sole, epiphallic parts positioned between BM and to side of RAM; GA bulbous, GP distinct, protrudes; AO indistinct, merges with bulbous GA; ED relatively short, narrow, twisted close to GA; EG large, unfolded, rounded; single long, uncoiled flagellum F1, extends from end of wider EG; AO, GA and ED all muscular white tissue; BD and CD junctions into GA side-by-side & close to opposing ED connection; BD longer, slightly narrower than CD without distal loop, both ducts, fused, smooth unfeatured, pass together through outer side of RAM connecting into folds of MG (BD above CD); BC translucent test, midsized, elongate bulbous, embedded in AG; large heavily coiled HD, connects soft white folded tissues of AG to smaller elongated brownish finely granulated HG; MG at distal end of AG; dark SV centrally embedded within AG near top of BC, AG larger than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 15J). Body cylindrical, thread-like (length = 6.1 ± 2.4 mm, n = 2), test thin, translucent; head tip tapered bluntly rounded, section containing a white gelatinous core, tapers to a thin flagellum & tip; both sections smooth, featureless; head longer, thicker than flagellum (head length = 5.27 ± 2.19 mm, ~ 86% of SPM length; head width = 89 μm ± 7 μm, flagellum width = 24 ± 10 μm, n = 2). Typically, SPM tightly coiled in BC, embedded in white gelatinous mass.

Radula (adapted from Jenkins 1983: 17). Mean dentition formula 35:1:35 (SD = 7.01) with 127 (SD = 7.33, n = 5) transverse rows; 35 half row laterals, of which 20 mid (SD = 4.98) and 15 outer (SD = 3.58) laterals (n = 5); central tooth single pointed mesocone, inner laterals absent, mid laterals with bluntly pointed mesocone and broad pointed ectocone (Jenkins, 1983, pl. 6d, e), ectocone strong, protrudes at acute angle halfway along the tooth's length; outer lateral with a 'chisel' shaped pointed mesocone flanked by small, irregularly pointed, single ecto and endocones (Jenkins 1983: pl. 6f), angle of separation of each cone from the mesocone varies. Dentition formula: 36:1:36 (Hutton, 1883: 142), 30:1:30 (Hubendick 1946: 49).

Comparative remarks. *Siphonaria australis* (*lateralis* group, unit 86) is the sister species of *S. propria* (Figs 1, 4). Both species form a subclade in Clade D together with *S. jeanae* and *S. diemenensis*. From its closest relative, *S. propria*, this species differs by COI distances of ≥ 10.4%. From other species, *S. australis* differs by distances of ≥ 19% (Table S8). Within its range *S. australis* is found in sympatry with two congeners: For comparison with *S. obliquata* refer to comparative remarks under that species. *Siphonaria propria* has a slightly smaller shell with a more prominent siphonal ridge, posteriorly left offset apex, regular ribbing and a consistently internal tan to off white siphonal groove, as well as a smaller to inconspicuous AO and longer F1**.**

Some authors were uncertain of the identity of *S. australis*. Specimens figured in Hubendick (1946: pl. 3, figs 28–31) have been correctly identified as *S. australis*; however, the corresponding description (Hubendick 1946: 49) incorrectly includes specimens from Port Jackson [Sydney], Australia (likely *S. denticulata*). Hubendick (1946) incorrectly included Port Jackson and Norfolk Island in the distribution of this species. The radula description matches that of Hutton (1883: 124, pl. 17, figs E–G).

Distribution and habitat. Recorded from New Zealand, North and South Islands, Chatham, Stewart, and Snares Islands, between latitudes of 34° and 48° S) (Fig. 16). In this study found to be common in sheltered positions (e.g., crevices, vertical faces) on exposed to semi-exposed rocky intertidal shores across upper and mid littoral levels (see also Jenkins 1983: 14).

Siphonaria capensis Quoy & Gaimard, 1833
(Figs 17L–N, 18F–G)

Siphonaria capensis Quoy & Gaimard 1833: 331, pl. 25, figs 32–34 (type locality: Cap de Bonne-Espérance, baie de la Table [Table Bay, Cape of Good Hope, South Africa]).—Lamarck 1836: 561; Anton 1838: 26; Lamarck 1839: 206; Jay 1839: 39; Catlow & Reeve 1845: 100; Krauss 1848: 58; Dunker 1853: 3; H. Adams & A. Adams 1855 (in 1853–1858): 271; Hanley 1858b: 151; H. Adams & A. Adams 1863: 271; Paetel 1873: 117; 1883: 178; 1889: 429; Sowerby III 1892: 53; Bartsch 1915: 10; Turton 1932: 10; Hubendick 1947a: 163; Braga 1956: 7, pl. 1 fig. 1; Allanson 1963: 70; Galindo 1977: 416; Richards 1981: 79; Kilburn & Rippey 1982: 134, pl. 32, fig. 13; Villiers & Hodgson 1987: 129; Teske *et al.* 2007: 223, fig. 2; Pinchuck & Hodgson 2009: 371; Teske *et al.* 2011: 5026; White & Dayrat 2012: 61.

Siphonaria (*Patelliopsis*) *capensis*—Hubendick 1945: 70, fig. 20; 1946: 33, pl. 1, figs 40–42, pl. 2, figs 1–4; Allanson 1958: 150, 157, pl. 1, fig. 1; Chambers & McQuaid 1994a: 265, figs 1E, 3A; 1994b: 418; Chambers *et al.* 1996: 3; 1998: 51.

Siphonaria kowiensis Turton 1932: 10, pl. 4, 84 (type locality: Port Alfred, SA [South Africa]).—Allanson 1958: 166.

Siphonaria capensis var. *lineolata* Krauss 1848: 58, pl. 4, fig. 2 (type locality: Tafelbai [Table Bay, SA]); invalid, preoccupied by Sowerby I, 1835).—Sowerby III 1892: 54; Bartsch 1915: 10; Turton 1932: 10; Hubendick 1945: 19; 1947a: 163.

Siphonaria (*Patelliopsis*) *capensis* forma *kraussi* Hubendick 1946: 34, pl. 2, figs 1–4 (nom. nov. pro *S. lineolata* Krauss, 1848 not Sowerby I, 1835).—Allanson 1958: 159.

Pachysiphonaria capensis—Trew 1983: 2.

Siphonaria kraussi—White & Dayrat 2012: 59, 64.

Material examined. *Type material.* Lectotype of *Siphonaria capensis* Quoy & Gaimard, 1833, present designation, from 'Cap de Bonne-Espérance, baie de la Table' [Table Bay, Cape of Good Hope, South Africa] (MNHN IM 2000-38235 Fig. 17L); Seven paralectotypes, same data as lectotype (MNHN-IM-2000-5042).

Other, non-type material. **Mozambique:** Inhaca, Ponta do Farol, 25°58.2'S, 32°59.4'E MM6 (MNHN IM-2019-1477 p [M584], Fig. 17N; IM-2019-1481 p [M585], Fig. 17M).

Taxonomic remarks. The lectotype is designated herein for the stabilisation of the name and to ensure the unambiguous identity of this taxon (Art. 74.1 of the Code). Krauss (1848: 58) introduced *Siphonaria capensis var. lineolata*; however, this name is preoccupied by *S. lineolata* Sowerby I, 1835 (Hubendick 1946: 33; White & Dayrat, 2012: 65) and *S. lineolata* Orbigny, 1841 (White & Dayrat, 2012: 65). Hubendick (1946: 33) introduced *S. capensis* forma *kraussi* as a replacement name. The taxonomic status of this taxon remains uncertain, but it is synonymized herein because of Hubendick's treatment as an infrasubspecific taxon (forma). Hubendick (1946: 33) synonymized *S. jonasii* Dunker, 1846 (probably a juvenile), *S. placentula* Menke, 1853, and *S. venosa* Reeve, 1856 with *S. capensis*. He also attributed the record of '*S. pectinata*' by Martens (1874) to *S. capensis*.

Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (e.g., Fig. 17M-N) and geographic series of additional specimens (Tables S1–2). The taxonomic status of *S. placentula, S. oculus, S. venosa* and *S. jonasii* has not been assessed herein. Therefore, Hubendick's (1946) treatment of these taxa stands. Trew (1983: 2) incorrectly treated *S. capensis* as a synonym of *S. funiculata*.

Chambers & McQuaid (1994a, b) reported that *S. capensis* deposits benthic egg masses from which planktonic veliger larvae hatch.

External morphology (preserved). Animal yellowish/ cream. Irregular, widely spaced dark/black markings/spots along foot wall and cephalic lobes; genital pore conspicuous, located on foot wall posterior to right cephalic fold; mantle edge thick, large lobes.

Shell (Figs 17L–N; Table S9). Small to medium sized, ovate, thick, medium height (max sl mean = 23.1 mm, SD = 3.3 mm, n = 13), exterior grey/light brown, fairly even, apical sides convex, almost straight on posterior; apex offset to left and posterior, often eroded, protoconch direction undetermined, body whorl dextral, growth striae clear with faint external colour banding aligning with growth stages; primary ribs touching, raised fairly evenly spaced, straight, broaden to shell edge, ridges rounded to flat, rib count (mean = 42.6, SD = 5.8, n = 13), few to no secondary ribs; ribs project weakly beyond shell edge, siphonal ridge indistinct, weakly raised, formed by multiple ribs; rib interstices dark brown, weakly furrowed; shell edge weakly corrugated and scalloped. Interior glossy, edge and margin chocolate brown to black at shell edge with white /cream rays aligning under ribs, extending and narrowing from shell edge over margin to ADM scar, spatula pale blue/tan, siphonal groove apparent, same as interior colour, CMS straight.

Reproductive system (Fig. 18F; n = 3). Positioned within coelom under the respiratory cavity and intestine, over foot muscle, against right side of foot wall; epiphallic parts positioned over BM and between RAM; single conspicuous GP, opening from GA through foot wall posterior to right cephalic fold, junction of AO, GA and ED close distinct; AO large broad and flat, larger than GA, thicker than ED; GA bulbous proximal to ED and BD/CD junctions, ED relatively long and twisted; EG very large, broad, lobed, flagellum (F1) indistinct; BD and CD closely coupled, of similar length and thickness, connect in parallel close together into GA between ED and GP, BD without distal loop or MA; both ducts smooth, featureless, pass together partially through RAM connecting into soft curved folds of MG, CD wider and dorsal to BD; CD connects to small, bulbous, thin test BC, partially embedded into folds of MG; HD short thick, brown markings, coiled, links AG to elongated narrow yellowish granulated HD; HG larger than AG, MG and AG folded, soft white tissue; SV embedded on left side of AG.

Spermatophore (Fig. 18G). Very small, drop-like with short flagellum (length = 0.41 ± 0.037 mm, n = 3); head section bulbous, rounded (head length = 0.31 ± 0.04 mm, head ~76% of SPM length, head width = 230 ± 37 µm; flagellum width = 17 ± 0 µm, n = 3), body and flagellum test fur-like, opaque, tapering to a pointed end; both sections featureless; 4 SPM in brown gelatinous mass in one BC (MNHN IM-2019-1481 [M585]) embedded in white gelatinous mass.

Radula. Dentition formula: 42:1:42 (Hubendick 1946: 34).

Comparative remarks. Analyses of mtDNA sequences supported a sister relationship of *S. capensis* (unit 96) with unit 4 (= *S. pectinata* from Spain and Ghana + *S. naufragum* from Trinidad and Tabago; not reviewed herein, see Giribet & Kawauchi 2016). Distances between units 96 and 4 were ≥ 10.7% in COI (Table S8). We found two sympatric congeners in Mozambique: *Siphonaria carbo* has a darker shell with a more central apex and finer ribbing, an indistinct AO, larger, elongate BC and longer, larger SPM. *Siphonaria plana* has a smaller, paler shell with coarser ribbing and a flared siphonal ridge, smaller AO, twisted ED, BD with bursal and distal loops, a larger BC and a longer, thread-like SPM. For comparisons with South African siphonariids, such as *S. serrata* (Fischer, 1807), *S. concinna* Sowerby I, 1825, *S. oculus* Krauss, 1848 and *S. carbo* Hanley, 1858, which occur within the distributional range of *S. capensis*, refer to the studies of Allanson (1958), Chambers & McQuaid (1994a) and Teske *et al.* (2007, 2011).

The RS figured in Hubendick (1945: 18, fig. 20) closely resembles the RS of *S. capensis* figured herein (Fig. 18F) except for one detail in the junctions of the CD/BD/GP/GA, which Hubendick portrays as wider and with ducts more separated. Apart from the absence of an AO, the RS of *S. capensis* figured in Allanson (1958: 165, fig. 10) matches well the RS figured herein (Fig. 18F). Figured specimens of '*S. capensis'* and *'S. capensis* v. *kraussi'* in Hubendick (1946: pl. 1, figs 40–42 from Cape, South Africa; pl. 2, figs 1–4 from Port Natal, respectively) corresponds well with shells shown herein (Fig. 17L–N). Similarly, specimens figured in Krauss (1848: 58, pl. 4, fig. 2), Braga (1956: 7, pl. 1 fig. 1), Allanson (1958: 150, 157, pls 1a–b, 2a–b), Kilburn & Rippey (1982: 134, pl. 32, fig. 13) and Chambers & McQuaid (1994a: 256, figs1E, 3A) correspond well with typical features of this species.

Distribution and habitat. Endemic to SE coast of Africa (Fig. 28). During this study, collected on intertidal rocks in Baie de Maputo, Mozambique.

Siphonaria atra Quoy & Gaimard, 1833
(Figs 19A–F, M–P, T–U, 21)

Siphonaria atra Quoy & Gaimard 1833: 337, pl. 25, figs 41–42 (type locality: Vanikoro [Solomon Islands]).—Lamarck 1836: 560; 1839: 206; Reeve 1842: pl. 138, fig. 1; Catlow & Reeve 1845: 100; Reeve 1856: pl. 8, species 14; Jay 1850: 104; H. Adams & A. Adams 1855 (in 1853–58): 271; Hanley 1858b: 151; H. Adams & A. Adams 1863: 271; Paetel 1873: 117; 1875: 92; Brazier 1878: 134; Dunker 1882: 169; Paetel 1883: 178; 1889: 428; Hedley 1909: 369; Singleton 1937: 396; Adam & Leloup 1939: 9, pl. 2, fig. 3a,b, text-fig. 2a,b; Marcus & Marcus 1960: 109; Firth & Calaby 1974: 57; Galindo 1977: 416; Coles 1981: 11; Jenkins 1983: 29; Short & Potter 1987: 122, pl. 60, fig. 4; Wells & Bryce 1995: 113; 1996: 63; Bryce 1997: 55; White & Dayrat 2012: 61; Willan *et al.* 2015: 330.

Siphonaria albicante Quoy & Gaimard 1833: 335, pl. 25; figs 38, 40 (type locality: Île de Vanikoro [Solomon Islands] et celle de la Nouvelle-Irlande [New Ireland, PNG] au halve Carteret [Carteret Islands, PNG]).—Trew 1983: 4; White & Dayrat 2012: 60.

Siphonaria albicans Lamarck 1836: 560.—Lamarck 1839: 485; Catlow & Reeve 1845: 99; H. Adams & A. Adams 1855 (in 1853–1858): 271; Reeve 1856: pl. 2, species 9; Hanley 1858b: 151; Chenu 1859: 206, figs 3577, 3578; H. Adams & A. Adams 1863: Paetel 1873: 117; 1875: 92; 1883: 178; 1889: 427; Galindo 1977: 416 (invalid; incorrect subsequent spelling of *S. albicante*).

Siphonaria sipho—Brazier 1878: 135 (not *S. sipho* Sowerby I, 1823).

Liphonaria siquijorensis Brazier 1878: 135 (invalid; incorrect subsequent spelling; not *S. siquijorensis* Reeve, 1856).

Mestosiphon eumelas Iredale 1940: 439, figs 5–6 (type locality: Snapper Island, North Queensland [Australia]).—Short & Potter 1987: 122; White & Dayrat 2012: 63.

Triellsiphon acervus Iredale 1940: 439, figs 22–23 (type locality: Canala, NC [France]).—White & Dayrat 2012: 60.

Siphonaria (*Siphonaria*) *eumelas*—Hubendick 1946: 52; 1955: 3.

Siphonaria (*Siphonaria*) *savignyi*—Hubendick 1955: 2 (not *S. savignyi* Krauss, 1848).

Siphonaria '*atra* group, unit 41'—Dayrat *et al.* 2014: 264, figs 5 V-X (in part).

Material examined. *Type material*. Lectotype of *Siphonaria atra* Quoy & Gaimard, 1833, present designation, from l'ile de Vanikoro [Vanikoro Island, Solomon Is]; coll. Expédition Durville, 1826 (MNHN IM-2000-35950, Fig. 19A). Two paralectotypes, same data as lectotype (MNHN IM-2000-5034).

Lectotype of *Siphonaria albicante* Quoy and Gaimard, 1833, present designation, from l'ile de Vanikoro et celle de la Nouvelle Iriande, au havre Carteret [Vanikoro Island, Solomon Is and New Ireland, PNG, at Carteret Harbour; thought to be Carteret Islands, PNG] (MNHN IM 2000-38234, Fig. 19M). Paralectotype, same data as lectotype (MNHN IM 2000-5026, Fig. 19N).

Holotype of *Triellsiphon acervus* Iredale, 1940 from Canala, NC; coll. 1928. (AM C.103716, Fig. 19D). Fifteen probable paratypes (AM C.140260), same data as holotype.

Probable holotype of *Mestosiphon eumelas* Iredale, 1940 from Snapper Island, [near Port Douglas], N Qld [Australia]; coll. 1928 (AM C.103711, Fig. 19C). Fifteen probable paratypes (AM C.140260), same data as probable holotype.

Other, non-type material. **Solomon Islands:** Santa Cruz Ids, Vanikoro off Sunday Reef, 11°42'S, 166°50'E (AM C.52095 d). **NC:** Tiari, 20°15.692'S, 164°24.664'E NC04-3 (AM C.585008 p [M361]); S of Pouebo, 20°25.950'S, 164°39.251'E NC04-2 (AM C.585005 p [M383]); Hienghène, 20°41.210'S, 164°59.108'E NC04-1 (AM C.585003 p [M391, SK173], C.585004 p [M392]); Ponerihouen, 21°05.644'S, 165°26.646'E NC03-1 (AM C.584977 p [SK059], C.584978 p [SK155], C.584980 p [M354], C.584981 p [M356], C.584982 p [M359] C.584983 p [M405, SK072], C.585329 p [SK040]); Poindimie, 21°55.901'S, 165°19.672'E NC03-2 (AM C.585967 20+p, C.584993 p [M351]); Ouassé nr Canala, 21°30.346'S, 166°03.732'E NC02-1 (AM C.585377 10+p, C.584973 p [M373], C.584974 p [M374], C.584975 p [M376], M378, C.584976 p [M411]; Bonhomme de Bourail, La Roche Percee, 20°36.487'S, 165°27.423'E NC06-3 (AM C.585011 p [M369]); Presqu'ile de Ouano La Foa, 20°51.434'S, 165°48.479'E NC06-4 (AM C.595912 8p); Port Quenghi nr marina, 21°54.405'S, 166°03.880'E NC07-1 (AM C.585018 p [M379], C.585019 p [M380]). **PNG:** New Ireland, Channel betw. Manne I. and New Ireland mainland, 02°43'S, 150°43.1'E (MNHN IM-2013-55761 p [M531], IM-2013-55762 p [M538], IM-2013-55763 p [M529], IM-2013-55764 p [M535]; Biliau I., 05°11.8'S, 145°48.2'E PM38 (MNHN IM-2013-15193 p [M559]). **Australia, Qld:** Somerset Bay, Cape York, 10°44.310'S, 142°35.637'E, Q47-2 (AM C.585177d [R12001]); Capt Billy Landing, 11°38.019'S, 142°51.472'E, Q46-1 (AM C.584791 p [M006, SK250]); Lizard Is, 14°40.908'S, 145°27.007'E; Q40-1 (AM C.584801 4p); Q40-5 (AM C.585166 p [SK218]); Cape Kimberley, 16°16.535'S, 145°28.737'E, Q35-1 (AM C.585412 10+p, C.585167 p [M454, SK178], C.585503 p [SK179]); Low Isles, 16°23.085'S, 145°33.596'E, Q34-1 (AM C.585704 4p, C.585160 p [M132], C.585873 p [M136]); Port Douglas, 16°28.697'S, 145°27.859'E, Q33-2 (AM C.585158 p [M134]); Red Cliff Pt, N of Cairns, 16°41.294'S, 145°35.080'E, Q33-3 (AM C.595969 3p); Gribble Pt Mission Bay Yarrabah, 16°53.781'S, 145°51.852'E, Q32-1 (AM C.585504 2p); Mourilyan Harbour, 17°35.951'S, 146°07.583'E, Q29-1 (AM C.585410 8p, C.585534 5p, C.585151 p [M004], C.585152 p [M401], C.585153 p [SK124], C.585154 p [SK217]); Horseshoe Bay Magnetic Is, 19°06.755'S, 146°51.875'E, Q27-2 (AM C.585345, p); Picnic Bay Magnetic Is, 19°10.757'S, 146°50.555'E, Q27-3 (AM C.585563 9p, C.595970 2p); Mackay breakwater wall, 21°06.415'S, 149°14.033'E, Q14-2 (AM C.585502 p; C.585639, 5p); Wreck Pt Yeppoon, 23°08.736'S, 150°45.865'E, Q08-4 (AM C.585562 3p, C.585132 p [M080]); Bagara Hervey Bay, 24°49.180'S, 152°28.011'E, Q06-1 (AM C.585699 8p); Drury Pt Scarborough, 27°12.255'S, 153°07.022'E, Q03-7 (AM C.585685 7p). **NT:** S Turtle Beach 12°18.852'S, 136°55.959'E NT04-2 (AM C.585666 6p, C.585073 p [M013], C.585074 p [M096]; Cape Wirawawoi Nhulunbuy, 12°09.513'S, 136°46.904'E NT05-A (AM C.585593 4p); Smith Pt, 11°07.360'S, 132°08.134'E NT21-2 (AM C.585667 6p); Nightcliff Darwin, 12°22.836'S, 130°50.402'E NT23-1 (AM C.585088 d). **WA:** Tait Point 1 Mission Bay, 14°05.442'S, 126°41.143'E, WA04-1 (AM C.584716 5p; WAM S74089 5p); Walsh Point, 14°33.998'S, 125°51.060'E, WA13-1 (AM C.584697 3p; WAM S74090 3p); Caffarelli Is, 16°01.991'S, 123°18.625'E, WA19-1 (AM C.584717 5+p, C.585012 p [SK034], WAM S74092 5p); Conilurus Is, 16°08.872'S, 123°35.205'E, WA18-2 (AM C.584721 5p, WAM S74091 4p); Catamaran Bay formal, 16°27.622'S, 123°00.242'E, WA22-3 (AM C.584703 4p, WAM S74094 3p); Catamaran Bay, 16°27.622'S, 123°00.242'E, WA22-1 (AM C.584737 27p, C.585300 p [SK189], WAM S74093 5p); Gantheaume Point, 17°58.384'S, 122°10.677'E, WA26-2 (AM C.584718 5p; WAM S74095 5p).

Taxonomic remarks. The largest syntype is herein designated as the lectotype of *Siphonaria atra* (MNHN IM-2000-35950) to ensure an unambiguous identity of this species and for the stabilisation of the name (Art. 74.1 of the Code). While topotypic specimens from Vanikoro are currently unavailable, the identity of *S. atra* (Fig. 19B) and its junior synonyms *Triellsiphon acervus* (Fig. 19F) and *S. albicante* (Fig. 19O) are each established based on the examination of specimens from NC that closely match the types. Furthermore, our delineation of this species is also based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes of *M. eumelas* (Fig. 19P) and *Triellsiphon acervus* (Fig. 19E) as well as geographic series of additional specimens (Table S1).

The shells figured as '*Siphonaria atra*' by Reeve (1856: pl. 3, fig. 14) exhibit a mixture of features typical for two species, *S. sirius* and *S. atra*. The description in Reeve mentioned features characteristic of *S. sirius* (i.e., shell pattern and single siphonal rib) but not *S. atra*. Furthermore, the initial two locations listed in Reeve (1956) are within the known distribution of *S. sirius* and well outside the known distribution of *S. atra*. Only Vanikoro, the type locality, is within the range of *S. atra*. Reeve (1956) incorrectly treated *S. coreensis* as a synonym of *S. atra*.

In several cases, the details of type locality in the original designations of Iredale (1940), differed from what appeared on the specimen labels. Iredale (1940: 438) specified 'type' in the original descriptions for *T. acervus* and *M. eumelas.* The figured specimens of *T. acervus* (Iredale, 1940: pl. 34, figs 22–23; Fig. 19D herein) and *M. eumelas* (pl. 34, figs 5–6; Fig. 19C herein) are considered as probable holotypes. Hubendick (1946: 50) listed amongst a number 'transitional' forms in an 'Indian-West Pacific form-group' a '*S. zanda* <> *S. atra*' form. The figured specimen (Hubendick 1946: 50, pl. 5, figs 3–4) is as a specimen of *S. atra*. Overall, it appears that the interpretation of *S. atra* in Hubendick (1946: 52) is uncertain. The specimens assigned to this species by him were from Mindanao, the Java Sea, and Osagawara [= Ryukyu, Japan] (Hubendick 1946: pl. 4, figs 5–7). None of these localities are within the known distribution of *S. atra* (Fig. 16) and therefore these are likely specimens of *S. alba* and *S. subatra*, respectively. Similarly, '*S. atra*' recorded from Nagasaki in Lischke (1871: 105) and from Okinawa in Kuroda (1960: 43) are likely *S. subatra.* A record of '*S. albicans*' in Hutton (1880: 36) from NZ is likely based on a misidentification of *S. australis*.

Mestosiphon eumelas has been synonymized with *S. atra* by Hubendick (1946: 52, 1955: 128), which is followed herein. Cernohorsky (1972: 210) also treated *M. eumelas* a synonym of *S. atra*; however, his figure of '*S. atra*' (pl. 60, fig. 1, Naviti Is, Fiji) shows a specimen of *S. vudaensis* **sp. nov.** Morrison (1972: 56–58) treated *S. atra* as a synonym of *S. laciniosa* based on similarity in the shell and for a 'common reproductive development'. This synonymy is rejected herein based on examination of type specimens and comparative morpho-anatomy. The unfigured records of '*S. atra*' in Chambers (1980: 141, 143), Christiaens (1980a: 78) and Chambers, McQuaid & Kirby (1998: 51) from Hong Kong are here attributed to either *S. alba* or *S. sirius*.

External morphology (Fig. 19U). Foot sole, foot wall, foot edge, cephalic folds and pneumostomal lobe evenly cream; mantle thick translucent in larger specimens, thin in smaller specimens, edge thickened, whitish, lobed, with very light black pigmentation at mantle edge aligning with large primary rib interstices; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two centrally touching, centrally black pigmented cephalic folds; pneumostomal lobe long, under the mantle, unpigmented, behind right cephalic fold.

Shell (Figs 19A–F, M–P, T; Table S9). Shell morphology displays wide intraspecific variability, medium sized (max sl mean = 21.7 mm, SD = 3.3 mm, n = 23), ovate; height low to medium; apex offset sightly posterior and central, apical sides convex, protoconch direction homostrophic (n = 3) shell whorl dextral; growth striae prominent in bands, shell thickness thick; exterior uneven, dark purple brown to pale tan, radial colour banding often present, protoconch area pale, central band darker and shell edge dark brown; rib count (mean = 49, SD = 6, n = 23), primary rib ridges pale, ribs fairly straight, increasingly raised and strongly protrude beyond shell lip (often > 1mm) to unevenly scallop and corrugate the edge; siphonal ridge often greatest protrusion, formed by paired primary ribs; 1–2 finer interspersed secondary ribs between primary, rib interstices darker. Interior shell margin dark chocolate brown to white, white rays on shell margin aligned under primary/secondary ribs dark chocolate brown to white, siphonal groove distinct, often same colour as shell margin, white forms with fringing dark brown markings; spatula dark chocolate brown to golden brown even whitish; ADM scar distinct, CMS straight, darker than shell lip; thickening of shell lip common, overcoats brown markings on shell margin with white, infills and reduces lip scalloping, and often spatula becomes whitened.

Reproductive system (Fig. 21; n = 19). HG/AG/MG complex positioned within right side of coelom, against foot wall over foot muscle, under the respiratory cavity; epiphallic parts positioned between BM and RAM; GA small, with singular GP through foot wall; AO large, broad, bluntly pointed, joined to upper GA; ED short, broad, centrally slightly bent, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG large, longer than ED, soft whitish tissue, folded, joins ED; single very broad flagellum (F1), similar length and width to ED, appears as an extension of ED. BD and CD connect side-by-side into GA between ED join and GP, both ducts short, straight, smooth, thickened, whitish, featureless, pass closely together through RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex relatively large; CD connecting to ducts, BC embedded in folds of AG/MG complex close to embedded blackish SV; BD with short distal twisted loop, similar thickness but longer than CD; BC relatively small, bulbous, thin whitish translucent test, HD short, wide, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobbed; AG usually larger than HG; genital pore inconspicuous, located on foot wall posterior to right cephalic fold.

Spermatophore (Figs 21C, G). Over half of length comprises a translucent cylindrical head section, tip bluntly rounded, central white core; flagellum very thin, transparent, tapering to a thread-like end; both sections smooth, featureless; test thin, translucent (head length = 10.58 ± 1.73 mm; head width = 188 ± 44 µm n = 2; flagellum width = 33 µm, n =1), possibly longer as flagellum appears incomplete); very short taper region into the filamentous transparent flagellum; three and 5 SPMs respectively tightly coiled and embedded in brown gelatinous mass in BC of 2 specimens [M391, M380].

Radula. Dentition formula: 35:1:35 (Hubendick 1946: 52).

Comparative remarks. *Siphonaria atra* (*atra* group, unit 41) forms a clade with unit 40 (*S. hienghenensis* **sp. nov.** + unidentified species from PNG and Qld) and *S. alba* (unit 39) (Figs 1, 2). It differs from these two units by COI distances of ≥ 11.1% (*S. hienghenensis* **sp. nov.**) and ≥ 8.3% (*S. alba*) (Table S3). The maximum distance among sequences in unit 41 (= *S. atra*) is 12.8% (Tabe S2). This is the highest intraspecific genetic divergence observed among all *Siphonaria* species examined herein. This exceptionally high divergence can partly be attributed to a single GenBank sequence from PNG (UF 332973), which is considered to likely represent a separate, unidentified species. When this sequence is excluded from *S. atra*, the maximum COI distance within unit 41 is 9%.

Siphonaria alba is indeed morphologically similar; however, it has a shell with a slightly less scalloped edge, a longer ED, larger BC, and longer SPM. Both species occur in sympatry in Timor-Leste and Western Australia. *Siphonaria hienghenensis* **sp. nov.** has a paler, grey-brown shell with a weaker scalloped edge, and a smaller AO. Both species are found in sympatry in New Caledonia. Throughout the range of *S. atra* we found twenty-two congeners within partly sympatric distributions. Eight congeners are sympatric with *S. atra* in NC: *Siphonaria namukaensis* **sp. nov.** has a smaller, paler, slightly taller shell with a weaker scalloped edge, a broader ED, and a longer SPM. *Siphonaria normalis* has a smaller, paler shell with a less prominent siphonal ridge and a weaker scalloped edge, a smaller AO and larger BC. *Siphonaria ouasseensis* **sp. nov.** has a smaller more evenly ribbed shell with a stronger offset apex, weaker scalloped edge, and a smaller AO. *Siphonaria caledonica* **sp. nov.** has a smaller shell with a greater offset apex and weaker scalloped edge, a longer ED, and longer SPM. *Siphonaria bourailensis* **sp. nov.** has a smaller shell with a greater offset apex and weaker scalloped edge, and a shorter F1. *Siphonaria poindimiensis* **sp. nov.** has a smaller, taller, and darker shell with external patterning, a larger, broader ED, and a longer SPM. *Siphonaria viridis* has a smaller, taller, and darker shell with external patterning, a larger, broader ED, and longer SPM.

Ten congeners are sympatric with *S. atra* in tropical Qld, NT and WA, Australia (along with *S. normalis* and *S. viridis*). *Siphonaria costellata* **sp. nov.** has a shell with a greater offset apex, weaker scalloped edge, a smaller AO, longer BC, and shorter BD. *Siphonaria denticulata* has a larger, paler, taller shell with narrower ribbing and without a scalloped edge, a smaller AO, and longer SPM. *Siphonaria gemina* **sp. nov.** has a smaller, paler shell with a weaker scalloped edge, a smaller AO, and a shorter BD. *Siphonaria jiigurruensis* **sp. nov.** has a smaller, taller shell with a greater offset apex, patterned exterior, a longer, broader ED, more bulbous AO, and a longer SPM. *Siphonaria oblia* has a far smaller, fragile and taller shell with a well offset apex, weaker scalloped edge, a longer, wider ED and smaller F1 (Jenkins, 2018: 278, figs 3C–D). *Siphonaria opposita* has a lower shell with paler interior, weaker scalloped edge, a larger BC, and longer ED and BD with bursal loop. *Siphonaria restis* **sp. nov.** has paler, taller shell with raised and uneven ribbing, a weaker scalloped edge, a smaller AO, longer ED and larger BC. *Siphonaria scabra* has a paler, taller shell with a weaker scalloped edge, a smaller AO, longer ED and larger BC. *Siphonaria zelandica* has a smaller, lower, thinner, paler shell with a weaker scalloped edge, a smaller AO, without distal loop on BD, and a shorter drop-like SPM. *Siphonaria forticosta* **sp. nov.**, along with *S. alba*, is sympatric in TL. It has a paler shell with weaker splayed siphonal ridge, a smaller AO, and larger BC. For a comparison with *S. javanica* found in sympatry in PNG refer to comparative remarks under that species.

Wide intraspecific variability occurs in shell morphology of *S. atra* (particularly characteristics of shell thickness, ribbing and interior colouration) irrespective of shell size or geographical distribution. Variability in shell morphology ranges from a dark (i.e., *S atra, S. eumelas*) to pale (i.e., *S. albicante, T. acervus*) forms. The RS anatomy of both forms is consistent, however (Figs 21A, F dark shell form, Fig. 21B, pale shell form).

Shell geometry, sculpture and colouration of *S. atra* resemble those of 13 other species in the *atra* group in the IWP region; *S. subatra* (unit **38**), co-occurring *S. forticosta* **sp. nov.** (unit **71**), *S. hienghenensis* **sp. nov.** (unit **40**) and *S. bifurcata* (unit **45**), *S. denticulata* (unit **33**), *S. scabra* (unit **50**), *S. pravitas* **sp. nov.** (unit **51**), *S. crenata* (unit **43**), *S. tenebrae* **sp. nov.** (unit **96**), *S. vudaensis* **sp. nov.** (unit **37**), *S. alba* (unit **39**) and *S. sirius* (unit **31**). However, all these species exhibit differences in the structure of RSs, some have finer shell features and all of them are genetically well-differentiated. Figured specimens of '*S. atra'* in Adam & Leloup (1939: 9, pl. 2, figs 3a, b) match the shell size, sculpture, and ribbing of *S. atra,* and align with its distributional range and radula dentition count (p. 10, text fig. 2a, b). Figured specimens of '*S.* (*S.*) *atra*' in Hubendick (1946: 91, pl. 4, fig. 5–7) from Mindanao are likely specimens of *S. alba*, not of *S. sirius* (with a single siphonal rib) or *S. atra* (with narrower, less protruding primary ribbing). A shell figured as *S. atra* in Tan & Chou (2000: fig. 117) corresponds with features of *S. alba* (i.e., shell exterior ribbing, interior colouration). Records of '*S. atra*' in Habe (1962: 96, pl. 44, fig. 17; 1964: 145, pl. 44, fig. 17) from Honshu, subsequently referenced also by Maes (1967: 119) are likely misidentifications of *S. subatra*. We could not confirm any records of *S. atra* from Japan or the Philippines. The records of '*S. atra*' in Maes (1967: 119) and Wells (1994: 18) are here attributed to *S. alba*. Way & Purchon (1981: 321) recorded '*S. atra*' from West Malaysia and Singapore, and Tan & Low (2014: 267) recorded '*S. atra*' from CKI, however, we are unable to confirm the occurrence of *S. atra* in these regions. Figured specimens of the '*atra* group, unit 41' in Dayrat *et al.* (2014) from Lizard Island (fig. 5W) and PNG (fig. 5X) are morphologically consistent with *S. atra.*

Distribution and habitat. Recorded from throughout

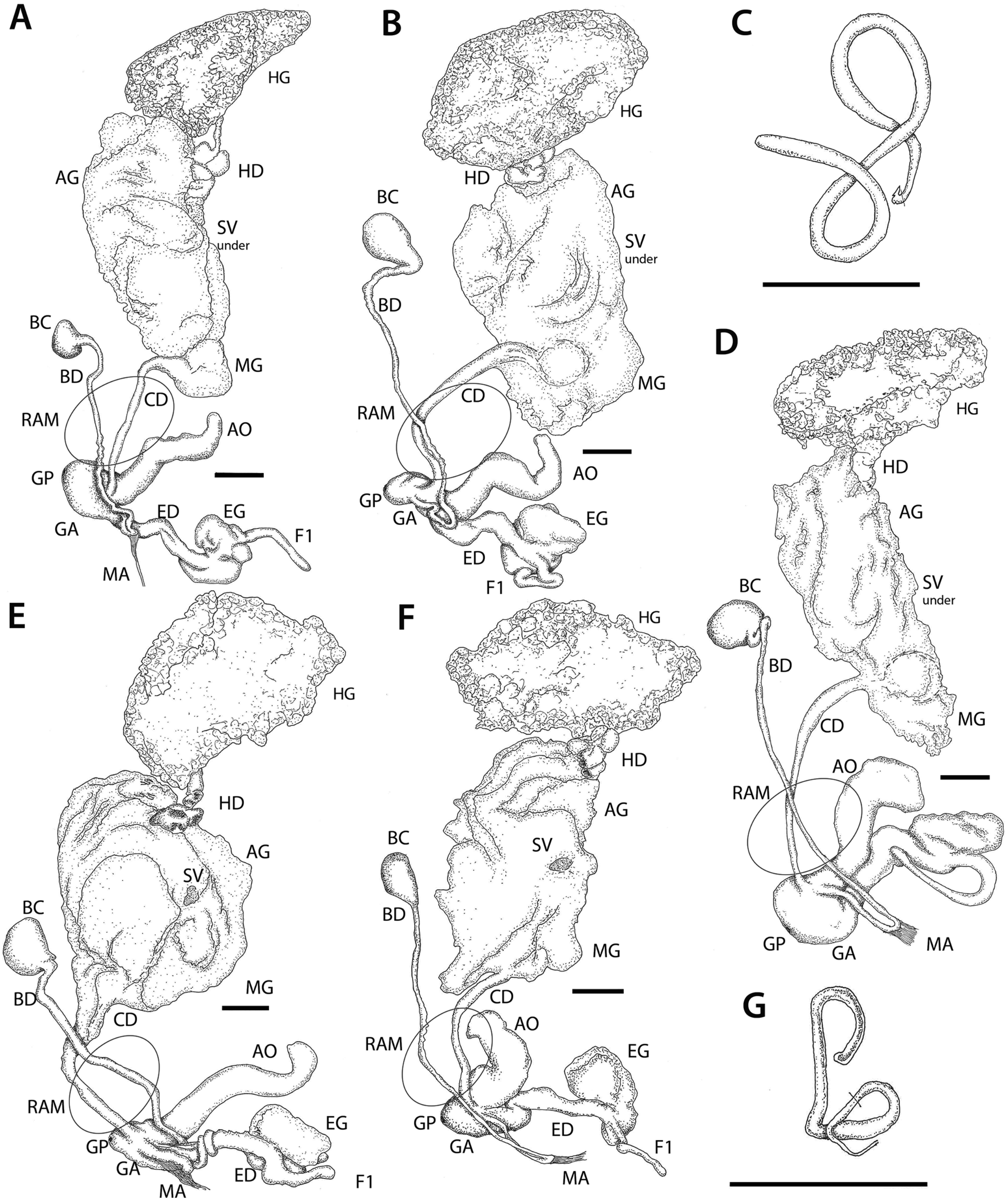

FIGURE 21. Reproductive morphology of *S. atra*. **A.** NC, La Roche Percee, AM C.585011, dark shell form [SK174]. **B–C.** NC, Ponerihouen, AM C.584978, pale shell form [SK155]. **D.** Qld, Cape Kimberley, TS of *M. eumelas* AM C.585167 [M454, SK178]. **E.** WA, Caffarelli Is, AM C.585012 [SK034]. **F–G.** NC, Hienghène, AM C.585003, dark shell form [M391, SK173]. Unlabelled scale bars = 1 mm.

large parts of Tropical IWP including Santa Cruz Islands, American Samoa, Solomons Islands, NC, PNG, northern Australia (Cape York Peninsula through to Kimberley, WA), and Timor-Leste (Fig. 16). In this study found to be common on exposed rocky shores across upper littoral levels (Fig. 19Q).

Siphonaria denticulata **Quoy & Gaimard, 1833**
(Figs 19G–L, R, 20D–H)

Siphonaria denticulata Quoy & Gaimard 1833: 340, pl. 25; figs 19–20 (type locality: Nouvelle-Hollande, port Western [Western Port, French Island, Vic, Australia]).—Lamarck 1836: 559, 1839: 206; Reeve 1842: pl. 138, fig. 2; Catlow & Reeve 1845: 100; Menke 1852: 38; H. Adams & A. Adams, 1855 (in 1853–58): 271; Reeve 1856 pl. 1, species 4; Hanley 1858b: 151; H. Adams & A. Adams 1863: 271; Angas, 1867: 232; Paetel 1873: 117; 1875: 92; Tenison Woods 1878b: 99; Paetel 1883: 178; Etheridge 1887: 29; Henn & Brazier 1894: 178; Brazier 1889; 25; Paetel 1889: 428; Whitelegge 1889: 117; Adcock 1893: 11; Hedley 1909; 369; 1918: M96; McAlpine 1952: 41; Ewers 1961; Galindo 1977: 416; Crease 1980: 38; Jenkins 1981: 2; Hochlowski *et al.*1983: 7413; Quinn 1983: 81; Trew 1983: 2; Jenkins 1983: 29; 1984: 113; Hochlowski & Faulkner 1984: 3839; Short & Potter 1987: 122, pl. 60, fig. 3; Jansen 1995: 89; Davey 1998: 118, text-fig.; Grove *et al.* 2006: 60; White & Dayrat 2012: 62; Colgan & da Costa 2013: 74.

Siphonaria denticula Anton 1838: 26 (invalid; incorrect subsequent spelling of *S. denticulata*).

Siphonaria atra—Angas 1867: 233; Whitelegge 1889: 117.

Siphonaria cochlearformis Whitelegge 1889: 117; Hedley 1918: M96 (invalid; incorrect subsequent spelling, not *S. cochleariformis* Reeve, 1856).

Ellsiphon marza Iredale 1940: 438 pl. 34, figs 1, 2 (type locality: Keppel Bay, Queensland).—McAlpine 1952: 42; White & Dayrat 2012: 57, 60, 63.

Siphonaria scabra—Iredale 1940: 438 (not *S. scabra* Reeve, 1856).

Siphonaria marza—Hubendick 1946: 61, pl. 5, fig. 27, 28; Galindo 1977: 416.

Siphonaria (*Ductosiphonaria*) *diemenensis* var. *denticulata*—Hubendick 1946: 38, pl. 2 fig. 17.

Ellsiphon denticulatus—McAlpine 1952: 41, fig. 1; Iredale & McMichael 1962: 82.

Siphonaria (*Siphonaria*) *currumbinensis* Hubendick 1955: 126–136, figs 4–8, pl. 1, figs 1–6 (type locality: Currumbin, Qld, Australia).—White & Dayrat 2012: 62, 70.

Ductosiphonaria denticulata—Cotton 1959: 411.

Siphonaria alternicosta—Cotton 1959: 411 (not *S. alternicosta* Potiez & Michaud, 1838).

Siphonaria ‘*atra* group, unit 33’—Dayrat *et al.* 2014: 264, fig. 5 J (not *S. atra* Quoy & Gaimard, 1833).

Material examined. *Type material.* Lectotype of *Siphonaria denticulata* Quoy & Gaimard, 1833, present designation, from ‘partie sud de la Nouvelle-Hollande, au port Western, et probablement aussi au port du Roi-Georges’ [southern part of Australia, at Western Port, Vic, Australia, and probably also at King George Harbour; see comments below] (MNHN IM 2000-35951, Fig. 19G). Two paralectotypes, same data as lectotype (MNHN IM 2000-5062).

Probable holotype of *Ellsiphon marza* Iredale, 1940 from Keppel Bay [Qld, Australia]; coll. H. Bernhard, 1940 (AM C.103715, Fig. 19K). Probable paratypes of *Ellsiphon marza* Iredale, 1940. Similar data to holotype label (refer Taxonomic remarks) (MV F13843, 3 d); Tampian Heads, Yeppoon, Keppel Bay; coll. H. Bernhard Dec 1938 (AM C.58529, 26 d); Four probable paratypes; coll. 1940 (AM C.106867).

Holotype of *Siphonaria currumbinensis* Hubendick, 1955 from Currumbin [28°07.83′S, 153°29.98’E, Qld, Australia]; coll. R. Endean & R. Kenny, 20-6-1952 (MV F15562, Fig. 19I). Probable paratypes, same data as holotype (MV F13953, 2 d, 3 p; MV F13948, 2 d, 3 p).

Other, non-type material. **Australia; Qld:** Wreck Pt Yeppoon, 23°08.736’S, 150°45.865’E, Q08-4 (AM C.585471 3p, C.584743 p [SK030 protoconch B7 jaw], C.585133 p [M081], C.585134 p [SK073]); Double Head Yeppoon, 23°09.908’S, 150°47.638’E, Q08-3 (AM C.585561 3p); Bagara Hervey Bay, 24°49.180’S, 152°28.011’E, Q06-1 (AM C.585961 p); Alexandra Mooloolaba, 26°40.342’S, 153°06.822’E, Q04-1 (AM C.585383 10p); Nth Reef Scarborough, 27°11.432’S, 153°06.755’E, Q03-5 (AM C.585560 4p); Drury Pt Scarborough, 27°11.836’S, 153°06.955’E, Q03-7 (AM C.585408 10+p); Scarborough Pt Scarborough, 27°12.168’S, 153°06.980’E, Q03-8 (AM C.585638 5p); Currumbin Point, 28°07.523’S, 153°29.203’E, Q02-2 (AM C.585536 20+p, C.585122 p [M073], C.585123 p [M074], C.585124 p [M183], C.585125 p [M184]). **NSW:** Brunswick Heads, 28°32.297’S, 153°33.444’E, NSW12-1 (AM C.585480 16p, C.585066 p [M077], C.585067 p [M079]); Evans River at South Evans Head, 29°6.82’S, 153°25.93’E (AM C.339263 p); Wooli Wooli River at Wooli, 29°53.27’S, 153°15.98’E (AM C.339285 4p; AM C.339287 2p); Redbank (Corindi) River at Red Rock, 29°59.03’S, 153°13.55’E (AM C.339288 3p); Urunga mangroves on S side of town just beyond footbridge ,30°29.92’S, 153°1.16’E (AM C.355024 8p); Camden Haven Inlet, 31°38.37’S, 152°49.63’E (AM C.339289 p); Fingal Bay nr Port Stephens, 32°44.087’S, 152°10.402’E, NSW09-2 (AM C.585683 7p), 32°44.990’S, 152°10.481’E, NSW09-1 (AM C.585065 p [M151]); Bolton Point Lake Macquarie, 33°0.389’S, 151°36.889’E, NSW08-3 (AM C.585737 2p, C.585058 p [M452]; C.585059 p [M453]); Bateau Bay Beach, 33°23.003’S, 151°29.197’E, NSW08-6 (AM C.595940 p [SK520]); Crackneck, Bateau Bay, 33°23.316’S, 151°29.139’E, NSW08-5 (AM C.585063 p [SK295], C.585064 p [SK296]); Broken Head Terrigal, 33°26.796’S, 151°27.030’E, NSW08-1 (AM C.585528 20+p, C.585050 p [M001]); Terrigal The Skillion, 33°27.008’S, 151°27.122’E, NSW08-2 (AM C.585558 3p, C.585053 p [M226], C.585054 p [M225]); Brisbane, WAter, 33°29.82’S, 151°18.18’E (AM C.355025 8p); Fairlight Sydney Harbour, 33°47.971’S, 151°15.990’E, NSW06-4 (AM C.585590 4p); Fairlight, North Harbour, 33°47.986’S, 151°16.837’E, NSW06-1 (AM C.585589 6p); 100m NW of Spit Bridge, Port Jackson, 33°48.210’S, 151°14.664’E (AM C.546770 2p); Spit Bridge, Port Jackson, 33°48.270’S, 151°14.520’E (AM C.546768 p); Wy-ar-gine Point Balmoral, 33°49.159’S, 151°15.195’E, NSW06-5 (AM C.585476 17p, C.585043 p [M158], C.585044 p [M159], C.585045 p [M160], C.585046 p [M161], C.595923 p [SK031]); Laings Point Sydney Harbour, 33°50.419’S, 151°16.638’E, NSW06-3 (AM C.585589 5p, C.585034 p [M193], C.585041 p [M165], C.585042 p [M167]); Bombo Kiama 34°39.232’S, 150°51.649’E, NSW03-1 (AM C.585403 10+p, C.585333 p [SK043]); Murunna Point Camel Head, 36°22.720’S, 150°04.766’E, NSW02-1 (AM C.585401 10+p). **Victoria:** Bastion Head Mallacoota, 37°34.429’S, 149°45.927’E, V09-1 (AM C.585787 5p, C.585294 p [M194], C.585295 p [M195]); Cape Conran, 37°48.798'S, 148°43.608'E, V08-2 (AM C.585292 p [M197]). **Tas:** T01-1 S of Granite Point Bridport, 40°59.739'S, 147°23.468'E (AM C.584834p [M173]).

Taxonomic remarks. The largest syntype with the clearest external sculpture (Fig. 19G) is herein designated as the lectotype of *S. denticulata* for the stabilisation of the name and to ensure the unambiguous identity of this taxon (Art. 74.1 of the Code). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes of *S. denticulata* (AM C.585303 [SK043], C.585044 [M159], C.585053 [M226]), Fig. 19H), *Ellsiphon marza* (AM C.584743 [SK030], C.585133 [M081], Fig. 19L) and *S. currumbinensis* (AM C.585123 [M074], Fig. 19J) and geographic series of additional specimens (Table S1). Quoy & Gaimard's (1833: 340) statement 'probably also at King George Harbour' is not considered as part of the type locality. While there is also a King George Harbour in Tas, the King George Harbour referred to by Quoy & Gaimard (1833) is probably that near Albany, WA. However, we have not found this species in WA. The type locality for *E. marza* is Keppel Bay and Caloundra as stated in the original description, yet some paratypes are from additional sites (Tampian Heads and Yeppoon). Noosa, Qld is mentioned by Hubendick as a site for '*S. currumbinensis*' The locality on the holotype label (MV F15562) is misspelled as Corrumbin (sic Currumbin) and the name is misspelled as *S. corrumbinensis*. Hutton (1873: 55) stated that *S. denticulata* and *S. diemenensis* occur in NZ; however, this is likely based on misidentifications of *S. australis* and/or *S. propria*.

External morphology (Fig. 19R). Foot sole smooth, evenly pale yellow grey; foot wall pale yellow grey with evenly spread white subepithelial pustules becoming more vivid and dense around pneumostomal lobe; foot wall shows black blotches; fringing mantle translucent, covers shell mantle, outer edge lobed, thickened, with black pigmented blotches aligning with rib interstices; pneumostomal lobe within mantle between the right ADMs, closes the pneumostomal and anal openings at the mantle edge; two small black epithelial eye spots centralised on two thick brownish yellow centrally touching cephalic folds; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold.

Shell (Figs 19G–L; Table S9). Medium to large sized (max sl mean = 24.46 mm, SD = 2.04 mm, n = 20), ovate; height medium; apex offset sightly posterior and central (usually eroded), apical sides strongly convex, protoconch direction undetermined, shell whorl dextral; growth striae prominent in bands, shell thickness thick; rib count (mean = 42.6, SD = 4.5, n = 20), primary ribs pale white, fairly straight, increasingly raised and protrude beyond shell lip to unevenly scallop and corrugate the edge; 1–2 interspersed pale white finer secondary ribs, rib interstices darker; paired primary ribs on siphonal ridge, no more prominent than other primary ribs. Interior shell margin dark brown to tan, white rays align on shell margin under primary/secondary ribs, siphonal groove distinct, same colour as shell edge, points to right anterior; spatula dark chocolate brown to mottled tan even whitish; ADM scar distinct, CMS straight, paler than shell lip; thickening of shell lip translucent, infills and reduces lip scalloping, spatula becomes whitened. The shells of *S. denticulata, S. scabra, S. pravitas* **sp. nov.** and *S. diemenensis* may appear similar and may be misidentified; external ribbing is similar. Differences exist in the sharpness and intensity of primary ribs and rib interstice colouration. In addition, the spatula colouration differs; *S. denticulata* and *S. scabra* dark chocolate to tan-brown, *S. diemenensis* and *S. pravitas* **sp. nov.** are more golden brown.

Reproductive system (Figs 20D, F, G; n = 3). Positioned within coelom under the respiratory cavity, over foot muscle, against right side of foot wall; epiphallic parts positioned between BM and RAM; single GP inconspicuous, opening from GA through foot wall posterior to right cephalic fold. Join of AO, GA and ED distinct, all whitish fibrous muscular tissue; AO elongated, bluntly pointed, folded, larger than GA, thicker than ED; ED relatively long, thick and twisted; EG broad, lobed, bluntly pointed with two curved, broad, flagellum (F1 and F2; F2 twice length of F1); BD and CD connect close together into GA between ED, AO and GP; BD noticeably longer and thinner than CD with a prominent twisted loop immediately before BC (no distal loop or MA), both ducts smooth, featureless, pass together through RAM connecting into soft curved folds of MG, BD dorsal to CD; BC large, bulbous, thin test, internally embedded into folds of MG; HD short thick, coiled, links AG to elongated narrow yellowish granulated HD; HG larger than AG, MG and AG folded, soft white tissue; SV embedded on left side of AG under BC; AG and HG sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Figs 20E, H). Head section over half of total length (head length = 8.08 ± 0.42 mm; ~ 43% of SPM length; head width = 119 ± 3 μm; flagellum width = 33 ± 1 μm, n = 3), cylindrically elongate, tip bluntly rounded, containing a white gelatinous mass; tapers quickly into consistently filamentous transparent flagellum; both sections smooth, translucent, test thin, featureless. multiple tightly coiled SPM in bursa, embedded in brown gelatinous mass. Seven and two SPM found in BC of two specimens [SK043, SK030].

Radula and jaw (Figs 83E–H). Mean dentition formula 31:1:31 (SD = 8.1), mean transverse rows 138 (SD = 20.1, n = 3, AM C.201775, C.201765, C.316303); single central rachidian tooth flanked squarely by 31 half row laterals, 0–4 are inner (SD = 4.98), 12–14 mid (SD = 4.98) and 15–19 outer (SD = 3.58) laterals (n = 5); central tooth with narrow unicuspid mesocone less than half length of basal plate, lower than laterals; inner laterals absent or few (Figs 83E–F), mid lateral mesocones generally unicuspid, however, maybe irregularly bicuspidate (Figs 83E–F), mid laterals with pointed ectocone; ectocone strong, protrudes at acute angle halfway along the tooth's length; outer laterals typically with a 'chisel' shaped mesocone flanked by small, pointed single ecto and endocones, endocone positioned higher on side of tooth than ectocone, angle of separation of each cone from the mesocone varies (Fig. 83G). Jaw located inside front of buccal cavity, orange-brown, arch shaped with 'shingle'-arranged cone-like rods, ~ 140 rods wide (~ 1.9 mm) by ~ 16 rods deep (mean length = 50 µm, SD = 6, mean width = 12 µm, SD = 3, n = 15); tip bluntly rounded [SK030].

Comparative remarks. *Siphonaria denticulata* (*atra* group, unit 33) is the sister taxon of a clade containing two species, *S. opposita* (unit 34) and *S. plana* (unit 35) (Figs 1–4). It differs from these species by COI distances of ≥ 14.8% (unit 35) and ≥ 15.8% (unit 34) (Table S3).

We found eight congeners with sympatric occurrences in SE Australia. For comparisons with *S. atra* and *S. diemenensis* refer to comparative remarks under these species. *Siphonaria stowae* has a smaller, more elongate, paler shell with a strongly offset apex, less prominent ribbing and edge scalloping, a smaller AO, shorter ED larger BC, and shorter SPM. *Siphonaria emergens* has a smaller, elongate, paler brown shell with a strongly offset apex, less prominent ribbing and edge scalloping. *Siphonaria funiculata* has a paler, taller shell with less raised ribs broadening to shell edge, a fainter scalloped edge, a larger AO, shorter BD and ED, absent to smaller F1, and larger, drop-like SPM. *Siphonaria pravitas* **sp. nov.** has a lower shell with greater raised ribbing and edge scalloping, no BD distal loop, a larger BC, wider F1, and shorter SPM. *Siphonaria scabra* has a paler shell with finer ribbing and coarser exterior, a longer AO, BC and F1, and a bursal loop. *Siphonaria zelandica* has a paler, lower shell with less prominent and finer narrower ribbing, a shorter ED and BD, and a short. drop-like SPM.

Menke (1851: 38) referred to the name *S. denticulata* for a specimen from Mexico. This reference was subsequently considered as a misidentification of *S. lecanium* var. *palmata* Carpenter, 1857 (Carpenter 1857: 183). Hubendick (1946: 40) treated this taxon as a junior synonym and subspecies of *S. maura* Sowerby I, 1835.

Erroneous records of '*S. denticulata*' from NZ (Hutton, 1873: 55) and Mozambique (Braga, 1956: 7, pl. 1, fig. 2) are herein attributed to *S. propria* Jenkins, 1983 and possibly *S. ferruginea* Reeve, 1856, respectively. We have not located any samples of this species from NZ nor Mozambique in any of the examined museum collections. The treatment of *S. denticulata* as a synonym or variety of *S. diemenensis* by several authors is refuted herein and both species are accepted as distinct species. Hedley (1915; 1918; M96) and Angas (1867: 232) incorrectly recorded *S. denticulata* from Port Jackson (= Sydney) and NSW.

A specimen figured as '*S. marza'* in Hubendick (1946: 61, pl. 5, figs 27–28) from Port Jackson [Sydney Harbour]) is herein identified as *S. denticulata*. McAlpine (1952: 40, 42, fig. 1) misidentified specimens of *S. scabra* as 'E*llsiphen*' (sic *Ellsiphon*) *denticulatus*. The RS figured herein (Figs 20D, G) matches closely the figure in McAlpine (1952: 43, fig. 1; as *Ellsiphon denticulatus*) and that shown in (Fig. 20F, from Currumbin) closely matches the distal RS figure of '*S. currumbinensis*' from in Hubendick (1955: fig. 4). A specimen from NZ labelled as '*S. denticulata*' in Davey (1998: 117) is herein identified as *S. funiculata*. Specimens stated to resemble either *S. diemenensis, S. denticulata* or *S. australis* by Dayrat *et al.* (2014) as 'unit 7' are herein identified as *S. diemenensis*. By contrast, the figured specimens of '*atra* group, unit 33' in Dayrat *et al.* (2014: fig. 5J, K) are morphologically consistent with *S. denticulata.*

Distribution and habitat. Endemic to temperate eastern and southeastern Australia, from Keppel Bay, Qld, south to Cape Conran, Vic, and Bridport, Tas (Fig. 16). In this study found in sheltered to moderately exposed sites on hard substrates (e.g., rocky shores, wooden pilings); upper and mid littoral levels; home scars prominent.

Siphonaria viridis Quoy & Gaimard, 1833
(Figs 22, 23, 24)

Siphonaria viridis Quoy & Gaimard 1833: 332, pl. 25, figs 30–31 (type locality: Amboine, aussi la Nouvelle-Guinée [Ambon, Maluku Islands, Indonesia, and New Guinea]).—Lamarck 1836: 156; 1839: 206; Catlow & Reeve 1845: 100; H. Adams & A. Adams 1855 (in 1853–1858): 271; Hanley 1858b: 561; H. Adams & A. Adams 1863: 271; Paetel 1889: 430; White & Dayrat 2012: 69.

Siphonaria sipho—Hedley 1909: 369 (not *S. sipho* Sowerby I, 1823).

Siphonaria (*Siphonaria*) *sipho*—Adam & Leloup 1939: 7, pl. 2, fig. 1a–d, text-fig. 1a–c (not *S. sipho* Sowerby I, 1823).

Siphonaria punctata Quoy & Gaimard 1833: 342, pl. 25, fig. 13–14 (type locality: 'On la trouve sur les rochers du port Louis de Île-de-France' [on rocks, Port Louis, Mauritius]).—Lamarck 1836: 559; 1839: 205; Catlow & Reeve 1845: 100; H. Adams & A. Adams 1855 (in 1853–1858): 271; 1863: 271; Martens 1880: 310; Paetel 1889: 429; Hubendick 1943: 47; Michel 1974: 274; Galindo 1977: 416; White & Dayrat 2012: 67.

Parellsiphon zanda Iredale 1940; 438, fig. 7–8 (type locality: Low Isles, North Queensland, [Australia]).—Hubendick 1945: 29; Morrison 1972: 57; White & Dayrat 2012: 69.

Parellsiphon promptus Iredale 1940: 438, fig. 24, 25 (type locality: Northwest Is, Capricorn Group [Qld, Australia]).—Hubendick 1946: 30; Morrison 1972: 57; White & Dayrat 2012: 67.

Legosiphon optivus Iredale 1940: 440, fig. 26, 27 (type locality: Magnetic Island, Queensland [Australia]).—Hubendick 1955: 7; Short & Potter 1987: 122; White & Dayrat 2012: 65.

Legosiphon mirificus Iredale 1940: 440, fig. 28, 29 (type locality: Magnetic Island, near Townsville, Queensland [Australia]).—White & Dayrat 2012: 66.

Legosiphon densatus Iredale 1940: 441, fig. 18–19 (type locality: Port Douglas, North Queensland, [Australia]).—Hubendick 1946: 47; White & Dayrat 2012: 62.

Siphonaria (*Siphonaria*) *optivus*—Hubendick 1946: 47.

Siphonaria (*Siphonaria*) *laciniosa*—Hubendick 1946: 47, pl. 3, fig. 18 (in part); 1955: 7 (not *S. laciniosa* (Linnaeus, 1758)).

Siphonaria (*Siphonaria*) *stellata*—Hubendick 1946: 48, pl. 3, fig. 22 (not *S. stellata* (Helbling, 1779)).

Siphonaria (*Siphonaria*) *laciniosa* var. *sipho*—Hubendick 1946: 52, pl. 4, fig. 8; 1955: 7 (not *S. sipho* Sowerby I, 1823).

Siphonaria (*Siphonaria*) *zanda*—Hubendick 1946: 52, pl. 4, fig. 8–11.

Siphonaria australis—Hubendick 1955: 7 (not *S. australis* Quoy & Gaimard, 1833).

Siphonaria laciniosa—Drivas & Jay 1988: 132, pl. 51, fig. 18 (not *S. laciniosa* (Linneaus, 1758)).

Siphonaria (*Mestosiphon*) *laciniosa*—Morrison 1972: 57 (not *S. laciniosa* (Linnaeus, 1758)).

Siphonaria laciniosa—Short & Potter 1987: 122, pl. 60, fig. 7; Wells & Bryce 1995: 113; 1996: 63; Bryce 1997: 55; Tan & Woo 2010: 61; Tan & Yeo 2010: 294; Willan *et al.* 2015: 330 (not *S. laciniosa* (Linnaeus, 1758)).

Siphonaria javanica—Tan & Chou 2000: 116, fig 116; 2010: 61 (not *S. javanica* (Lamarck, 1819)).

Siphonaria 'laciniosa group, unit 25'—Dayrat *et al.* 2014: 261, fig 4K–R (in part).

Material examined. *Type material.* Lectotype of *Siphonaria viridis* Quoy & Gaimard, 1833, present designation, from 'rade d'Amboine, aussi la Nouvelle-Guinée' [on rocks, Amboina] (MNHN-IM-2000-35958; Fig. 22A). Three paralectotypes MNHN-IM-2000-5042, same data as lectotype. Holotype of *Parellsiphon zanda* Iredale, 1940 AM C.l03706 (from GBR and Michaelmas Cay, N Qld, [Australia]; coll. May 1926; Fig. 22B). Lectotype of *Siphonaria punctata* Quoy & Gaimard, 1833, present designation, from Île-de-France [Mauritius, Indian Ocean] (MNHN-IM-2000-35957, Fig. 23A). Two paralectotypes, same data as lectotype (MNHN-IM-2000-5053). Syntype of *Parellisiphon promptus* Iredale 1940 AM C.103707 (from North West Island [23°18'S 151°42'E], Capricorn Group, [Qld, Australia]; coll. May 1931; Fig. 22C). Holotype of *Legosiphon densatus* Iredale, 1940 AM C.103716 (from Port Douglas, N Qld, [Australia]. Holotype of *Legosiphon optivus* Iredale, 1940 AM C.103719 (from Magnetic Island, Qld, [Australia]; coll. A.F. Basset Hull, May 1924; Fig. 22H). Seventeen probable paratypes of *Legosiphon optivus* Iredale, 1940 AM C. 153469, same data.

Syntype of *Legosiphon mirificus* Iredale, 1940 AM C.103718 (from Magnetic Island, near Townsville, Qld, [Australia]; coll. A.F. Basset Hull, May 1924; Fig. 22G). Five probable paratypes of *Legosiphon mirificus* Iredale, 1940 same data as probable holotype, AM C.153362).

Probable holotype of *Legosiphon densatus* Iredale, 1940 from Port Douglas, N Qld, [Australia]; coll. Nov 1929, (AM C.103717, Fig. 22D). Two questionable paratypes, same locality data, Nov 1928 (AM C.106998).

Other, non-type material. **Mauritius:** Trou-aux-Biches, 20°02.488'S, 57°32.353'E, MRU04-1 (AM C.585972 20+p, C.585834 p [M246], C.585835 p [M247], C.585836 p [M248]). **PNG:** New Ireland, NW side of Big Nusa Island, 02°34.1'S, 150°46.7'E KM12 (MNHN IM-2013-55336 p [M534]); Lemus Island, 02°38'S, 150°37.5'E KM24 (IM-2013-53728 p [M533]; IM-2013-53874 p [M530]); Ta Island, 02°41.6'S, 150°44.3'E KM22 (MNHN IM-2013-51004 p [M537]; IM-2013- 55767 p [M536]; IM-2013- 55768 p [M539]; IM-2013- 55765 p [M540]; IM-2013- 55766 p [M541]; IM-2013- 55770 p [M542]; IM-2013- 55769 p [M543]; IM-2013- 50993 p [M544]); Rempi Area, S Dumduman Is., 05°00,2'S, 145°47,6'E PM12 (MNHN IM-2013-11999 p [M561]); Riwo waters, 05°08.9'S, 145°48.2'E PM40 (MNHN IM-2013-15249 p [M553]) ; Biliau Island, 05°11.8'S, 145°48.2'E, PM38 (MNHN IM-2013-14828 p [M549], PM39 (IM-2013-15190 p [M556]). **Australia, Qld:** Cape York Peninsula, Bamaga, Umagico, 10°53.125'S, 142°20.799'E, Q50-1 (AM C.585181 [M179], C.585599 4p, C.585180 p [M104], C.585182 p [M433, SK140 (RS), C.595938 p [SK539], C.595939 p [SK540], C.585184 p [SK352], C.585185 p [SK353]). Bathurst Head, 14°15.912'S, 144°11.598'E, Q41-2 (AM C.585973 10p); S of Bathurst Head, 14°17.583'S, 144°11.845'E, Q41-1 (AM C.585948 4p); Lizard Island, 14°40.908'S, 145°27.007'E, Q40-1 (AM C.585642 5p); Cape Kimberley, 16°16.535'S, 145°28.737'E, Q35-1 (AM C.585903 2p, C.585173 p [M084], C.585174 p [M085]); Low Isles, 16°23.085'S, 145°33.596'E, Q34-1 (AM C.585384 10p, C.585161 p [M137], C.585162 p [M138], C.585163 p [M139], C.585165 p [M432, SK137]); Port Douglas, 16°28.697'S, 145°27.859'E, Q33-2 (AM C.585962 6p, C.585963 5p, C.585157 p [SK217], C.585159 p [SK219], C.585871 p [M131, SK218], C.585872 p [M133]); Bingil Bay, E of El Arish, 17°49.563'S 146°06.131'E (AM C.420154 2d). Magnetic Is., Balding Bay, 19°06.651'S, 146°52.260'E, Q27-1 (AM C.585904 15p), Horseshoe Bay, 19°06.755'S, 146°51.875'E, Q27-2 (AM C.585900 6p), Geoffrey Bay, 19°09.142'S, 146°52.125'E, Q27-4 (AM C.585902 7p C.585533 d [R4108], C.585869 p [M482], C.585870 p [M483]); Rocky Bay, 19°10.43'S, 146°50.73'E (AM C.459332 1d). Hamilton Is., Catseye Bay, 20°20.831'S, 148°58.002'E, Q18-1 (AM C.585463 15p). **NT:** N Turtle Beach, 12°18.816'S, 136°55.930'E NT04-1 (AM C.585069 p [M086], C.585070 p [M148], C.585071 p [M149], C.585072 p [SK079], C.585079 p [SK077]). Nhulunbuy, Cape Wirawawoi, 12°09.513'S, 136°46.904'E NT05-1A (AM C.585594 4p), East Woody Islet 12°09.695'S, 136°45.075'E NT05-2 (AM C.585632 5p, C.585078 p [M462, SK196]). Cobourg Peninsula, Kuper Pt 3, 11°10.688'S, 132°13.711'E NT21-7 (AM C.585390 10+p, C.585086 p [M093], C.585087 p [M142]), Kuper Pt 2, 11°10.877'S, 132°13.554'E NT21-6 (AM C.585084 d [M035], C.585085 p [M150]), Smith Pt, 11°07.360'S, 132°08.134'E NT21-2 (AM C.585634 5p), Smith Pt 2, 11°07.466'S, 132°08.538'E NT21-3 (AM C.585081 p [M463, SK198], C.585317 p [M034]); Sandy Is Pt, 11°07.862'S, 132°11.187'E NT21-1 (AM C.585468 15+p, C.585080 p [M023], C.585842 p [M095]). Cox Peninsula, 12°24.824'S, 130°40.921'E NT25-1 (AM C.585407 10+p); Luxmore Hd, Melville Is, 11°20.639'S, 130°23.149'E NT24-1 (AM C.585595 4p). **WA:** Caffarelli Is, 16°01.991'S, 123°18.625'E, WA19-1 (AM C.584739 10+p, C.584659 p [M465, SK200], C.584660 p [M466, SK201], C.584661 p [SK290], C.584662 p [SK291], C.584784 p [SK221], C.585297 p [SK220],C.585298 p [SK360]); Conilurus Is, 16°08.875'S, 123°35.234'E, WA18-1 (AM C.585654 5p); Catamaran Bay, 16°27.622'S, 123°00.242'E, WA22-3 (AM C.584663 p [M026]); Emeriau Point Middle Lagoon, 16°46.351'S, 122°34.200'E, WA23-1 (AM C.584674 d [M396]; C.585884 d [M393]); Broome, between Crab Creek and Broome, 17°58'S, 122°14'E (WAM S76939

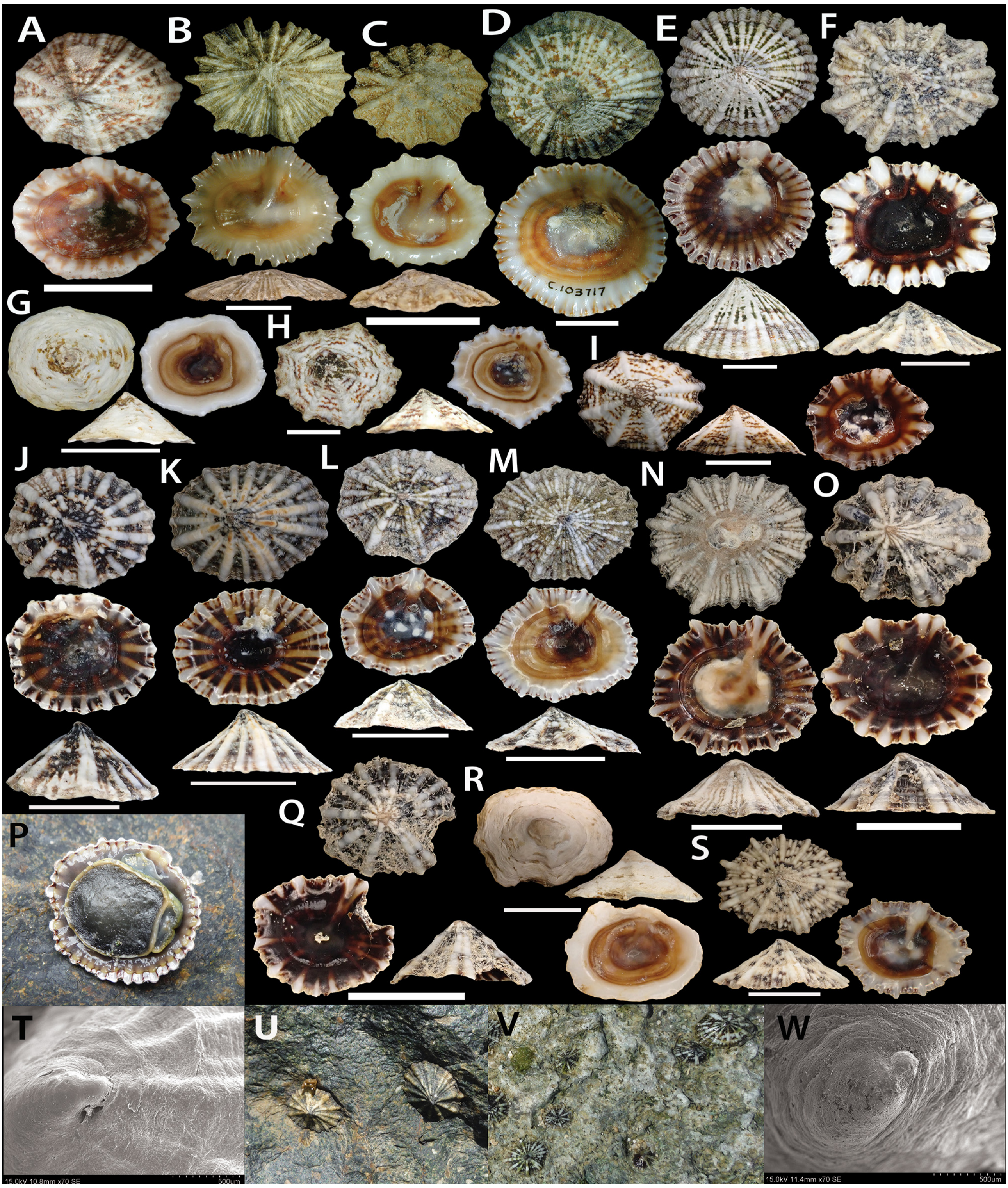

FIGURE 22. Shell of *S. viridis*. **A.** Lectotype of *S. viridis* MNHN-IM-2000-35958. **B.** Probable holotype of *Parellsiphon zanda* AM C. l03706. **C**. Syntype of *P. promptus* AM C.103707. **D.** Probable holotype of *P. densatus* AM C.l03717. **E.** Qld, Port Douglas, TS of *P. densatus* AM C.585872 [M133]. **F.** WA, Tantabiddi, AM C.584676 [M205]. **G.** Syntype of *Legosiphon mirificus* AM C.103718. **H.** Probable holotype of *L. optivus* AM C.103719. **I.** Qld, Magnetic Is, TS of *L. optivus* AM C.585869 [M483, SK293]. **J.** WA, Caffarelli Is, AM C.584659 [M465]. **K.** Singapore, St Johns Island, AM C.585224 [M324]. **L–M.** Qld, Low Isles, TS of *P. zanda***, L.** AM C.585161 [M137], **M**. AM C.585161 [M139]. **N–O, Q.** PNG, New Ireland, MNHN IM 2013 55767 [M536], IM 2013 50993 [M544], IM 2013 55770 [M542], **P.** Animal, **R.** Malaysia, Pulau Tioman, ZRC.MOL.24898 [SK373]. **S.** PNG, Bilau, IM 2013 14828 [M549]. **T.** Protoconch, AM C.585157 [SK217]. **U.** Singapore, *in situ*. **V.** TS of *P. zanda*, *in situ*. **W.** Protoconch, AM C.585084 [M035]**.** Unlabelled scale bars = 10 mm.

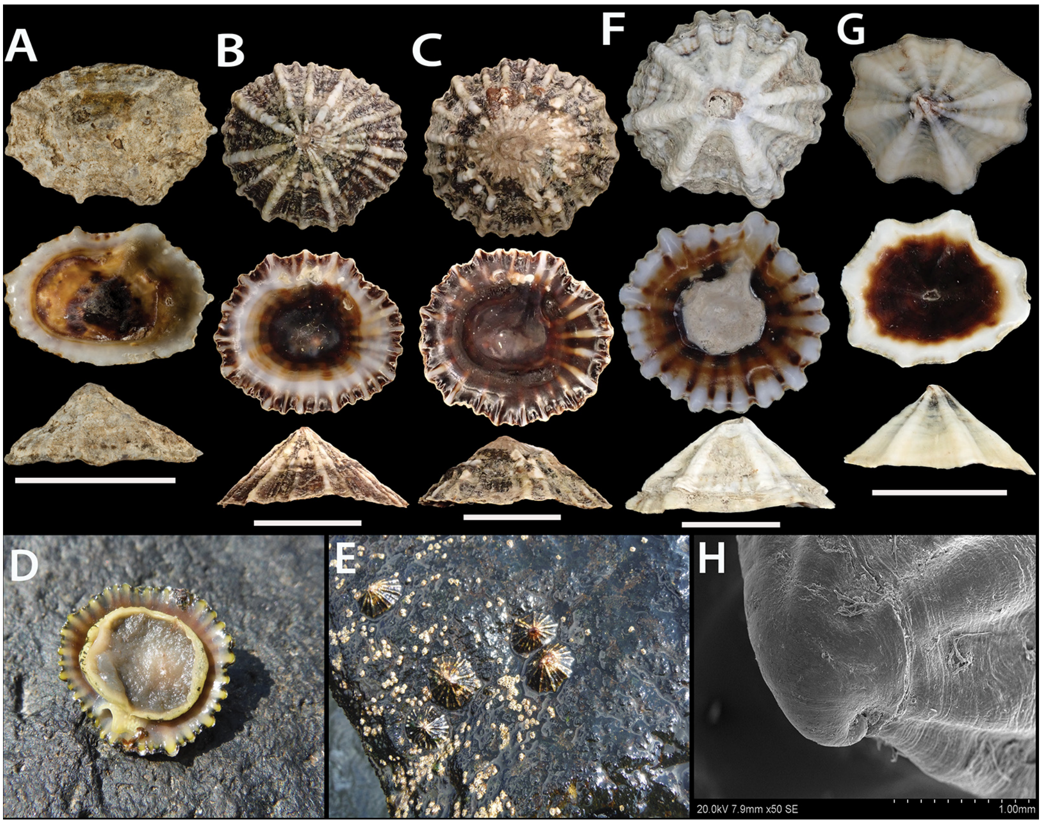

FIGURE 23. Shell of *S. viridis*. **A.** Lectotype of *S. punctata* MNHN-IM-2000-35957. **B–E.** Mauritius, Trou-aux-Biches, TS of *S. punctata*. **B.** AM C.585835 [M247]. **C.** AM C.585834 [M246]. **D.** Animal. **E.** *In situ*. **F–H.** Qld, Cape York Peninsula. **F.** AM C.585181 [M179]. **G.** AM C.585180 [M104]. **H.** Protoconch, AM C.585182 [M433]. Scale bars = 10 mm.

11p, p [SK065]); Cape Latouche Treville nr Gourdon Bay, 18°27.101'S, 121°48.911'E, WA27-2 (AM C.585795 20p, C.584675 p [SK149], C.585306 p [M066], C.585307 p [M067]); Hearson Cove, Dampier, 20°38.079'S, 116°48.031'E, WA33-2 (AM C.585309 p [SK064]); Gnoorea Point 2 20°50.333'S, 116°20.825'E, WA36-2 (AM C.585885 d (M105)); Tantabiddi, 21°54.739'S, 113°58.706'E, WA42-1 (AM C.584676 p [M205]; C.585886 p [M206]). **Timor-Leste:** Dolokoan Beach, N of Dili, 8°31.424'S, 125°37.091'E TL01-1 (AM C.585745 10+p, C.584796 p [M478, SK285], C.584821 p [SK299], C.584822 p [SK300], C.585388 p [SK558], C.585880 p [M442], C.585881 p [M443], C.585882 p [M444], C.585883 p [M450], C.595948 p [SK563]). **Indonesia, Bali:** Tanah Lot IND03 8°37.25967′S, 115°5.22967′E (ZRC.MOL.24913 p [M473]). **Singapore:** St Johns Island, Peninsula Lokos 01°12.824'N, 103°51.076'E SI04-1 (AM C.585224 p [M324], C.585225 p [M325]); Lazarus Island channel headland, 1°13.085'N, 103°51.429'E SI04-4 (AM C.585604 10p, C.585164 p [SK166], C.585243 p [M330], C.585244 p [SK167],C.585245 p [M329], C.585246 p [M331], C.585486 p [M336]); Lazarus Island causeway, 01°13.288, 103°51.195'E SI04-3 (AM C.585982 4p, C.585240 p [M328], C.585241 p [M333], C.585242 p [SK143]); Lazarus Island, 01°13.355'N, 103°51.148'E SI04-2 (AM C.585228 p [SK184]. **Malaysia**: Palau Tioman 2°49′N, 104°11′E ZRC 1999-1781 7p, ZRC.MOL.24897 p [SK374], ZRC.MOL.24898 p [SK373]).

Taxonomic remarks. The lectotype of *S. viridis* is designated herein for the stabilisation of the name and to ensure the unambiguous identity of this taxon (Art. 74.1 of the Code). In addition, we designate the syntype of *S. punctata* with the clearest external sculpture (Fig. 23A) as the lectotype of *S. punctata* for the stabilisation of the name (Art. 74.1 of the Code). The labels associated with the type specimens give 'Île-de-France' [Mauritius].

Paetel (1889: 429) listed *S. punctata* 'Quoy. I. Maurit.' as an accepted species. However, Reeve (1856), Hanley (1858b: 152) and Hutton (1880: 36) treated *S. punctata* as a synonym of *S. sipho*. Finally, Hubendick (1946: 47) listed *S. punctata* as a synonym of *S. laciniosa*. We recognise *S. punctata* as a synonym of *S. viridis* mainly based on genetic evidence. We found that topotypic specimens that closely match the shell morphology of the types fall within unit 25 (Fig. 3: genetic vouchers M246–M248 from Mauritius) and exhibit morphological and anatomical features that are consistent with that of *S. viridis*.

The type locality of *P. zanda* given on the specimen label of the types ('GBR and Michaelmas Cay, N Qld' [Australia]) differs from that given in the original description ('Low Isles, N Qld'). The original descriptions of *P. zanda* and *P. promptus* each appear to be based on a single specimen. Iredale (1940: 438) referred to 'type' in the original descriptions of *P. zanda, L. densatus* and *L. optivus* but not in that of *L. mirificus* nor *P. promptus.*

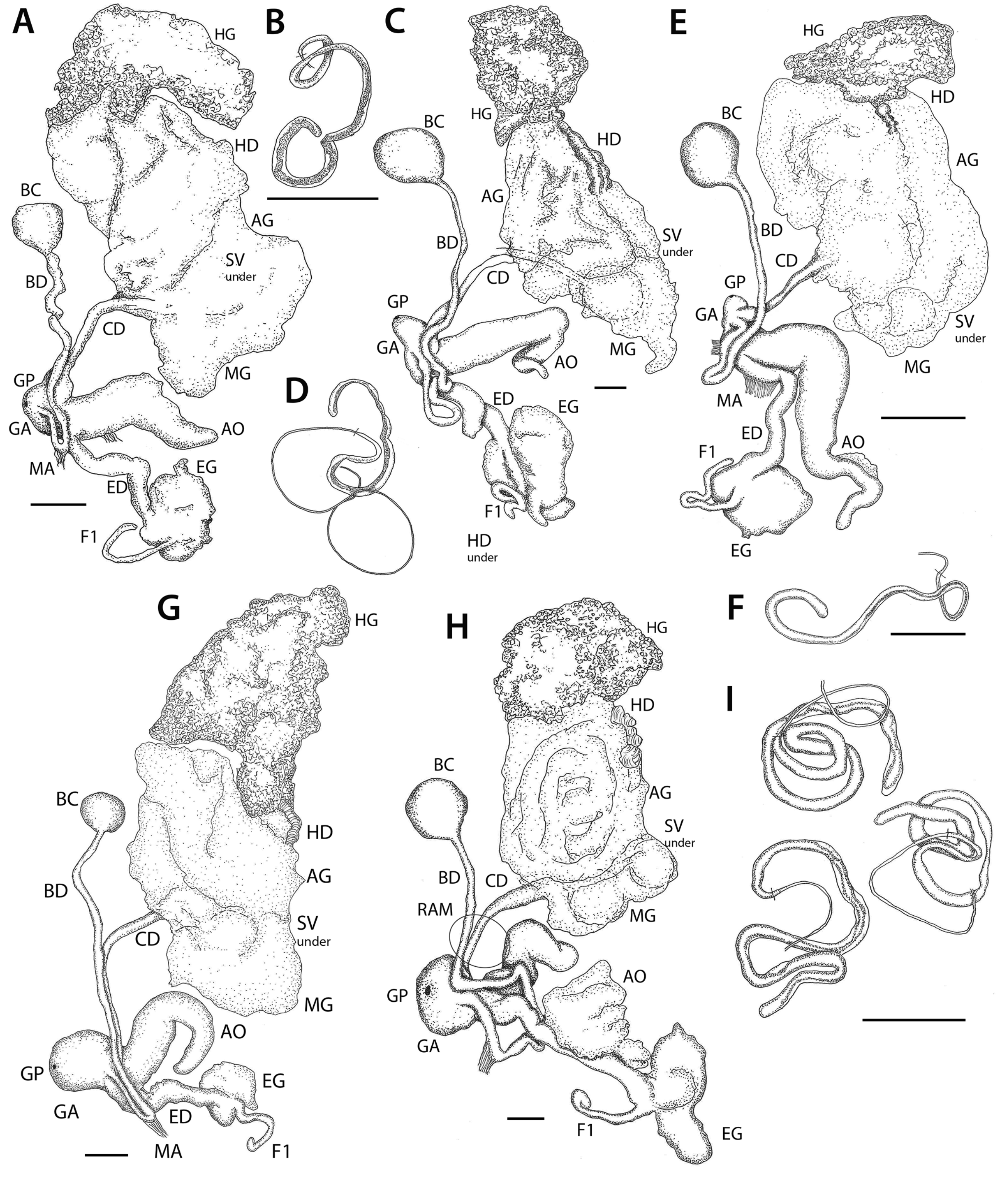

FIGURE 24. Reproductive morphology of *S. viridis*. **A–B.** Qld, Low Isles, TS of *Parellsiphon zanda* AM C.585165 [M432, SK137]. **C–D.** Qld, Port Douglas, TS of *Legosiphon densatus* AM C.585872 [M133, SK219]. **E–F.** Qld, Magnetic Is, TS of *L. optivus* AM C.585872 [M482]. **G.** Qld, Cape York Peninsula, AM C.585182 [M433 SK140]. **H–I.** Mauritius, Trou-aux-Biches, TS of *S. punctata* AM C.585835 [M247]. Scale bars = 1 mm.

Therefore, we consider the single type specimens of *P. zanda, L. densatus, and L. optivus* as holotypes, but the types of *L. mirificus* and *P. promptus* as syntypes. No additional types are known to exist.

Hubendick (1946: 47) incorrectly considered *S. viridis*, *L. optivus* and *L. densatus* as synonyms of *S. laciniosa* based on shell colouration and shape. The interpretation of *S. zanda* in Hubendick (1946: 52) is likely based on a misidentification. While reference to the original designation is correct, the specimens examined and figured are from the Java Sea and Madagascar (Hubendick 1946: pl. 4, figs 8–11) and clearly differ from the type (Fig. 22B) (refer to Comparative remarks). Hubendick (1946: 53) incorrectly considered *L. mirificus* as a possible synonym of '*S. ferruginea'* (= *S. plana*). The specimens figured in Hubendick (1946: pl. 4, fig. 16–19) do not resemble the type of *L. mirificus*. Morrison (1972: 56–58) synonymized '*Parellsiphon zanda*' and '*P. promptus*', with *S. laciniosa* based on similarities in shell shape and 'common reproductive development'. These synonymies are rejected herein based on examination of type specimens and comparative morpho-anatomy.

Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes of all synonymized taxa and geographic series of additional specimens (Tables S1–2).

External morphology (Figs 22P, 23D). Foot sole, foot wall, pneumostome lobe and cephalic folds evenly grey or cream in colour, darker to centre of foot sole, paler to foot edge, cephalic folds cream to mouth; irregular black blotches cover all but foot sole, concentrated to centre of cephalic folds; mantle narrow than foot wall, evenly grey, edge thickened, with white band, lobed; pneumostome lobe large, under mantle.

Shell (Figs 22–23; Table S9). Small to medium sized (max sl mean = 13.8 mm, SD = 3.6 mm, n = 21), elongate ovate; height tall; medium thickness; apex offset weakly posterior and left (frequently eroded), apical sides weakly concave, protoconch direction homostrophic (n = 6; Fig. 22T, W), shell whorl dextral; growth striae prominent, irregular, uneven; rib count (mean = 37, SD = 7.6, n = 21), primary ribs prominent, white, protrude slightly beyond shell edge, often wider than rib interstices, ridge edge rounded, fused pair highlight siphonal ridge; few secondary ribs, 0–3 secondary ribs between anterior primary ribs, dark brown/black radial bands in rib interstices overlaying interstices and secondary ribs; shell edge fragile, weakly scalloped and corrugated at primary rib end. Interior shell lip to margin dark brown and white, white rays align on shell margin under furrowed primary/secondary ribs, dual brown rays aligning under interstices extend from lip over margin to merge into a single brown ray to evenly brown spatula; siphonal groove distinct furrow; ADM scar distinct, CMS straight. Growth thickening and whitening of the shell lip, with retention of axial brown markings, is common in larger specimens. The holotype specimen is an example of shell thickening.

Reproductive system (Fig. 24; n = 21). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts positioned between BM and RAM. GA small, with singular GP through foot wall; AO very large, wide, bluntly pointed, joined to upper GA, muscle attachment at side; ED elongated, thickened, centrally bent, joins to lower side of GA; GA, AO, ED all white muscular fibrous tissue; EG large, soft whitish tissue, slightly folded, joins ED; single narrow flagellum (F1), similar length and width to ED, appears as an extension of ED. BD and CD connect in opposing directions into GA between ED join and GP, CD join is bulbous, both ducts long straight smooth whitish, pass together on outer side of RAM (BD over thicker CD) into soft white folded tissues of MG; BD long narrow with prominent distal loop with MA to inner anterior foot wall, bent and twisted before BC; CD long, wider than BD; CD connecting to MG ducts, BC embedded in folds close to embedded blackish SV; BC relatively small bulbous, thin whitish translucent test, 2 SPM in BC of topotypic specimen (AM C.585165 Q34-1 [M432, SK137]); MG/AG complex relatively large; HD short narrow coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; AG/MG larger than HG, sides match curvature of inner foot wall.

Spermatophore (Figs 24B, D, F, I). Thread-like; head section (head length = 9.74 mm, head width = 94.6 µm, n = 1, flagellum incomplete) cylindrical, bulbous, bent, rounded tip, tapers to flagellum; test thin, smooth, featureless, translucent encasing a white opaque central core; a short tapering section merges head to filamentous flagellum; head section wider than translucent flagellum (complete flagellum unavailable). We found two SPMs tightly coiled in brown gelatinous mass in bursa [M432, SK137], two SPM coiled, embedded in white gelatinous mass in each [SK079, SK077], a single SPM in white gelatinous mass in one bursa [SK149].

Radula. Dentition formula: 20-25:1:25-20 (Adam & Leloup, 1939: 8, as '*S. sipho*'), 40:1:40 (Hubendick 1946: 47).

Comparative remarks. In our molecular phylogenetic tree (Figs 1–4), *Siphonaria viridis* (*laciniosa* group, unit 25) is closely related to *S. umagicoensis* **sp. nov.** and *S. punctata*. These species are separated from each other by average genetic p-distances in COI of 6.5% to 8.1%. All three species together form a well-differentiated clade. Sequences from Sulawesi and Bali clustering within this clade and attributed to "unit 25" by Dayrat *et al.* (2014) are of uncertain identity and require further scrutiny for lack of morpho-anatomical study. *Siphonaria viridis* has a variable shell (Figs 22–23) across its wide distribution throughout tropical Australia, PNG and Singapore (Fig. 25). Within this range, we found twenty-three sympatric congeners. Three congeners are sympatric in NC: *Siphonaria hienghenensis* **sp. nov.** has a slightly larger, darker shell with a flared siphonal ridge, a smaller AO, and shorter SPM. *Siphonaria poindimiensis* **sp. nov.** has a taller, darker shell with fused siphonal ribs, stronger edge scalloping, and longer ED. *Siphonaria bourailensis* **sp. nov.** has a shell with a more posteriorly offset apex, uneven ribbing, stronger edge scalloping, a smaller AO, and shorter SPM. Nine congeners are sympatric with *S. viridis* in PNG and TL: *Siphonaria atra* has a larger, lower shell with stronger edge scalloping, flared siphonal ridge, and larger BC, and shorter SPM. *Siphonaria opposita* has a lower, pale to dark brown shell, a larger BC, pointed AO, and longer ED. *Siphonaria madangensis* **sp. nov.** has a slightly smaller and lower shell with greater raised ribbing and stronger edge scalloping, a smaller, less prominent AO, larger BC, and shorter, bulbous, threadlike SPM. *Siphonaria nusalikensis* **sp. nov.** differs by being much smaller shell, with a darker interior, and BD without distal loop. *Siphonaria planucosta* **sp. nov.** has smaller, lower, darker shell with unpatterned interstices, a smaller AO, larger BC, and shorter SPM. *Siphonaria forticosta* **sp. nov.** has a larger shell with darker spatula, and a smaller AO. *Siphonaria alba* has larger, lower shell with stronger edge scalloping, a flared siphonal ridge, and a longer SPM. *Siphonaria campestra* **sp. nov.** has smaller shell without exterior patterning, with darker interior, a smaller AO, shorter BD and SPM. For comparison with *S. javanica* refer to comparative remarks under that species.

Siphonaria maloensis **sp. nov.** (sympatric in Vanuatu) is of similar shell size but has a darker, grey-brown shell with slightly stronger edge scalloping, an apex offset to posterior and left, and a golden-brown interior. A further eight species are sympatric with *S. viridis* in tropical Australia (along with *S. alba*, *S. atra*, *S. campestra* **sp. nov.** and *S. opposita*). *Siphonaria costellata* **sp. nov.** has a larger, darker shell with a darker interior, a smaller AO, shorter BD, and shorter, wider SPM. *Siphonaria gemina* **sp. nov.** has paler shell with stronger edge scalloping and flared siphonal ridge, a smaller AO, and shorter SPM. *Siphonaria jiigurruensis* **sp. nov.** has taller shell with more posteriorly offset apex, and paler whitish brown spatula, and a broader ED. *Siphonaria oblia* has a far smaller shell, weakly ribbed, with strongly posteriorly offset apex, and a smaller to indistinct AO (Jenkins 2018: 278, figs 3C–D). *Siphonaria restis* **sp. nov.** has a shell with stronger edge scalloping, more strongly raised ribbing, a smaller AO, and larger BC. *Siphonaria zelandica* has lower, paler shell with finer ribbing and a less prominent siphonal ridge, smaller AO and BC, and a smaller, drop-like SPM. Two species are sympatric with *S. viridis* in Singapore (including *S. alba and S. costellata* **sp. nov.**). *Siphonaria sirius* has lower shell with single rib siphonal ridge, stronger edge scalloping and a paler spatula, a smaller AO, longer ED, shorter BD, larger BC, and a longer SPM. *Siphonaria normalis* has a smaller, lower shell with a more posteriorly offset apex and less raised ribbing, a smaller AO, larger BC and shorter F1.

Topotypic specimens of *L. mirificus* (AM C.585869), *L. optivus* (Fig. 22I) and *P. densatus* (Fig. 22E) are conspecific based on mitochondrial phylogenetics and comparative morphology.

The record of '*S. sipho'* in Adam & Leloup (1939: 7, pl. 2, fig. 1a–d) from Java, Bali, Mansinan, PNG and of '*S. funiculata*' (9, pl. 2, figs 2a, b) from Iles Psang, PNG are here attributed to *S. viridis* and are well within its distributional range (Fig. 25). Hubendick (1946: 30–32, 63) considered the validity of '*Parellsiphon promptus'* (= *S. viridis*) doubtful, revealing considerable resemblance in shell characters and possible synonymy with *S. acmaeoides*. Hubendick (1946: 53) further indicated that the mollusc is 'Entirely yellowish white' (i.e., likely discolouration in preserved material; external foot dark grey in live *S. viridis*). The specimen from Queensland figured in Hubendick (1946: 47, pl. 3, fig. 18) as '*S. laciniosa* v. *sipho'* is attributed here to *S. viridis*. References to '*S. laciniosa*' (in part) in Hubendick (1946: 47, from New Guinea and Huon Is) and '*S. laciniosa*' in Hubendick (1955: 7, from Cairns (MV F15031, MV F13925, MV F13923) are also most likely specimens of *S. viridis*. Hubendick's (1946: pl. 3, fig. 22) specimen of '*S. stellata*' from Broome and Thursday Island (pl. 3, fig. 20) are likely specimens of *S. viridis*, too. A specimen of '*S. zanda*' from 'Java Sea' figured in Hubendick (1946: 91, pl. 4, fig. 8–11) is likely a specimen of *S. alba* and a specimen from Madagascar (figs 10–11) is likely *S. madagascariensis*. Specimens of '*S. australis*' from Masthead and Heron Islands (MV F.13924, 15032, 15034, 15038) mentioned by Hubendick (1955: 7) are likely *S. viridis*. Reference to '*S. laciniosa*' from New Guinea in Hubendick (1947b: 3) is likely of *S. viridis*. The records of '*S. laciniosa*' from East coast Malaysia in Way & Purchon (1981: 321) are most likely of *S. viridis*. Figured specimens of '*laciniosa* group, unit 25' in Dayrat *et al.* (2014) from Timor (fig. 4J), Singapore (fig. 4L), Magnetic Is (fig. 4P), Broome, WA (fig. 4N), PNG (fig. 4Q) and Vanuatu (fig. 4R) correspond well with typical features of *S. viridis*.

Distribution and habitat. Tropical IWP, including Palau, Singapore (St Johns Island), Vanuatu, and northern Australia (Qld through to Kimberley, WA) as well as Mauritius, Indian Ocean (Fig. 25). Records from Sulawesi, Bali, and PNG arebased on specimens sequenced by Dayrat *et al*. (2014) and found to be members of unit 25. In this study found in protected positions (e.g., hollows) on moderately exposed rocky boulder shores, mid littoral level (upper oyster zone).

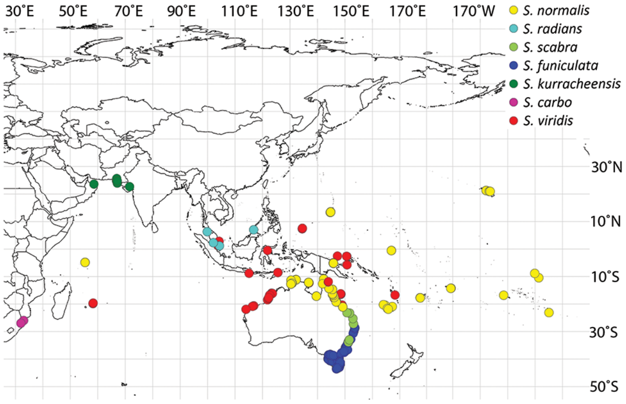

FIGURE 25. Known occurrence records of *S. viridis*, *S. normalis*, *S. radians*, *S. scabra*, *S. funiculata*, *S. kurracheensis* and *S. carbo.*

Siphonaria guamensis Quoy & Gaimard, 1833
(Figs 26A–E, 27A–B)

Siphonaria guamensis Quoy & Gaimard 1833: 343, pl. 25, figs 15–16 (type locality: 'Port d'Humata' [Umatac Bay, Guam]).—Lamarck 1836: 558; Catlow & Reeve 1845: 100; H. Adams & A. Adams 1855 (in 1853–58): 271; Hanley 1858b: 152; Paetel 1889: 428; White & Dayrat 2012: 63.

Siphonaria (*Sacculosiphonaria*) *guamensis*—Hubendick 1945: 72, fig. 33, 37; 1946: 41, pl.6, fig. 30–32; Marcus & Burch 1965: 256, figs 40–43.

Material examined. *Type material.* Lectotype of

Siphonaria guamensis Quoy & Gaimard, 1833, present designation, from 'Est tres-commune dans l'ile dont elle porte le nom, surtout au port d'Humata' [is very common in the island of which it is named, especially at the port of Humata, Iles Mariannes [Umatac Bay, Guam] (MNHN IM 2000-35953, Fig. 26A). Ten paralectotypes, same data as lectotype (MNHN IM 2000-5054).

Other, non-type material. **Guam:** Umatac Bay Nth point, 13°17.917'N, 144°39.494'E GM01-1 (AM C.585553 10+p, C.584911 p [SK142], C.584929 p [SK378], C.584928 p [SK379], C.585031 p [SK426]); Umatac Bay, Sth point, 13°32.549'N, 144°48.443'E GM01-3 (AM C.585392 10p, C.584870 p [M344], C.584871 p [M345], C.584872 p [M346]).

Taxonomic remarks. The largest syntype with clearest external sculpture is herein designated as the lectotype of *Siphonaria guamensis* for the stabilisation of the name (Art. 74.1 of the Code). Labels associated with type specimens just give 'Iles Mariannes'. Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes specimens (Figs 26B–C) and a series of additional specimens (Table S1). The topotypes studied here match characteristics mentioned in the original description, such as 'raised and distinctive ribbing, prominent dark radial banding and the slightly hooked apex anteriorly [sic! posteriorly]'.

External morphology. Foot sole, foot wall, pneumostome, cephalic folds and mantle evenly cream/light grey; genital pore inconspicuous, located on foot wall posterior to right cephalic fold; mantle narrower than foot wall, thin translucent, edge weakly lobed with light black bands aligning to rib interstices extends to shell edge, pneumostomal lobe thin and within mantle between the right ADMs, closes the pneumostomal and anal openings at the mantle edge; two small black epithelial eye spots centralised on two thick centrally touching cephalic folds; light black pigmentation over posterior foot wall and centre of cephalic folds.

Shell (Figs 26A–C, E; Table S9). Small sized (max sl mean = 10.96 mm, SD = 1.6 mm, n = 6), height medium; ovate; apex offset weakly to posterior and left; apical sides convex, posterior concave to straight; protoconch hooks to posterior, area black colouration, protoconch direction weakly homostrophic (n = 2; Fig. 26E), shell whorl dextral; growth striae weak; shell thickness thin; colouration uneven with some radial banding; rib count (mean = 38, SD = 4.9, n = 6); slightly raised, pale white, fairly straight, faintly protrude beyond shell lip; predominantly primary ribs, in parts interspersed with 0–2 finer secondary ribs, rib interstices darker; siphonal ridge indistinct. Interior evenly dark brown to black from margin to spatula, paler on shell lip aligning under rib ends, siphonal groove clear; ADM scar indistinct, CMS weakly convex; No evidence of growth variations in shell thickness or shell margin colouration.

Reproductive system (Fig. 27A; n = 2). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned over and looped/folded in front of BM and to side of RAM; AO large, elongated, bluntly pointed (embeds into MG), centrally bent with MA, merges with indistinct GA; ED relatively short, slightly twisted, thick with side appendage; EG relatively large, folded, elongated and pointed; single short narrow bent flagellum F1 on EG; AO, GA and ED all muscular white tissue; BD and CD with opposing connections (bulbous at CD) into GA between ED, AO and GP; BD longer and narrower than CD with a prominent distal loop, top of loop attached via a long MA to inner foot wall in front of BM, both ducts smooth and pass together through RAM connecting into folds of MG (BD above CD), BC translucent test, midsized and bulbous; HD brownish long coiled links AG to a small elongated narrow brownish finely granulated HG; MG and AG small folded soft white tissue; dark SV embedded within AG, AG larger than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 27B). Thread-like, test thin, smooth, featureless, translucent (length = 9.38 mm, n = 1), head bulbous, tip bluntly rounded, containing a white gelatinous mass; taper region into the filamentous transparent flagellum is extended; both sections smooth, featureless; head longer and much thicker than flagellum (head length = 7.00 mm, head ~75% of SPM length; head width = 80 μm; flagellum width = 13 μm); three SPM tightly coiled in a brown gelatinous mass found in one BC [SK241].

Radula. Dentition formula 26:1:26 (Hubendick 1946: 42).

Comparative remarks. Based on our molecular phylogeny (Figs 1, 3), *S. guamensis* (*plicata* group, unit 70) is the sister species of an unidentified *Siphonaria* species from Rarotonga (unit 17). The next most closely related species is *S. nusalikensis* **sp. nov.** (unit 89). The minimum distance between *S. guamensis* and these species is 9.6% (unit 17) and 11.1% (unit 89) in COI. The minimum distance to any other species is at least 25% (Table S7).

Three congeners occur in sympatry with *S. guamensis* in Guam: *Siphonaria lirata* is very similar, but has finer ribbing, paler interior colouration, a non-hooked protoconch, and a shorter, wider ED, and longer F1. *Siphonaria normalis* is extremely variable, but has less raised ribbing, a non-hooked apex, paler interior, a shorter, wider ED and F1, larger BC, and shorter SPM. *Siphonaria tanguissonensis* has more raised and prominent ribbing, an unhooked apex, paler golden-brown interior with more prominent dark rays on shell lip, a smaller AO, longer BD, F1 looped, and a longer SPM. None of these species are closely related to *S. guamensis* (Figs 1, 3).

RS figures of '*S. guamensis*' in Hubendick (1945: 26, fig. 33, 37) correspond well with *S. costellata* **sp. nov.**, but not *S. guamensis*. Correspondingly, specimens from 'Billiton, Paudua, The Sunda Islands' depicted as '*S. guamensis*' by Hubendick (1946: 93, pl. 6, fig. 30–32) are likely *S. costellata* **sp. nov.** for resembling shell characteristics of this species, but not of *S. guamensis.* '*Siphonaria guamensis*' recorded from Singapore (Tan & Chou, 2000: 115, fig 115) is also likely *S. costellata*

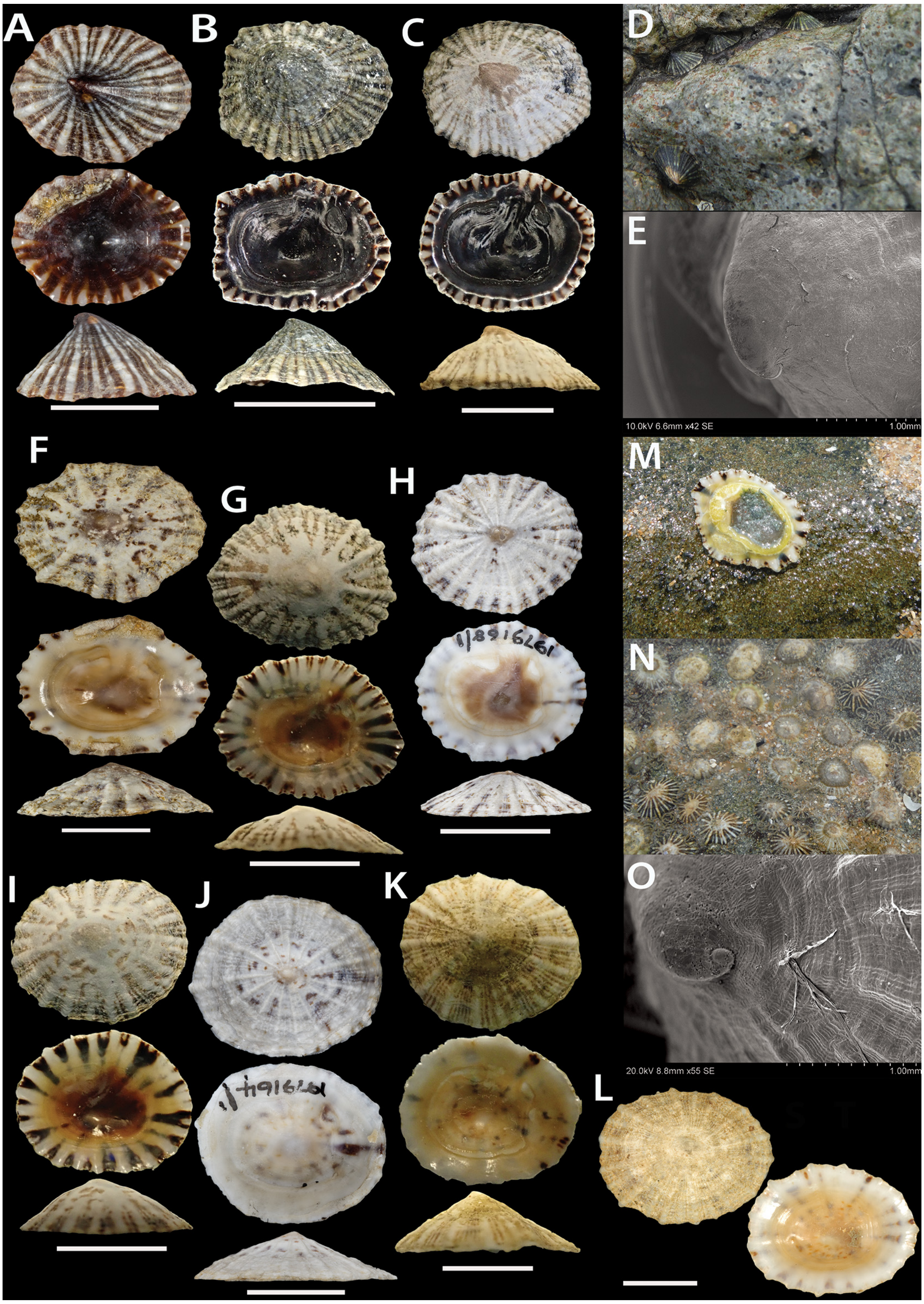

FIGURE 26. Shells of *S. guamensis* and *S. zelandica*. **A–E.** *S. guamensis*. **A.** Lectotype MNHN-IM-2000-35953. **B–C.** Guam, Umatac Bay, TS. **B.** AM C.584870 [M344]. **C.** AM C.584872 [M346, SK241]. **D.** Guam, in situ. **E.** Protoconch, AM C.584911 [SK142]. **F–O.** *S. zelandica*. **F.** Lectotype MNHN-IM-2000-5055. **G.** WA, Cape Latouche Treville, AM C.584342 [SK067]. **H.** Lectotype of *S. zebra* NHMUK 1979168.1. **I.** NSW, Sydney Harbour, TS of *S. zebra* AM C.585047 [M155]. **J.** Lectotype of *S. baconi* NHMUK 1979164.1. **K.** WA, Point Brown, TS of *S. baconi* AM C.585935 [M127, SK243]. **L.** Syntype of *P. elegans* AM C.103710. **M.** NSW, Bateau Bay, animal. **N.** NSW, Inverloch, *in situ*. **O.** Protoconch, AM C.585216 [SK024]. Scale bars = 10

sp. nov. based on shell characteristics, such as interior colouration, protoconch shape, which differs in *S. guamensis*. Unfigured records of ‘*S. guamensis*’ from Hong Kong (Christiaens, 1980a: 81), Anambas and Natuna Islands (Tan & Kastoro, 2004: 50; Chim & Tan, 2009: 269) are mis-identified specimens of *S. sipho*. The identity of ‘*S. guamensis*’ reported from Visakhapatnam, India by Murty *et al.* (2013: 104, fig. 1) is erroneous and outside of the range of this species.

Distribution and habitat. Endemic to Guam (Fig. 28), found in crevices on rock platforms and boulders on exposed rocky shores at mid to upper littoral levels (Fig. 26D).

***Siphonaria zelandica* Quoy & Gaimard, 1833**

(Figs 26F–O, 27C–E)

Siphonaria zelandica Quoy & Gaimard 1833: 344, pl. 25; figs 17–18 (type locality: Nouvelle-Zélande [New Zealand]).—Lamarck 1839: 205; Catlow & Reeve 1845: 100; H. Adams & A. Adams 1855 (in 1853–58): 271; 1863: 271; Iredale 1915: 478; Hanley 1858b: 153; Jenkins 1983: 4, pls 1a–h, 2a–h, 6a–c. fig. 3a–d; Paul 1984: 28; Wells 1984: 53; Phillips *et al.* 1984: 78, fig. (unnumbered); Villiers & Hodgson 1987: 135; Short & Potter 1987: 122, pl. 60, fig. 6; Ludbrook & Gowlett-Holmes 1989: 612, fig. 11.29 j, k; Jansen 1995: 90, fig. 376; Wilson 2002: 172, text-fig.; Wells *et al.* 2003: 289; White & Dayrat 2012: 69; Colgan & da Costa 2013: 74; Dayrat *et al.* 2014: 268, fig. 5 B, C.

Siphonaria bifurcata—Hanley 1858b: 151; Angas 1867: 232; Tenison Woods 1878b: 100; Paetel 1873: 173; 1883: 117; 1889: 428; Whitelegge 1889: 117; Hedley 1917b: M95, 1918: M95; Iredale 1924: 276; Hubendick 1955: 4; Berry 1977: 209, fig. 19; Short & Potter 1987: 122 (not *S. bifurcata* Reeve, 1856).

Siphonaria australis—Lamarck 1836: 562; Hanley 1858b: 151; Hochlowski & Faulkner 1984: 3838 (not *S. australis* Quoy & Gaimard, 1833).

Siphonaria baconi Reeve 1856: pl. 6, species 30 (type locality: Swan River, New Holland [Perth, WA, Australia]).—Hanley 1858b: 151; Paetel 1883: 178; 1889: 428; Angas 1865: 189; Tenison Woods 1878b: 100; Pritchard & Gatliff 1903: 221; Verco 1907: 104; 1912b: 204; Iredale 1924: 276; Cotton & Godfrey 1932: 154; Macpherson & Chapple 1951: 142; Hubendick 1955: 129; Macpherson & Gabriel 1962: 264, fig. 302; Hodgkin *et al.* 1966: 27, pl. 8, fig. 4; Galindo 1977: 416; Mapstone 1978: 85; Jenkins 1981: 12, pl. 1 b, c; Roberts & Wells 1981: 72, pl. 30; Trew 1983: 4; Jenkins 1983: 5; Paul 1984: 28; Short & Potter 1987: 122; White & Dayrat 2012: 61.

Siphonaria zealandiae Paetel 1889: 430 (invalid; incorrect subsequent spelling of *zelandica*).

Siphonaria zebra Reeve 1856: pl. 5, species 22 [not species 21] (type locality: Port Jackson [Sydney Harbour], Australia).—Hanley 1858b: 153; Paetel 1889: 430; Hedley 1918: M95; Iredale,1924: 276; Hubendick 1955: 4; Galindo 1977: 416; Jenkins 1983: 5, 12, pl. 1 e–h; Trew 1983: 7; White & Dayrat 2012: 69.

Siphonaria (*Ductosiphonaria*) *baconi*—Hubendick 1945: 70; 1946: 37, pl. 6, fig. 10, 11.

Siphonaria luzonica—Adcock 1893: 11; Shikama 1964: 6, pl. 2, fig. 7 (not *S. luzonica* Reeve, 1856).

Planesiphon elegans Iredale 1940: 441, figs 3–4 (type locality: Keppel Bay, Queensland).—Marcus & Marcus 1960: 122; Jenkins 1983: 5, 12, pl. 1 d, pl. 2 g–h; Short & Potter 1987: 122; White & Dayrat 2012: 63.

Siphonaria (*Ductosiphonaria*) *bifurcata*—Hubendick 1945: 22, 70; 1946: 37, pl. 2, figs 9–13 (not *S. bifurcata* Reeve, 1856).

Siphonaria (*Siphonaria*) *elegans*—Hubendick 1945: 29, 72, fig. 44, 46, 47.

Siphonaria (*Siphonaria*) *australis*—Hubendick 1945: 72; 1946: 49, pl. 3, fig. 28–31 (not *S. australis* Quoy & Gaimard, 1833).

Ductosiphonaria bifurcata—McAlpine 1952: 42, fig. 3 (not *S. bifurcata* Reeve, 1856).

Siphonaria elegans—McAlpine 1952: 42.

Siphonaria (*Pachysiphonaria*) *zealandica* Hubendick 1955: 129–136, figs 5–8 (invalid; incorrect subsequent spelling of *zelandica*).

Ductosiphonaria baconi—Cotton 1959: 411.

Ellsiphon denticulata—Cotton 1959: 411 (not *S. denticulata* Quoy & Gaimard, 1833).

Planesiphon bifurcata—Iredale & McMichael 1962: 82 (not *S. bifurcata* Reeve, 1856).

Siphonaria bifaciata Galindo 1977: 416 (invalid; incorrect subsequent spelling, not *S. bifurcata* Reeve, 1856).

Material examined. *Type material.* Lectotype of *Siphonaria zelandica* Quoy & Gaimard, 1833, from Nouvelle Zealandie [New Zealand (in error for Australia, see Jenkins, 1983: 5)] (MNHN IM 2000-5055, Fig. 26F). Two paralectotypes, same data as lectotype (MNHN IM 2000-5135).

Lectotype of *Siphonaria baconi* Reeve, 1856 from Swan River [Perth, WA] (NHMUK 1979164.1, Fig. 26J). Two paralectotypes of *Siphonaria baconi* Reeve, 1856. Same data as lectotype (NHMUK 1979164.2 and 1979164.3).

Lectotype of *Siphonaria zebra* Reeve, 1856 from Port Jackson [on type label; ‘Philippine Islands’ in Conch. Icon. incorrect—see Taxonomic remarks below] [Sydney, Australia], (NHMUK 1979168/1, Fig. 26H). Three paralectotypes of *Siphonaria zebra* Reeve, 1856. Same data as holotype (NHMUK 1979168/2-4).

Syntype of *Planesiphon elegans* Iredale, 1940 from Keppel Bay, Qld; coll. H. Bernhard, Sept 1935 and 1936 (AM C.103710, Fig. 26L).

Syntypes of *P. elegans* Iredale 1940. Expanded syntype data (AM C.108528, 6d, locations on label of North Keppel Island and Emu Park; AM C.126707, 5d, location on label of Emu Park; MV F13845, 1d, location on label of Emu Park).

Other, non-type material. **Australia, Qld:** Keppel Bay, 23°25’S, 150°55’E (AM C.103710 d); Emu Park, 23°15’S, 150°49’E (AM C.126707 5d); North Keppel Is & Emu Park 2, 3°25’S, 150°55’E (AM C.108528 6d). Caloundra Shelly Beach, 26°48’S, 153°9’E (AM C.391924 d). **NSW:** Fingal Bay nr Port Stephens, 32°44.990’S, 152°10.481’E, NSW09-1 (AM C.585559 3p); Broken Head Terrigal, 33°26.796’S, 151°27.030’E, NSW08-1 (AM C.585380 10p, C.585052 p [M098]);

Terrigal The Skillion, 33°27.008’S, 151°27.122’E, NSW08-2 (AM C.585591 4p, C.585057 p [M222]); Wy-ar-gine Point Balmoral, 33°49.159’S, 151°15.195’E, NSW06-5 (AM C.585445 11p, C.585047 p [M155], Fig. 26I, C.585048 p [M156], C.585049 p [M157]); Bombo Kiama, 34°39.232’S, 150°51.649’E, NSW03-1 (AM C.585557 3p); Murunna Point Camel Head, 36°22.720’S, 150°04.766’E, NSW02-1 (AM C.595960 2p). **Vic:** Bear Gully, 38°53.519’S, 145°59.029’E, V07-3 (AM C.585572 3p); Caves, Inverloch 38°39.777’S, 145°40’871’E, V07-2 (AM C.585359 p); San Remo, headland, 38°31.913’S, 145°22.209’E, V07-4 (AM C.585582 34p); San Remo, 38°31.489’S, 145°21.858’E, V07-1 (AM C.585358 p); Frankston, 38°09.236’S, 145°06.457’E, V06-1 (AM C.585651 5p); West Head Flinders, 38°28.883’S, 145°01.727’E, V06-3 0 (AM C.585717 8p); Point Lonsdale (nr Queenscliff), 38°17.276’S, 144°36.977’E, V05-1 (AM C.585608, 4 p); Roadknight Point, 38°25.707’S, 144°11.102’E, V04-1 (AM C.585474 16p); Marengo Rocks Apollo Bay, 38°46.772’S, 143°39.997’E, V03-1 (AM C.585650 5p); Crofts Bay, 38°35.363’S, 142°50.633’E, V01-3 (AM C.585607 4p, C.585284 p [M177]); Armstrong Bay, 38°21.012’S, 142°21.633’E, V01-2 (AM C.585726 9p). **SA:** Cape Northumberland, 38°03.503’S, 140°40.378’E, SA15-1 (AM C.585351 p); Cape Northumberland Port Macdonnell, 38°03.308’S, 140°39.398’E, SA15-2 (AM C.585723 9p, C.585223 p [M200]); Cape Thomas, 37°04.461’S, 139°44.659’E, SA14-1 (AM C.585766 7p, C.584893 d [R3032], C.584935 p [SK038], C.585218 p [M199]); Fisheries Bay Lands End, 35°37.999’S, 138°06.921’E, SA13-2 (AM C.585713 8p, C.584900 p [SK509], C.585216 p [SK024]); Groper Bay nr West Cape, 35°14.108’S, 136°49.883’E, SA10-1 (AM C.585601 4p); Pondalowie Bay, 35°13.989’S, 136°49.892’E, SA10-2 (AM C.585473 16p, C.585492 p); Port Neill, 34°07.102’S, 136°21.271’E, SA06-1 (AM C.585710 8p); Port Moonta, 34°03.273’S, 137°33.592’E, SA09-1 (AM C.585647 5p); Salmon Point, 33°38.547’S, 134°51.916’E, SA04-2 (AM C.585688 7p); Whyalla, 33°02.539’S, 137°35.511’E, SA07-1 (AM C.585675 6p); Rocky Point, 32°12.250’S, 133°14.861’E, SA02-4 (AM C.585687 7p); Ceduna, 32°07.438’S, 133°40.260’E, SA03-2 (AM C.585707 8p); Denial Bay Ceduna, 32°05.886’S, 133°34.817’E, SA03-1 (AM C.585762 10p); Port Le Hunte Point Sinclair, 32°05.554’S, 132°59.476’E, SA02-2 (AM C.585706 8p); Wandrilla Beach, nr Cape Nuyts 32°01.894’S, 132°16.052’E, SA01-1 (AM C.585522, 20 p). **WA:** Cave Point, 35°06.965’S, 117°54.080’E, WA62-1 (AM C.584768 5p, WAM S74186 5p); Waterbay Point, 35°05.540’S, 117°56.963’E, WA62-2 (AM C.584684 2p, WAM S74187 2p); Peaceful Bay, 35°02.989’S, 116°55.769’E, WA60-7 (AM C.584744 4p, WAM S74183 4p); 35°02.865’S, 116°55.722’E, WA60-8 (AM C.585579 8p); Wilson Head Ocean Beach, 35°02.250’S, 117°19.894’E, WA61-1 (AM C.584730 10p, WAM S74185 5p); Cape Riche 34°36.213’S, 118°45.401’E, WA62-5 (AM C.584714 5p, WAM S74188 5p); Bremer Bay Boat Harbour, 34°25.613’S, 119°23.818’E, WA63-2 (AM C.584773 5p, WAM S74189 5p); Sarge Bay Cape Leeuwin, 34°22.091’S, 115°08.820’E, WA60-4 (AM C.585371 p); Augusta, 34°20.451’S, 115°10.069’E, WA60-5 (AM C.584699 3p, WAM S74182 3p); Alexander Bay 2, 33°53.467’S, 122°44.995’E, WA64-4 (AM C.584776 5p, 74191 5p); Alexander Bay, 33°53.374’S, 122°44.922’E, WA64-3 (AM C.584774 5p, 74190 5p); Salmon Beach Esperance, 33°53.254’S, 121°50.381’E, WA64-2 (AM C.585580 3p); Blue Haven Beach Esperance, 33°53.105’S, 121°51.687’E, WA64-1 (AM C.585314 p [M097]); Cowaramup Point, 33°51.934’S, 114°58.904’E, WA60-3 (AM C.585521 2p); Yallingup, 33°38.358’S, 115°01.481’E, WA60-9 (AM C.584696 3p, WAM S74184 2p); Point Dalling Dunsborough, 33°35.955’S, 115°06.315’E, WA59-4 (AM C.584750 5p, C.595950 p [M129], WAM S74180 5p); Point Casuarina Bunbury, 33°18.544’S, 115°38.201’E, WA59-3 (AM C.585578 3p); groyne nr Robert Point Mandurah, 32°31.270’S, 115°42.409’E, WA59-1 (AM C.585437 5p, WAM S74179 5p); Fremantle Hbr breakwater 32°03.342’S, 115°43.987’E, WA58-5 (AM C.585612 4p); Longreach Bay point, Rottnest Is, 31°59.333’S, 115°32.063’E RI01 (AM C.584783 4p, WAM S74164 4p); Point Brown Swan River, 32°02.344’S, 115°45.471’E, WA59-5 (AM C.584709 4p, C.584899 p [SK039], C.585935 p [M127, SK243], WAM S74181 4p); Grey, 30°39.968’S, 115°08.072’E, WA58-2 (AM C.585367 p); Jurien Bay 30°17.244’S, 115°02.482’E, WA58-1 (AM C.585576 3p); Cambawarra Head Green Head, 30°04.136’S, 114°57.830’E, WA57-6 (AM C.585518 2p); Illawong, 29°42.254’S, 114°57.542’E, WA57-5 (AM C.584708 4p, WAM S74178 4p); Illawong bch rocks, 29°42.198’S, 114°57.551’E, WA57-4 (AM C.584705 4p, WAM S74177 3p); S end Leander Point Port Denison, 29°16.725’S, 114°54.918’E, WA57-2 (AM C.584682 2p, WAM S74176 2p); Leander Point Port Denison, 29°16.568’S, 114°54.858’E, WA57-1 (AM C.584692 3p, WAM S74175 2p); Cape Burney Geraldton, 28°52.084’S, 114°38.056’E, WA54-1 (AM C.584748 3p, WAM S74174 3p); Turtle Bay East Wallabi Is, 28°25.804’S, 113°44.538’E, WA55-1 (AM C.585658 5p); Horrocks, 28°21.469’S, 114°24.751’E, WA53-1 (AM C.584681 2p, WAM S74173 2p); Red Bluff, 27°44.627’S, 114°08.576’E, WA52-2 (AM C.584741 10p, C.595943 p [M124], WAM S74172 10p); Chinamans Rock Kalbarri, 27°42.776’S, 114°09.361’E, WA52-1 (AM C.584740 10p, WAM S74171 10p); Pepper Point (Zuytdorp), 26°23.826’S, 113°18.268’E, WA51-1 (AM C.584756 5p, WAM S74170 5p); Bottle Bay Cape Peron, 25°32.566’S, 113°29.467’E, WA49-1 (AM C.585364 p); Point Quobba, 24°29.124’S, 113°24.501’E, WA45-1 (AM C.584707 4p, WAM S74169 4p); Point Maud, 23°08.322’S, 113°46.294’E, WA44-1 (AM C.584723 5p, WAM S74168 4p); Pt S of Bruboodjoo Pt Bateman Bay, 23°02.991’S, 113°49.371’E, WA43-1 (AM C.584733 12p, WAM S74167 6p); Tantabiddi, 21°54.739’S, 113°58.706’E, WA42-1 (AM C.584691 3p, C.585121 p [SK188], C.585310 p [M207], C.585311 p [M208], WAM S74166 2p); NW Cape Exmouth, 21°48.360’S, 114°07.665’E, WA41-1 (AM C.585363 p); Cape Keraudren, 19°57.393’S, 119°46.358’E, WA29-2 (AM C.584706 4p, WAM S74165 4p); Cape Latouche Treville nr Gourdon Bay,18°27.457’S, 121°48.725’E, WA27-1 (AM C.584342 p [SK067], C.584927 p [SK066]); Catamaran Bay formal, 16°27.622'S, 123°00.242'E, WA22-3 (AM C.585304 p [M045]).

Taxonomic remarks. The original description of *P. elegans* contains no type designation. Hence, we consider all types as syntypes. Jenkins (1983) designated the lectotypes of *S. zelandica* (5, pl. 1, fig. a), *S. baconi* (10, pl. 1, fig. b) and *S. zebra* (11, pl. 1, fig. e). Anatomical and molecular analyses of freshly preserved topotypic specimens matching type specimens of each nominal species and geographical series validate the identity and occurrence of *S. zelandica* and confirm that *S. zebra*, *Planesiphon elegans* and *S. baconi* are junior synonyms. The descriptions of *S. zebra* and *S. bifurcata* were mixed up in Reeve's monograph: The types of '*S. zebra'* match the description of *S. bifurcata* (species 22, figure 21) while the types of '*S. bifurcata'* match the description of *S. zebra* (species 21, figure 22) (see Jenkins, 1983: 28; White & Dayrat, 2012: 60). As a result, the correct type locality of '*S. zebra'* is Port Jackson instead of the Philippines Islands. The labelling errors in Reeve (1856) confused many subsequent authors. Iredale (1924: 276) also noted the transposition and correctly considered that *S. zebra* referred to the same species as *S. baconi. Siphonaria zebra* has been treated as a synonym of *S. sipho* by Reeve (1856), repeated in Schrenck (1867: 306). Hutton (1883: 143) refrained from accepting Reeve's (1856) synonymy. The record of '*S. luzonica*' in Adcock (1893, 11, SA) and listing of *S. stellata, S. exigua, S. baconi* and *S. kurracheensis* as its synonyms are incorrect. Herein we demonstrate that '*S. luzonica*' (= *S. sipho*) and *S. zelandica* are distinct species with different distributions.

Paetel (1883: 178, 1889: 430) and Galindo (1977: 416) incorrectly recorded *S. zebra* from the Philippines. Verco (1907: 104) incorrectly considered *Trimusculus albida* (Angas, 1878) as a possible white form of *S. baconi*. Hubendick (1946: 37) pointed out that Adcock's (1893: 11) synonymisation of *S. baconi* with *S. luzonica* was questionable. The record of '*S. zebra*' in Kuroda (1941: 137, pl. 3, figs 49–50) is a misidentification of *S. rucuana*. Hubendick (1946: 49) treated *S. zelandica* Quoy & Gaimard, 1833 as a synonym of *S. australis* Quoy & Gaimard, 1833. McAlpine (1952: 42) compared the conchology and anatomy of *P. elegans*, *S. diemenensis* and *S.* '*bifurcata'* and species interpretations by Iredale and Hubendick, from which Hubendick (1955: 4–5) subsequently indicated *P. elegans* was a synonym of *S. zelandica*. Confirmed in Jenkins (1983: 4–5, 28) reviewing the type specimens and redescribing the anatomy and distributions. Hubendick (1946: 69) uncertain of the identity of *S. zebra*, suggested it may be identical with *S. plana*. Morrison (1972: 56–58) assigned *S. elegans*, along with 29 other nominal species (*S. zelandica* not mentioned), to *S. laciniosa* without specific explanation other than based on similarity to a '*laciniosa*' shell form and 'common reproductive development'. These synonymies are not supported by examination of type specimens and morpho-anatomy. '*S. zelandica'* in Berry (1977: 204–5, pl. 1), based on Hutton (1882: 343, correctly as *S. australis*) refers to *S. australis*. Trew (1983: 7) considered *S. zebra* a synonym of *S. kurracheensis,* probably following Hubendick (1946: 54), however, is presently indeterminable as location of the material in the collection is not indicated. Jenkins (1983: 5, 10–11, 28) and Wells (1984: 52), treated *S. baconi* as a synonym of *S. zelandica*. The taxon was redescribed by Jenkins (1983: 6, fig. 1C). Here we utilise and expanded the information provided there.

External morphology (Fig. 26M). Foot sole evenly dark grey, foot wall, foot edge mantle, cephalic folds and pneumostome lobe evenly yellow; cephalic folds large; mantle wider than foot wall, thin, translucent; mantle edge unthickened, black edge bands absent; faint irregular black blotches on foot wall and centre of cephalic folds, touch and extend over the mouth region; two small black subepithelial eye spots are centrally located cephalic folds.

Shell (Figs 26F–O; Table S9). small to medium sized, ovate, (max sl mean = 17.2 mm, SD = 1.6 mm, n = 12), height low; apex offset posterior and left, apical sides straight to concave; shell whorl dextral, protoconch direction homostrophic (n = 2; Fig. 26O); growth striae fine to inconspicuous; thickness fine; outer lip is uneven, often broken and finely scalloped with primary ribs extending past the outer lip; rib count (mean 48, SD = 5.1, n = 12), white primary ribs slightly raised, mainly broad, apically continuous, radiate from the apex with black to light brown interstices finely striated with four to six apically discontinuous secondary ribs; exteriorly the siphonal ridge is indistinct; pneumostomal margin of the shell slightly raised and the outer edge extends weakly out to the right side; interior smooth with brown to white spatula, slightly swollen margin; brown apical rays are often presented extending from the spatula to slightly swollen lip margin corresponding with exterior rib interstices; siphonal groove (fig. 1C, sg) is shallow, smooth, of a similar colouration to the spatula; CMS (fig. 1C, cms) is shallow and weakly concave to straight; ADM scars are similarly shallow, may be darker or lighter brown than the spatula. Juvenile shells are miniature adults displaying similar ribbing but with paler interiors and exteriors.

Reproductive system (Figs 27C–D; n = 5). HG (ovotestis), large yellow, granular and AG both located in posterior region of coelom, against inner foot wall and under the respiratory system; HG joined to anterior of soft folds of AG by a short pink lobed HD, passes and between the translucent soft white semicircular folds of the MG and the white AG; thin white CD emerges from MG. SV small ovate pinkish, connected via a short thin duct to the junction of the HD and CD. BD long thin white, passes alongside but dorsal to the much thicker CD through the adductor muscle and both enter adjacently into the GA; both CD and BD smooth, non-looped, featureless; BC small, brown, appears spherical when holding SPM but deflated when empty; ED long, thick, white and may be centrally looped (Jenkins, 1984: fig 1b), enters the GA almost opposite the BD and CD juxtaposed points of entry, no AO present; EG, cream, soft, lobed, longer than ED; single F1, short, broad, white, branching from the

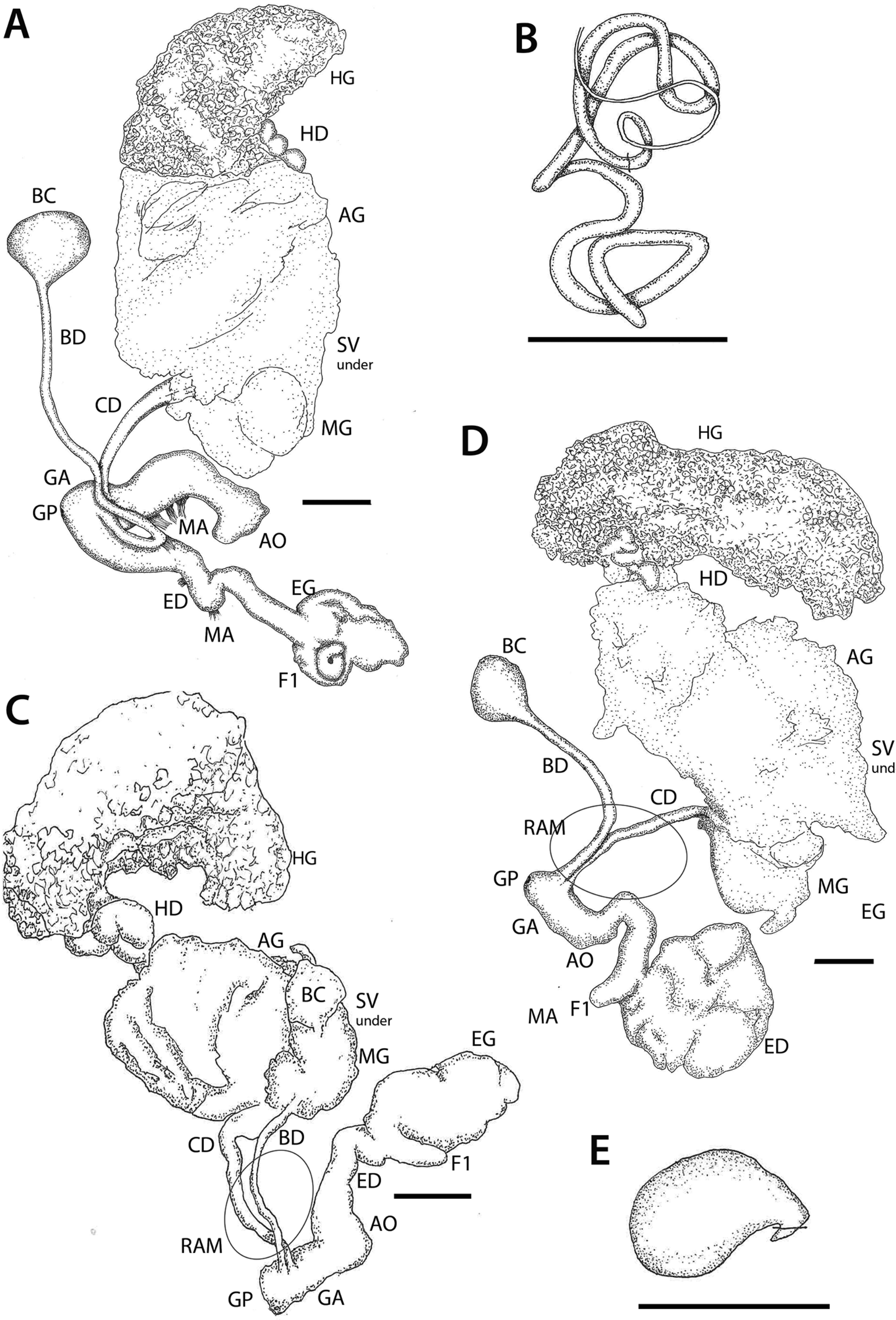

FIGURE 27. Reproductive anatomy of *S. guamensis* and *S. zelandica*. **A–B.** *S. guamensis*, Guam, Umatac Bay, TS, AM C.584872 [M346, SK241]. **C–E.** *S. zelandica*, **C**. WA, Cape Latouche Treville, AM C.584342 [SK067]. **D.** NSW, Sydney Harbour, TS of *S. zebra* AM C.585047 [M155, SK235]. **D.** SA, Cape Thomas, AM C.584935 [SK038]. Scale bars = 1 mm.

junction of the EG and ED. GP small, opens from GA through the foot wall, under the mantle and posterior to the right cephalic fold.

Spermatophore (Fig. 27E). Drop-like with short, hooked flagellum (length = 1.12 mm, n = 1); head section bulbous, round tip (head length = 1.0 mm, head ~86% of SPM length; head width = 150 µm; flagellum width = 34 µm), body and flagellum test opaque, thick, tapering to a pointed end; both sections featureless; 1 SPM in brown gelatinous mass in one BC.

Radula (in Jenkins, 1983: pl. 6, fig. a–c). Wide intraspecific variation exists in the number of transverse rows and the number of inner, mid and outer lateral teeth in longitudinal rows. The mean dentition formula is 28:1:28 (SD = 3.8, n = 7) with 122 parallel and slightly curved (anteriorly convex) transverse rows (SD = 6.5, n = 8). Of the 28 half row laterals, 10 (SD =2.4) are inner, 2 (SD = 0.8) mid and 16 (SD = 1.5) outer teeth means respectively (n = 8). In each longitudinal row a gradual reduction in tooth size and an increase in distance between transverse rows occurs from the central tooth to the outer laterals. All teeth are bluntly concave posteriorly. The central tooth has a lower profile than the flanking laterals and a short pointed mesocone less than half the base length. The anterior is forked and wider than the notched posterior. The narrow base interlocks and articulates with the adjacent central teeth. Lateral teeth have broad bases. The mesocone of the inner laterals is either pointed or bicuspidate. The inner cusp is always longer and usually overlapping the posterior of the inner lateral in front. Ecto and endocones are absent. The mid laterals have an ectocone and a bluntly bicuspidate mesocone with the inner cusp being longer. Outer laterals have a square shaped base with a broad blunt mesocone flanked by short pointed ecto and endocones. The clefts between the mesocones and the side denticles of the outer laterals are widely variable in width and angle of separation. Around the third or fourth outer longitudinal row, often aberrant outer lateral teeth appear as fused teeth with double mesocones.

Comparative remarks. *Siphonaria acmaeoides* from Japan is the closely related sister species of *S. zelandica* (*atra* group, unit 26) (Figs 1, 2). Both species differ from each other by a genetic distance of at least of 5.8% (Table S4). The next closely related species are *S. restis* **sp. nov.** (distance = 23%) and *S. stowae* (distance = 17.7%) (Table S4). Examination of the type specimens and topotypic specimens of *S. zelandica* and *S. acmaeoides* revealed differences in shell geometry, the spacing of ribs, secondary ribbing, colouration, and reproductive features. Both taxa occur in splendid isolation from each other and are maintained as distinct species. Throughout the range of *S. zelandica*, we found seventeen congeners with partly sympatric distributions. Five species are sympatric in southern Qld. For comparisons with *S. atra*, *S. denticulata*, and *S. viridis* refer to comparative remarks under these species. *Siphonaria hienghenensis* **sp. nov.** has a larger, darker shell with more raised ribbing, a more prominent siphonal ridge, darker interstices, and interior colouration, a larger AO and BC, BD with distal loop, and a thread-like SPM. *Siphonaria opposita* has a larger shell with a more prominent and flared siphonal ridge, and stronger edge scalloping, a larger AO, ED and BC, and a thread-like SPM. *Siphonaria scabra* has a larger, taller, darker shell with more raised ribbing, rougher exterior, stronger edge scalloping and a darker interior, larger AO and BC, longer ED, and a long thread-like SPM.

Seven congeners are sympatric in NSW (along with *S. denticulata* and *S. scabra*). For comparison with *S. diemenensis* refer to comparative remarks there. *Siphonaria emergens* has a much smaller, orange-brown shell with less raised ribbing and an apex more posteriorly offset. *Siphonaria funiculata* has a shell with paler ribs and with dark brown interstices, a larger AO and BC, shorter BD, and a longer ED. *Siphonaria pravitas* **sp. nov.** has a taller shell with more raised prominent ribbing and siphonal ridge, stronger edge scalloping, a larger BC, and a thread-like SPM. *Siphonaria stowae* has a taller and much smaller, yellowish-cream shell, a larger BC, and a thread-like SPM.

Six congeners are sympatric in Vic and SA Australia (along with *S. denticulata, S. diemenensis, S. funiculata* and *S. stowae). Siphonaria jeanae* has a smaller, darker, grey blue shell with brown ribs and purplish spatula, a very small to absent AO, broader and twisted ED, and a bulbous SPM. *Siphonaria tasmanica* has a taller, blue grey shell with a more central apex and less distinct siphonal ridge, a shorter BD, and smaller BC.

Six congeners are sympatric in WA (along with *S. atra*, *S. jeanae* and *S. stowae*). *Siphonaria alba* has a larger shell with central apex, raised ribbing and stronger edge scalloping, a larger AO and BC, longer ED, and a longer, thread-like SPM. *Siphonaria gemina* **sp. nov.** has taller darker shell with more prominent siphonal ridge and stronger edge scalloping, a larger ED and BC, shorter BD, and a thread-like SPM. *Siphonaria restis* **sp. nov.** has a taller shell with more prominent and raised ribbing and siphonal ridge, stronger edge scalloping, a larger AO, BC and ED, long narrow F1, and a thread-like SPM.

Siphonaria zelandica displays a shell morphology like other species in the *plicata* group, but the structure of RS in each of these species differs (mainly size of BC; epiphallus parts of ED and F1).

Hubendick (1945: 29, 72, figs 44, 47; 1946: 56–57, pl. 4, figs 32–34) treated *S. elegans* as an accepted species. However, he mis-identified specimens of either *S. sipho* or *S. bifurcate S. zelandica*. The RS of '*S. elegans'* figured in Hubendick (1945: 30–31, figs 44, 47) corresponds to *S. zelandica* depicted herein (Fig. 27C–D). The RS of '*D. bifurcata*' figured by McAlpine (1952: 43, fig. 3) does also closely resemble that of *S. zelandica*.

The records of *S. zelandica* by Lamarck (1836: 558), Hutton (1873: 55, 1878: 41; 1880: 36; 1883: 143, pl. 17, figs H–M; 1904: 68), Suter (1904: 68; 1913: 600; 1915), Iredale (1915), Oliver (1923: 498), Odhner (1924: 55), Bucknill (1924: 84), Powell (1933: 186; 1937: 86; 1939: 217; 1946: 91), Borland (1950: 386), Knox (1955: 86), Powell (1955: 120; 1957a: 114), Dell (1960: 147, 1963: 227), Morton & Miller (1968: 83, pl. 19, fig. 8, 8a), Galindo (1977: 416), Powell (1979: 292, pl. 54, fig. 10), Trew (1983:7) and Wells & Wong (1978: 417) are all misidentifications of *S. australis* (refer Jenkins, 1983: 1).

Hubendick (1946) was uncertain about the identities of *S baconi* and *S. zebra*; probably because of the mix-up of the figures in Reeve's descriptions of both species). Hubendick (1945: 80; 1946: 37) treated '*S. baconi'* as accepted, but Hubendick (1946: 37, pl. 2, figs 9–13) tentatively placed it under '*S. bifurcata*'. The figures of '*S. baconi*' in Hubendick (1946: 92, pl. 4, figs 33–34) are specimens of *S. zelandica*. Hubendick (1946: 54) also tentatively placed *S. zebra* in synonymy of '*S. kurracheensis*' and listed the variant of *S. kurracheensis* var. *zebra* (pl. 2, fig. 37). This figure is attributed here to *S. belcheri*. Figures of '*S. elegans*' in Hubendick (1946: pl. 4, fig. 33–34) from 'Kupang, Timor and Java Sea' are likely specimens of *S. viridis*. Specimens figured as '*S. baconi'* in Hubendick (1946: 91, pl. 6, fig. 10–12) are specimens of *S. zelandica*. The SPM depicted herein (Fig. 27E) resembles that figured in Hubendick (1955: 10, fig. 8) of '*S. zealandica*' apart from a shorter flagellum (possibly broken). The record of *S. zelandica* in Davey (1998: 117) is a specimen of *S. denticulata*. Figured specimens 'unit 26' in Dayrat *et al.* 2014: fig. 5B, C) correspond well with *S. zelandica*.

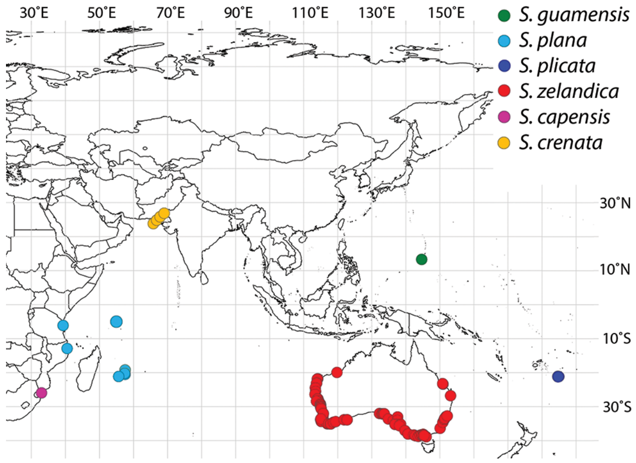

FIGURE 28. Known occurrence records of *S. crenata*, *S. capensis*, *S. guamensis*, *S. zelandica*, *S. plana* and *S. plicata*

Distribution and habitat. Endemic to Australia, from Keppel Bay, Qld, south along NSW, Victorian and SA coasts to Broome, WA (Fig. 28). Reasonably common in sheltered positions, often within runoff areas and shallow platform pools (Fig. 26D), on exposed to moderately exposed rocky intertidal marine shores across upper and mid littoral levels.

Siphonaria plana Quoy & Gaimard, 1833

(Figs 29A–D, M, 30A–B)

Siphonaria plana Quoy & Gaimard 1833: 342 pl. 25, fig. 21, 22 (type locality: 'lle de France, dans les environs du Port Louis' [Mauritius, in the vicinity of Port Louis]).—Lamarck 1836: 558; Anton 1838: 26; Lamarck 1839: 205; Catlow & Reeve 1845: 100; H. Adams & A. Adams 1855 (in 1853–1858): 271; 1863: 271; Gould 1852: 359, Hanley 1858b: 152; Deshayes 1863: 83; Paetel 1873: 117; 1875: 92; Martens 1880: 310; Paetel 1883: 178; 1889: 429; Hubendick 1946: 69); Michel 1974: 243; Galindo 1977: 416; Trew 1983: 6, 8; Subba Rao & Dey 2000: 190; White & Dayrat 2012: 67.

Siphonaria ferruginea Reeve 1856: pl. 5, species 26 (without type locality).—Deshayes 1863: 82; Lienard 1877: 59; Martens 1880: 310; Paetel 1883: 178; 1889: 428; Dall 1890: 299; Hubendick 1945: 29; 1946: 53; Michel 1974: 243; Galindo 1977: 416; Trew 1983: 5; Drivas & Jay 1988: 132, pl. 51, fig. 17; White & Dayrat 2012: 63.

Siphonaria feruginea Hanley 1858b: 152.—Paetel 1873: 117; 1889: 428 (invalid; incorrect subsequent spelling of *ferruginea*).

Siphonaria atra—Dautzenberg 1923: 24; Drivas & Jay 1988: 132, pl. 51, fig. 19 (not *S. atra* Quoy & Gaimard, 1833).

Siphonaria (*Siphonaria*) *ferruginea*—Hubendick 1946: 53, pl. 4, figs 16–19.

Siphonaria 'atra group, unit 35'—Dayrat *et al.* 2014: 262–263, fig. 5M–N; Ossenbrügger *et al.* 2023: 38, figs 3–4.

Material examined. *Type material.* Lectotype of *Siphonaria plana* Quoy & Gaimard, 1833, present designation, from Île-de-France [Mauritius] (MNHN IM 2000-35955, Fig. 29A). Two paralectotypes, same data as lectotype (MNHN IM 2000-5056).

Three syntypes of *Siphonaria ferruginea* Reeve, 1856 (NHMUK 1981001, Fig. 29B).

Other, non-type material. **Mauritius:** Souillac, 20°31.467'S, 57°31.582'E, MRU01-2 (AM C.584968 p [M254]); Nth Albion, MRU02-1 (AM C.585734 21p, AM C.584969 p [M251]; C.584970 p [M252]).

Taxonomic remarks. The largest syntype of *S. plana* is herein designated as the lectotype for the stabilisation of the name (Art. 74.1 of the Code). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 29C) and geographic series of additional specimens (Table S1). We establish *S. ferruginea* (Fig. 29B) as a new synonym. Reeve (1856) treated *S. plana* as a synonym of *S. lineolata* Sowerby I, 1835 based on specimens from Chile and Central America; which were misidentified (see Hubendick 1946: 68). Later, Carpenter (1864a 545) incorrectly considered *S. ferruginea* as a variety of the New World species *S. lecanium* Philippi, 1846, intermediate between *S. maura* and *S. palmata*. Hubendick (1946: pl.4, figs 16–19) depicted specimens from Mauritius that closely resemble the type of *S. ferruginea* (Fig. 29B). However, his interpretation of this species is confused. He stated that *S. plana* was a 'non-defined or insufficiently defined' species that may be identical with '*S. kurracheensis var. luzonica* or *zebra*'. He also assigned specimens from Queensland figured by Iredale (1940: pl. 34, figs 26–27) as '*L. optivus'* under *S. ferruginea*. However, we treat *L. optivus* as a junior synonym of *S. viridis*. Morrison (1963: 8) erroneously considered *S. ferruginea* as a synonym of the New World species *S. alternata* (Say, 1826). Subsequently, Morrison (1972: 56–58) treated *S. plana* as a junior synonym of *S. laciniosa* based on similarity in the shell and a 'common reproductive development'. This synonymy is not accepted herein based on examination of types and supplementary material.

External morphology. Foot sole, foot wall, mantle, cephalic folds and pneumostomal lobe evenly pale grey/cream, paler at edge foot/wall; blotches of black pigmentation on centre of cephalic folds, faintly on foot wall; mantle narrower than width of foot wall, non-translucent, covers exposed inner shell lip, edge thickened, lobed, vertical bands of black pigmentation aligned with shell rib interstices; genital pore indistinct, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two centrally touching cephalic folds; pneumostomal lobe long under the mantle between the right ADMs.

Shell (Figs 29A–D; Table S9). Small to medium sized (max sl mean = 16.8 mm, SD = 2.1 mm, n = 3), circular ovate; height low; apex offset left central and slightly to posterior, apical sides weakly convex, straight to concave at posterior; shell edge uneven; protoconch direction heterostrophic (n=3), shell whorl dextral; growth striae prominent, exterior brown, radial colour banding often present, edge dark, mid pale, protoconch area darker; shell thickness medium; rib count (mean = 39.3, SD = 1.7, n = 3), ~ 20 distinct primary ribs, white to pale, fairly straight, rib growth uneven, ridges rounded, broaden to scallop and protrude beyond shell edge (< 1 mm); 2 interspersed pale white finer secondary ribs, rib interstices darker; paired primary ribs on siphonal ridge, more prominent and extend further than other primary ribs. Interior shell dark chocolate brown, maybe mottled whitish; white rays extend from the shell lip to over the shell margin fading to the spatula, align under primary/secondary ribs, spatula dark chocolate brown; siphonal groove distinct, similar colour to margin and spatula; ADM scar distinct, CMS concave, variable colouration of shell interior common (e.g., Fig. 29D).

Reproductive system (Fig. 30A; n = 1). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior over back of BM and between RAM; size of RS small to animal size; GP singular, positioned through foot wall behind right cephalic fold, GA very small; AO short, narrow, bluntly pointed, joins at top underside of GA in conjunction with ED; ED elongated, broad, joins to back side of GA alongside AO; single short broad blunt centrally bent flagellum (F1), same width as ED, appears as extension of ED, marked by connection of very small white folded EG; AO, GA and ED all muscular white tissue; BD and CD connect closely side-by-side into upper GA, CD connection bulbous, BD twisted with distal loop and MA over ED, both ducts narrow smooth featureless, pass together through RAM connecting into MG (BD above CD), BD often looped immediately in front of BC and longer than increasingly broader CD; BC large, elongated, embedded in folds of AG/MG; SV embedded on left side of AG; HD short, thick uncoiled, links AG to smaller yellowish granular HG; MG and AG folded, soft white tissue; both curved reflecting the close positioning to curvature of inner foot wall on right posterior of coelom; outer edge of small MG lobed.

Spermatophore (Fig. 30B). Thread-like, test thin, translucent (length = 10.17 mm, n = 1, AL = 14 mm); head section cylindrical, bulbous, centrally bent, rounded tip; test thin, smooth, featureless, translucent, tapers into short flagellum; head slightly shorter, wider than translucent flagellum (head length = 4.31 mm, ~ 42% of total length, head width = 103 µm, flagellum width = 17 µm, n = 1); six tightly coiled SPMs found in a single BC of a topotypic specimen (AM C.584970).

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 2), *Siphonaria plana* (*atra* group, unit 35) is the sister taxon of unit 34 (= *S. opposita* **sp. nov.**). Both species are separated by COI distances of ≥ 8.1% (Table S3). *Siphonaria plana* differs from *S. denticulata* by COI distances of ≥ 14.8% and from other species by distances of ≥ 20% (Table S3).

Throughout the range of *S. plana* we found six congeners to occur in partial sympatry. Three are sympatric in Mauritius: For comparison with *S. viridis* refer to comparative remarks under that species. *Siphonaria griffithsorum* **sp. nov.** has a smaller, taller shell with weaker edge scalloping, larger AO, longer BC and F1. *Siphonaria gemina* **sp. nov.** has a smaller shell with more raised ribbing and weaker edge scalloping, a smaller BC, shorter BD, and shorter SPM. *Siphonaria incerta* has a smaller, taller shell with less raised ribbing and weaker edge scalloping, a larger AO, smaller BC, and longer F1. Two species are sympatric in Mozambique: For comparison with *S. capensis* refer to comparative remarks under that species. *Siphonaria carbo* has a smaller, darker shell with finer ribbing and weaker edge scalloping, an indistinct AO, larger, elongate BC, BD without bursal or distal loops, and a smaller, bulbous SPM.

Figured specimens '*atra* group, unit 35' in Dayrat, Goulding & White (2014: 263, fig. 5M, Q) as well as Ossenbrügger *et al*. 2023 (figs 3–4) correspond well with *S. plana* and fall into the same genetic cluster, unit **35**, as topotypic specimens examined herein.

Distribution and habitat. Indian Ocean: recorded from Mauritius, Réunion, the Seychelles (Ossenbrügger *et al*. 2023), and eastern Africa (Pemba Bay, Zanzibar) (Fig. 28). Dayrat *et al.* (2014: 255) listed a single sequenced but unfigured specimen from Rangong Kampuan, Thailand in 'unit 35'. The occurrence of *S. plana* in Thailand requires confirmation. Common in sheltered positions on moderately exposed inner-lagoon rocky intertidal marine shores across upper littoral levels.

Siphonaria plicata Quoy & Gaimard, 1833

(Figs 29E–G, N–O, Q–R, 30C–D)

Siphonaria plicata Quoy & Gaimard 1833: 346, pl. 25, figs 26–27 (type locality 'Île de Tonga-Tabou au village de Hifo' [= Hihifo, Tongatapu, Tonga]).—Lamarck 1836: 557; Anton 1838: 26; Lamarck 1839: 205; Catlow & Reeve 1845: 100; H. Adams & A. Adams 1855 (in 1853–58): 271; Hanley 1858b: 152; H. Adams & A. Adams 1863: 271; Paetel 1873: 117; 1875: 92; 1883: 178; 1889: 429; Galindo 1977: 416; White & Dayrat 2012: 67.

Siphonaria tongensis Hubendick 1943: 6, figs 4, 8 (type locality Foua, Tonga-Inseln [Tonga]).—Hubendick 1946: 63, pl. 5, figs 29–31; White & Dayrat 2012: 68.

Siphonaria sipho—Reeve 1856: pl. 2, species 9; Hanley 1858b: 152 (not *S. sipho* Sowerby I, 1823).

Siphonaria (*Siphonaria*) *laciniosa*—Trew 1983: 6 (not *S. laciniosa* (Linnaeus, 1758)).

Material examined. *Type material*. Lectotype of *Siphonaria plicata* Quoy & Gaimard, 1833, present designation, from 'Île de Tonga-Tabou au village de Hifo' [Hihifo, Tongatapu, Tonga] (NMHN IM 2000-35956, Fig. 29E). Two paralectotypes, same data as lectotype (NMHN IM 2000-5057). Holotype of *Siphonaria tongensis* Hubendick, 1943 from 'Foua, Tonga-Inseln' [Foua Island, Tonga]; coll. Eugenie Expedition, 1851–1853 (UUZM

1576, Fig. 29N). Paratype, same data as holotype (UUZM 1576).

Other, non-type material. **Tonga:** Tongatapu, Ha'atafu Beach Hihifo, 21°04.140'S, 175°20.048'W, TO02-1 (AM C.585539 20+p, C.585275 p [M418, SK104], C.585276 p [M419, SK106], C.585277 p [SK105], C.585278 p [SK225]); Mau'i Rock, W coast Tongatapu, 21°08.154'S, 175°20.706'W, TO01-1 (AM C.585431 20+p); Halafuoleva Beach, S coast Tongatapu, 21°08.358'S, 175°02.443'W, TO03-1 (AM C.585947 20p, C.585283 p [SK223[]); nr Kolonga, N coast Tongatapu, 21°12.021'S, 175°14.680'W TO04-2 (AM C.585432 10+p, C.585432 p [SK380]).

Taxonomic remarks. The largest syntype with best preserved external sculpture (Fig. 29E) is herein designated as the lectotype of *S. plicata* for the stabilisation of the name (Art. 74.1 of the Code). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 29F–G) and geographic series of additional specimens (Table S1). We establish *S. tongensis* as a junior synonym based on the examination of the types (Fig. 29N). Reeve (1856) erroneously considered *S. plicata* as a synonym of *S. sipho,* a view adopted by Hanley (1858b: 152). Hubendick (1946) and Trew (1983: 6) placed *S. plicata* in the synonymy of *S. laciniosa* without providing an explanation or having examined the types. Morrison (1972) treated *S. tongensis* as a junior synonym of *S. laciniosa* based on similarity in shell form and for a 'common reproductive development'.

External morphology (Fig. 29R). Foot sole centrally dark grey fading to yellowish at foot/wall edge; intensity of tissue colouration (i.e. of foot edge, foot wall and mantle) varies between paler and darker shell forms; external morphology is otherwise consistent; paler form (LIF01 and FI03-2)—foot wall and mantle intense yellow; darker form (TO03-1 and LIF02-1)—foot wall and mantle more greenish; both forms possess black pigmentation spots on foot wall, paler to foot edge; fringing mantle weakly lobed, translucent and reflects foot wall colouration, covers exposed inner shell lip; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two centrally touching cephalic folds; pneumostomal lobe thin, part of the mantle, between the right ADMs, closes the pneumostome at the mantle edge.

Shell (Figs 29E–G, N, Q; Table S9). Small to medium sized (max sl mean = 14.9 mm, SD = 0.4 mm, n = 6), ovate; height medium to tall; apex offset weakly posterior and to left, apical sides strongly convex, posterior side concave close to protoconch convex to margin; protoconch direction homostrophic to central (n = 3; Fig. 29Q); shell whorl dextral; growth striae prominent in bands, shell thickness thick; ribs fairly even in width, rib count (mean = 56.3, SD = 1.7, n = 6), exterior uneven without prominent radial colour bands; primary ribs pale grey, fairly straight to wavy, slightly broaden increasingly raised to shell edge, ridges rounded narrow; edge finely scalloped and unevenly corrugated; 6–8 prominent spread radial ridges, one being siphonal ridge, each formed by 3–5 primary ribs; few finer secondary ribs, rib interstices darker grey; interior shell margin white, dark brown rays from shell lip over shell margin to spatula, align under rib interstices, siphonal groove distinct, same colour as shell margin; spatula golden brown to white; ADM scar distinct, darker brown, CMS convex; thickening and whitening of shell lip occurs (Fig. 29E).

Reproductive system (Fig. 30C; n = 3). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned over back of BM, close to BC and to side of RAM; AO medium, broad, blunt, merges with MA, joins to inner side of a small GA; ED relatively short, centrally twisted, bent; EG folded, bulbous with pointed tip; single long narrow looped or bent flagellum F1 on EG; AO, GA and ED all muscular white tissue; BD and CD with opposing connections (bulbous at CD) into GA between ED, AO and GP; BD longer and narrower than CD with a prominent distal loop, top of loop attached via a long MA to inner foot wall in front of BM; both BD and CD smooth and pass together through RAM connecting into folds of MG (BD above CD), BC small, translucent test and bulbous drop shaped; HD brownish, broad coils, links AG to a small elongated narrow brownish granulated HG; MG and AG small folded soft white tissue; dark SV embedded within AG, AG larger than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 30D). Test thin, translucent (length = 10.89 ± 1.66 mm, n = 2); head bulbous, tip bluntly rounded, containing a white gelatinous mass; taper region into the filamentous transparent flagellum is extended; both sections smooth, featureless; head longer and much thicker than flagellum (head length = 6.09 mm, head ~57% of SPM length; head width = 64 µm, SD = 1 µm; flagellum width = 1 µm); Six SPM tightly coiled in brown gelatinous mass in BC (AM C.585275).

Comparative remarks. In our mitochondrial phylogeny, *S. plicata* (*plicata* group, unit 56) is genetically well-differentiated. It is related to several species from Pacific Islands, such as Guam, New Caledonia and Hawaii (Figs 1, 3). The species differs from other species by COI distances of ≥ 25% (Table S7). In Tonga we found one sympatric congener, *S. tongatapuensis* **sp. nov.** which differs by having a more prominent dual ribbed siphonal ridge, a more central apex, lower height, paler interior colouration, a shorter wider ED, a larger pointed AO and longer BD. with bursal loop. Generally, the shell of *S. plicata* is similar to that of other species in the *plicata* group.

Distribution and habitat. Known only from Tonga (Fig. 28). In this study found in sheltered positions (i.e., hollows on beach rock platforms, small pools, hollows of rocky cliff bases) on exposed rocky shores or landside of lagoons at mid and lower littoral levels. Two distinct forms appear to occupy different substrates: a smaller, taller shell morph ('*monticulus*'-morph) occupies pits or hollows in vertical limestone cliffs, the larger, flatter shell morph was ('*plicata*'-morph) is found on rock platforms, in hollows or on flat surfaces.

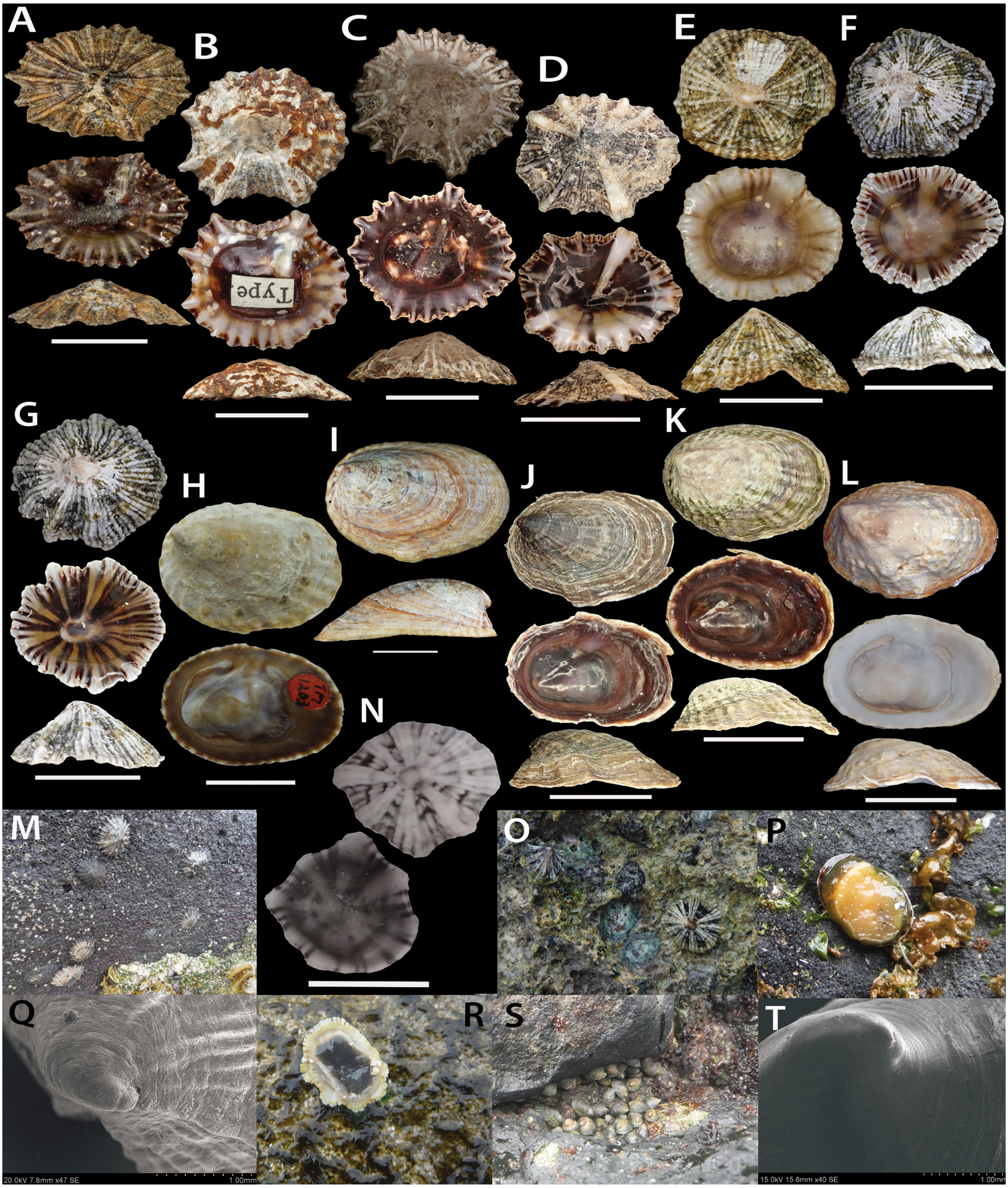

FIGURE 29. Shells of *S. plana*, *S. plicata* and *S. lateralis*. **A–D, M.** *S. plana*. **A.** Lectotype MNHN-IM-2000-35955. **B.** Syntype of *S. ferruginea* NHMUK 1981001. **C–D.** Mauritius, Nth Albion, TS. **C.** AM C.584970 [M252]. **D.** AM C.584970 [M254]. **M.** *In situ*. **E–G, N–O, Q–R.** *S. plicata*. **E.** Lectotype MNHN-IM-2000-35956. **F–G.** Tonga, Ha'atafu Beach, TS of *S. tongensis*. **F.** AM C.585275 [M418]. **G.** AM C.585276 [M419]. **N.** Holotype of *S. tongensis* UUZM 1576. **O.** *In situ*. **Q.** Protoconch, AM C.585278 [SK225]. **R.** Animal, Halafuoleva Beach. **H–L, P, S–T.** *S. lateralis*. **H.** Lectotype of *K. innominata* GNS TM1203. **I.** Holotype of *Kerguelenia macquariensis* AWMM MA.70376. **J–T.** Macquarie Is, TS of *K. innominata*. **J.** AM C.584961 [M469, SK271]. **K.** AM C.584960 [M468, SK270]. **L.** AM C.91959 [SK202]. **P.** Animal. **S.** *In situ*. **T.** Protoconch, AM C.584962 [SK272]. Scale bars = 10 mm.

Siphonaria lateralis Gould, 1846
(Figs 29H–L, P, S–T, 30E–G)

Siphonaria lateralis Gould 1846: 11 (type locality: Burnt Island, Orange Harbor [Tierra del Fuego, Argentina]).—Gould 1848: 153; 1852: 363; 1856: 12, fig. 462 a,b; Hanley 1858b: 152; H. Adams & A. Adams 1855 (in 1853–58): 271; 1863: 271; Rochebrune & Mabille 1888: H.29; Paetel 1889: 428; Lamy 1910: 202; Iredale 1915: 478; Lamy 1915: 74; 1931: 581; Powell 1937: 86; Gaillard 1954: 525; Powell 1955: 122; 1960: 163; Simpson 1976: 11; White & Dayrat 2012: 64; Güller *et al.* 2015: 87, fig. 6A, E, I; González-Wevar *et al.* 2018: 3.

Siphonaria redimiculum—Hutton 1880: 36; 1883: 143; Hedley 1916: 61; Filhol 1880: 552; Melvill & Standen 1907: 142; Dell, 1964: 290 (not *S. redimiculum* Reeve, 1856).

Siphonaria (*Liriola*) *lateralis*—Dall 1870: 32; Suter 1909a: 33; 1913: 601; Tomlin 1948: 229; Christiaens 1980a: 81.

Kerguelenia redimiculum—Suter 1909a: 37; Iredale 1915: 478; Hedley 1916a: 61; Powell 1937: 86 (not *S. redimiculum* Reeve, 1856).

Siphonaria tristensis—Suter 1904: 68 (not *Siphonaria tristensis* Sowerby I, 1823).

Kerguelenia redemiculum Lamy 1910: 202 (invalid: incorrect subsequent spelling of *redimiculum*; not *S. redimiculum* Reeve, 1856).—Powell 1937: 86; 1939: 237.

Kerguelenia innominata Iredale 1915: 478 (type locality: subantarctic Islands of New Zealand).—Hedley 1916a: 62; Odhner 1924: 55; Finlay 1927: 442; Powell 1937: 86; 1939: 237; 1955: 122; Hubendick 1945: 66; White & Dayrat 2012: 64.

Kerguelenia lateralis—Hedley 1916a: 62.

Kerguelenia macquariensis Powell 1939: 328, pl. 49, figs 9–10 (type locality: Macquarie Island [Australia]).—Hubendick 1945: 66; Powell 1946: 91; Dell 1964: 290; White & Dayrat 2012: 65.

Siphonaria (*Kerguelenia*) *lateralis*—Hubendick 1945: 66, fig. 15, 59; 1946: 26, pl. 1, figs 22–25; Marcus & Marcus 1960: 114.

Kerguelenella lateralis—Carcelles 1953: 206; Powell 1957a: 114, pl. 31, figs 9, 10; 1957b: 137; Dell 1964: 290; 1971: 215; Gaillard 1971: 298; Arnaud 1974: 452; Simpson 1977: 126, 132, fig. 7; Powell 1979: 279, pl. 54, figs 18, 19; Branch *et al.* 1991: 55; Forcelli 2000: 132, fig. 423; Griffiths & Waller 2016: 1147.

Kerguelenella redimiculum—Powell 1955: 122.

Kerguelenella innominata—Boreham 1959: 71; Powell 1957a, 114; 1979: 293, pl. 54, figs 16–17; Raven & Bracegirdle 2010: 46.

Siphonaria (*Pugillaria*) *lateralis*—Morrison 1963: 8.

Siphonaria magellanica—Dell 1964: 290 (not *S. magellanica* Philippi, 1857).

Kerguelenella lateralis macquariensis—Powell 1946: 91, figs 9–10; 1955: 122; 1957b: 140; 1960: 163.

Siphonaria lateralis macqueriensis—Galindo 1977: 416 (incorrect subsequent spelling of *macquariensis*).

Pugillaria lateralis—Trew 1983: 3.

Siphonaria (*Kerguelenella*) *lateralis*—Chambers & McQuaid 1994b: 418; Chambers *et al.* 1998: 51.

Siphonaria '*lateralis* group, unit 6'—Dayrat *et al.* 2014: 266, fig. 3F–G.

Material examined. *Type material*. Holotype of *Siphonaria lateralis* Gould, 1846 from 'Burnt Island, Orange Harbor' [Tierra del Fuego, Argentina]; coll. Carpenter (USNM 5853, figured in Güller *et al.* 2015: 88, figs. 6A, E, I).

Eight syntypes of *S. macgillivrayi* Reeve, 1856 from Island of St. Paul's [Indian Ocean] (NHMUK 1981003).

Lectotype of *S. redimiculum* Reeve, 1856, designated by Güller *et al.* (2015: 92, fig. 8O, T), without type locality (NHMUK 1981004/1). Four paralectotypes of *S. redimiculum*, same data as lectotype (NHMUK 1981004/2-5; figured by Güller *et al.* 2015: fig. 8P–S).

Lectotype of *Kerguelenella innominata* (Iredale, 1915), designated by Boreham (1959: 71), from Disappointment Island, Auckland Islands [New Zealand] (GNS TM1203, Fig. 29H); two paralectotypes, from Auckland Is; coll. Capt Bollons (AM C.43852).

Holotype of *Kerguelenia stewartiana* Powell, 1939 from Akers Point, Stewart Island, NZ; coll. R.H. Harrison (AWMM MA.70377); paratypes of *K. stewartiana*; same data as holotype, one (MA71589), two (GNS TM1969, TM 1970), 10 (AM C.585966); one from Akers Island, Stewart Island, New Zealand; coll. R.H. Harrison (USNM 880297).

Holotype of *Kerguelenia macquariensis* Powell, 1939: 238 from Macquarie Island, Australia; coll. H.J. Finlay (AWMM MA.70376; Fig. 29I). Two paratypes of *K. macquariensis*, same data as holotype (GNS TM1969–1970).

Holotype of *Kerguelenella flemingi* Powell, 1955 from Bay S of Crozier Pt, Auckland Island, NZ (GNS TM1204). Two paratypes of *K. flemingi*, same data as holotype (GNS TM1205, TM 1208).

Other, non-type material. **South Georgia Islands:** Grytviken Bay, 54°16′53.4"S, 36°30′28.8″W SGI01 (WAM S101182 p [M475, SK282]); Husivk 54°10.76'S, 36°42.68'W (NHMUK 1994092 p [SK204]). **NZ:** Auckland Island, 50°34'38.4"S 166°10'01.5"E (AM C.43852 2d; C.586004, 2 p). **MI:** (AM C.46754 p [SK550 K9200 protoconch F12]). Garden Cove, 54°30'S, 158°57'E (AM C.265944 4d, C.220182 d [R.211181], C.91954 10+p, C.91973 p, C.91974 p, C.46727 d, C.46701 3d); North Garden Cove, 54°29.91'S, 158°56.45'E (AM C.91965 10+p, C.91964 10+p, C.91963 10+p, C.91966 10+p); Hasselborough Bay, 54°29.91'S, 158°56.08'E (AM C.91970 10+p, C.91971 10+p, C.91969, C.91967 10+p), Hasselborough Corner (AM C.91968 10+p); Buckles Bay, 54°30.04'S, 158°56.18'E (AM C.91962 10+p, C.585698 MI02 8p, C.584960 p [M468], C.584961 p [M469], C.584962 p [SK272]); Opposite Tern Rock (AM C.91959 10+p, p [SK202], C.91958 10+p, C.99957 6p); Cosray Rocks (AM C.91955 10+p); Mawson Point, (AM C.91952 10+p); Sandy Bay, 54°34'S 158°56'E (AM C.91953 10+p, C.586003 p). **Taxonomic remarks.** The type of *S. lateralis* was subsequently figured in Gould (1856: 12, pl. 30, fig. 462, 462a–b). The holotype matches shell profile, dimensions and colouration of the figured specimen well. In an integrated morphological and molecular study Güller *et al.* (2015) established the identity of *S. lateralis* and its distinction from *S. lessonii* and *S.*

fuegiensis. Hubendick (1946: 27) pointed out that various nominal species with shells resembling *S. lateralis* have been reported from the south Pacific between Australia, NZ and the Kerguelen. Building on the findings of Güller *et al.* (2015), our anatomical and molecular analyses of freshly preserved topotypic specimens matching the types of each nominal species validate the identity and occurrence of *S. lateralis* and establish *K. innominata* (TS, Fig. 29K) and *K. macquariensis* (TS, Fig. 29J) as new synonyms. The identity of other nominal species described from this region, such as *S. flemingi*, *S. stewartiana, S. redimiculum* and *S. macgillvrayi* remain uncertain and are not reviewed herein. Güller *et al.* (2015: 88) stated that due to provenance issues and character differences, the name *S. redimiculum* is likely not applicable to *Siphonaria* species from the South American region, while assigning the Magellanic records of *S. macgillivrayi* in Hubendick (1945; 1946) to *S. fuegiensis*. Iredale (1915: 478) introduced the new name *Kerguelenia innominata* for '*Siphonaria lateralis* from the subantarctic islands of New Zealand' as described by Suter (1913: 601, pl. 49, fig. 10). Subsequently, Powell (1955: 122) considered *Kerguelenia innominata* Iredale 1915 as a *nomen nudum*. However, it is a replacement name based on a detailed description (of *S. lateralis*) by Suter (1913) and therefore an available name (Art. 12.2. of The Code). Suter (1913: 601) also included *S. redimiculum* Reeve, 1856 and *S. tristensis* Leach (not Sowerby I, 1823) in the synonymy of *S. lateralis*. However, Tasmania is considered as an unlikely occurrence for a species otherwise distributed through the sub-Antarctic. The genus name *Kerguelenella* was introduced by Powell (1946: 91) as a replacement name for *Kerguelenia* with *S. redimiculum* Reeve, 1856 as the type species by original designation. Powell (1955: 120–122; 1979: 293–294), Dell (1964: 290–292), and Forcelli (2000: 132) treated this taxon as an accepted genus. Powell (1955: 122) treated *K. macquariensis* as a subspecies of *K. lateralis* stating that *K. macquariensis* is 'closer to *K. lateralis* than any other NZ form'. This was followed by Powell (1960: 168) and Dell (1964: 291). However, subsequently (Powell, 1979: 293) synonymised *K. macquariensis* with *K. lateralis*.

Boreham (1959: 71) subsequently designated the lectotype of *Kerguelena innominata* restricting the type locality to Disappointment Island, Auckland Islands. A note on the lectotype label (GNS TM1203) indicates 'nom. nov. for *Siphonaria lateralis* Suter (not *S. lateralis* Gould, 1846) (in part) Ex Suter colln 4015'. Powell (1979: 293, pl. 54, figs 16–17) considered *Kerguelenella innominata* as an accepted species. Dell (1964: 290) considered *S. magellanica* as a synonym of *S. lateralis*; however, Güller *et al.* (2015: 83) showed it to be a synonym of *S. lessonii* instead.

External morphology (Fig. 29P). Foot sole orange grey, paler to foot edge; foot wall grey to yellow green, cephalic folds and pneumostomal lobe paler, fold small; irregular blotches of black pigmentation around foot wall and cephalic folds.

Shell (Figs 29H–L; Table S9). Medium to large sized (max sl mean = 15.8 mm, SD = 2.3 mm, n = 8, MI specimens), elongate ovate; height medium; exterior uneven, smooth to undulating often wrinkled, radially ribbed, reddish to greenish brown, apex offset strongly posterior and left, anterior and right apical sides strongly convex, posterior and left apical sides shorter straight to concave; protoconch hooked, below apex, close to posterior edge; protoconch direction weakly heterostrophic (n=1; Fig. 29T); growth striae prominent in bands, shell thin, lip even fragile, periostracum freely extending; rib count (mean = 31, SD = 2.5, n = 8), primary ribs flatly rounded, not protruding beyond shell lip; often interspersed finer secondary ribs, rib interstices darker; siphonal ridge indistinct but may be bulged, formed by paired primary ribs. Interior glossy, shell margin dark brown to tan, lip paler, paler markings weakly highlight under ribs, siphonal groove distinct, shallow, same colour as margin; spatula mottled tan, uneven darker markings; ADM scar distinct, CMS straight; thickening of shell lip not observed.

Reproductive system (Figs 30E, G; n = 3). RS positioned within right side of coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned between over rear of BM and side RAM, tip of AO embedded in EG; ED large wide short centrally curved, EG indistinct and curved continuation at top of ED, no flagellum (F1); AO and GA merged in base of ED as protruding bulb with MA; epiphallic parts all muscular tissue; CD and BD both short wide muscular wall featureless slightly curved, jointly connect to AO on inner side, BD over CD; pass just within outer side of RAM, BC large rounded, positioned between footwall and AG, test thick opaque, filled with orange-brown gelatinous mass; CD enters AG close to BD; single puckered GP at end of GA; HD small, brownish coils, links AG to brownish finely granulated HG; MG and larger AG small folded soft white tissue, MG at anterior of AG; dark SV embedded within AG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 30F). Elongated drop shaped, test thin, translucent (length = 4.4 ± 1.5 mm, n = 2), head bulbous, broad, tip bluntly rounded, containing a white gelatinous mass; taper region to flagellum reduced; both sections smooth, featureless; head much larger than flagellum (head length = 3.9 ± 1.3 mm, head length of SPM length ~88 %; head width = 1.06 ± 0.7 mm, flagellum width = 0.14 ± 0.03 mm, n = 2).

Radula and jaw. Described and figured in Güller *et al.* (2015: 87, figs 2D–F, 3G–H). Dentition formula 46:1:46 (Hubendick 1946: 27).

Comparative remarks. *Siphonaria lateralis* (*lateralis* group, unit 6) is the sister species of *S. fuegiensis*; both species together form a well differentiated subclade in the mitochondrial tree (Figs 1, 4). They differ by COI distances of ≥ 6.9% (Table S8). *Siphonaria lateralis* differs from other species by COI distances of ≥ 18% (Table S8). Within the Australian and New Zealand subantarctic distribution of *S. lateralis*, we found one sympatric congener on Auckland Island, *S. obliquata* (refer to comparative remarks under that species). No

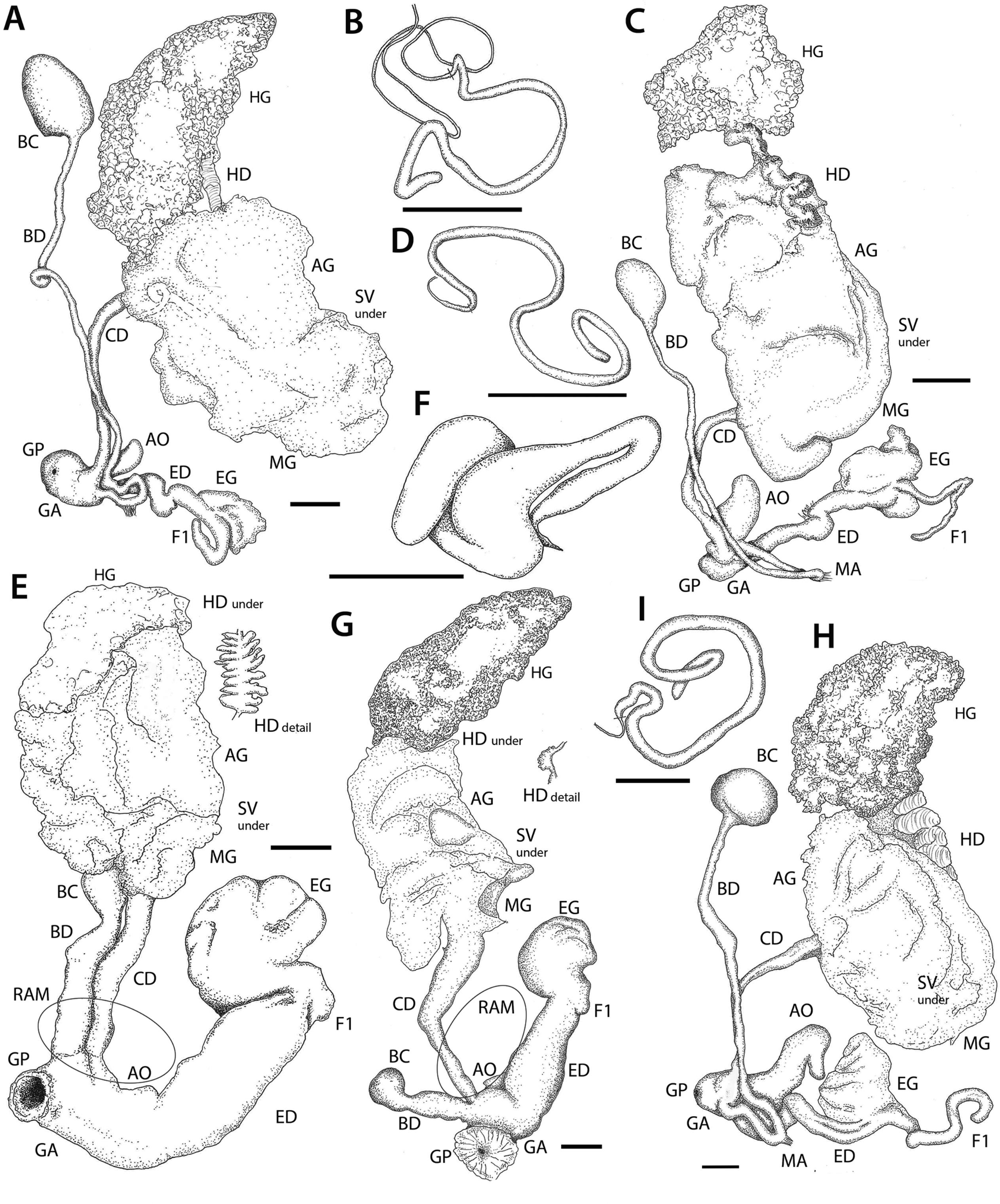

FIGURE 30. Reproductive morphology of *S. plana*, *S. plicata*, *S. lateralis* and *S. radians*. **A–B.** *S. plana,* Mauritius, AM C.584970 [M252]. **C–D.** TS of *S. plicata,* Tonga, Tongatapu. **C**. AM C.585276 [SK106, M419]. **D.** AM C.585275 [SK104, M418]. **E–G.** S. *lateralis,* Macquarie Island, TS of *Kerguelenella innominata.* **E–F.** AM C.91959 [SK202]. **G**. AM C.584960 [M468, SK270]. **H–I.** Indonesia, Riau Islands, Neotype of *S. radians* ZRC.MOL.24912 [M519, SK435]. Scale bars = 1 mm.

congeners were found on MI. Topotypic specimens of *K. innominata* (Fig. 29H, lectotype) and *K. macquariensis* (Fig. 29K) reveal typical features of *S. laterialis*, such as a relatively smooth (Fig. 29I) or rough shell (Fig. 29J), and corresponding RS structure, size and shape of epiphallic parts. They fall well within a very tight genetic cluster with sequences from South Georgia (unit 6; Dayrat *et al.* 2014: 266). Güller *et al.* (2015: 93) appeared to have mixed-up the species identifications when differentiating 'units 5 and 6' delineated in Dayrat *et al.* (2014: 259).

Figured specimens in Hubendick (1946: pl. 1, figs 22–25, from South Georgia) match shells of this species figured here (Figs 29H–L). The RS depicted herein (Fig. 30E, G) corresponds well with that depicted by Hubendick (1945: fig. 15) and Simpson (1977: 126, fig. 7). We found no noteworthy anatomical differences between specimens from South Georgia and MI (Figs 30E, G).

Distribution and habitat. Recorded from MI, south Pacific, southern Argentina and New Georgia, south Atlantic Ocean. In this study found at sheltered positions, clustered in crevices and hollows, on rocky shores at upper to mid littoral levels (Fig. 29S).

Siphonaria normalis Gould, 1846

(Figs 31A–I, O, S–U, 32A–D)

Siphonaria normalis Gould 1846: 12 (type locality: 'Sandwich Islands' [Hawaii]).—Gould 1848: 154; 1852: 359; H. Adams & A. Adams 1855 (in 1853–1858): 271; Gould 1856: 13, fig. 468a–b; Hanley 1858b: 152; H. Adams & A. Adams 1863: 271; Paetel 1883: 178; 1889: 429; Pilsbry 1920b: 379; Edmondson 1946: 188, fig. 102a; Hubendick 1946: 63; 1947b: 2, figs 3a–i, 4a–i, 5, 8–10; Morris 1952: 206, pl. 40, fig. 17; Johnson 1964: 116; Cook 1969: 679; Cernohorsky 1972: 210, pl. 60, fig. 2; Cook 1976: 34; Galindo 1977: 416; Coles 1981: 11; Trew 1983: 8; Jenkins 1984: 117; White & Dayrat 2012: 62, 2014: 266; Gonzàlez-Wevar *et al.* 2018: 5, fig. 1; Krug *et al.* 2022: 5.

Siphonaria normalis var. *lirata*—Pilsbry 1920b: 37980 (not *S. lirata* Reeve, 1856).

Planesiphon soranus Iredale 1940: 441, fig. 20, 21 (type locality: Townsville, Queensland).—White & Dayrat 2012: 67.

Siphonaria '*normalis* group, unit 14' (in part)—Dayrat *et al.* 2014: 267, fig. 3 P–S.

Siphonaria cf *normalis* (unit 52)—Ossenbrügger *et al.* 2023: fig. 2c–o.

Material examined. *Type material*. Syntype of *Siphonaria normalis* Gould, 1846 from Hawaii, United States, North Pacific Ocean; coll. Carpenter (USNM 15346, Fig. 31A).

Lectotype of *P. soranus* Iredale, 1940, present designation, from Townsville Qld, Australia; coll. 1929 (AM C.103709, Fig. 31D). Seven paralectotypes, same data as lectotype (AM C.124989). Two paralectotypes, same data as lectotype (MV F13840).

Other, non-type material. **Marquesas:** Baie des Vierges, Fatu Hiva, 10°27,84'S, 138°39,97'W (MNHN IM-2013-74897 p [M570, SK508], IM-2013-74898 p [M569], IM-2013-74899 p [M565]). **Hawaii, Oahu:** N end Waikiki Beach, 21°15.743'N, 157°49.307'W (AM C.584887 p [M293]); N end Waikiki, 21°16.646'N, 157°50.048'W (AM C.585622 5p, C.584886 p [SK210], C.585930 p [SK209]). **Maui:** Hanakao'o Beach, 20°54.564'N, 156°41.310'W (AM C.585929 p [M296]); Makalua-puna Point, 21°54.586'N, 156°41.338'W (AM C.585555 3p); Ho'okipa Beach, 20°56.029'N, 156°21.411'W (AM C.584892 p [SK212]). **Guam:** Umatac Bay, N end, 13°17.917'N, 144°39.494'E (AM C.585325 p C.584869 p [SK142], C.585493 p [M347], C.585494 p [M348]); Pago Bay, below UoG Marine Lab, 13°25.645'N, 144°47.927'E (AM C.585996 10+p); Tanguisson Beach, S end, 13°32.549'N, 144°48.443'E (AM C.585994 2p, C.584873 p [M343], C.584874 p [M439]). **Fiji, Viti Levu:** Vuda Point Marina seawall, 17°40.878'S, 177°23.009'E (AM C.585970 20+p, C.584866 p [SK115 protoconch C9], C.584867 p [M286], C.584868 p [M287]). **PNG:** Sek Is., 05°04,7'S, 145°48,9'E (MNHN IM-2013-13133 p [M558], IM-2013-13135 p [M562]); Wonad I., 05°08,1'S, 145°49,3'E (MNHN IM-2013-15280 p [M563]); Riwo waters, 05°08,9'S, 145°48,2'E (MNHN IM-2013-15250 p [M555] IM-2013-15251 p [M554]). **NC, Lifou:** We Baie de Chateaubriand E coast (AM C.585396 10p, C.584946 p [M388], C.584947 p [M389]). S of Pouebo 20°25.950'S, 164°39.251'E NC04-2 (AM C.585006 p [M381], C.585007 p [M382]); Bonhomme de Bourail, La Roche Percee, 21°36.487'S, 165°27.423'E (AM C.585013 p [M370], C.585014 p [M371]); Presqu'ile de Ouano La Foa, 20°51.434'S, 165°48.479'E (AM C.595911 6p). **Australia, Qld:** Umagico, 10°53.125'S, 142°20.799'E (AM C.585178 p [SK195]); Capt Billy Landing, 11°38.019'S, 142°51.472'E (AM C.585415 10+p, C.584792 p [M180], C.584793 p [M181], C.584794 p [M402]); S of Bathurst Head, 14°17.583'S, 144°11.845'E (AM C.585348 10p); Lizard Is, bch rock, 14°40.730'S, 145°26.838'E (AM C.585643 5p); Lizard Is, 14°40.908'S, 145°27.007'E (AM C.585566 4p, C.585175 p [M030]); Cape Kimberley, 16°16.535'S, 145°28.737'E (AM C.585720 9p, C.585168 p [M041], C.585169 p [M394], C.585170 p [M395], C.585171 p [M397]); Pebbly Beach Yule Reef Trinity Bay, 16°35.031'S, 145°30.823'E (AM C.585703 8p); Gribble Pt Mission Bay Yarrabah, 16°53.781'S, 145°51.852'E (AM C.585347 p); Mourilyan Harbour, 17°35.951'S, 146°07.583'E (AM C.585411 10+p, C.585155 p [M012], C.585156 p [SK123]); W side Kissing Pt Townsville, 19°14.332'S, 146°48.040'E (AM C.585672 6p, C.585146 p [M083], C.585147 p [M186], C.585148 p [M187], C.585149 p [M188], C.585931 p [SK197], C.585932 p [SK075]); Slade Pt Mackay, 21°03.813'S, 149°13.527'E (AM C.585501 2p). **Gulf of Carpentaria:** Mutee Head, 10°54.682'S, 142°15.204'E (AM C.585416 10p); Weipa, 12°37.795'S, 141°51.853'E, Q52-1 (AM C.585450 12p); **Sweers Is:** 17°07.029'S, 139°35.805'E (AM C.585645 5p), 17°07.413'S, 139°35.816'E, Q56-2 (AM C.585350 p), Inspection Pt, 17°08.471'S, 139°36.868'E (AM C.585417 15+p). **NT:** Cape Wirawawoi Nhulunbuy, 12°09.513'S, 136°46.904'E (AM C.585530 20+p); Sandy Is Pt 11°07.862'S, 132°11.187'E (AM C.585406 10+p); Smith Pt 2, 11°07.466'S, 132°08.538'E (AM C.585636 5p); Luxmore Hd Melville Is, 11°20.639'S, 130°23.149'E (AM C.585349 7p); Nightcliff Darwin, 12°22.836'S, 130°50.402'E (AM C.585977 10+p); Cox Peninsula, 12°24.824'S, 130°40.921'E (AM C.585978 10+p); N of Native Pt Dundee Bch, 12°42.182'S, 130°20.881'E (AM C.585668 6p) ; Native Pt oyster reef Dundee Bch, 12°42.906'S, 130°20.653'E (AM C.585413 8p); Native Pt reef Dundee Bch, 12°42.981'S, 130°20.807'E (AM C.585381 10p).

Taxonomic remarks. *Siphonaria normalis* was subsequently figured by Gould (1856: 13, pl. 30, figs 468, 468a–b). The syntype corresponds well with this figure in shell profile, dimensions and colouration. The description of *P. soranus* does not contain an original type designation. The figured specimen of *P. soranus* (Iredale, 1940: pl. 34, figs 20–21) is herein designated as the lectotype for the stabilisation of the name (AM C.103709). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes of *S. normalis* and *P. soranus* and geographic series of additional specimens (Table S1). We stablish *P. soranus* as a junior synonym of *S. normalis*.

Pilsbry (1920b: 379) erroneously considered *S. amara*, *S. nuttallii*, *S. lirata*, *S. crebricostata* and *S. normalis* f. *chirura* as synonyms of *S. normalis*. This was followed by Cernohorsky (1972: 210). Dayrat *et al.* (2014: 267) recognised several independent molecular units within the *normalis* group (i.e., unit 12 from Thailand, unit 13 from Singapore, and unit 14 from Hawaii). These units are herein recognised as three distinct species, *S. radiata* (unit **12**), *S. costellata* **sp. nov.** (unit **13**), and *S. normalis* (unit **14**).

External morphology. Foot sole, foot wall, mantle, cephalic folds and pneumostomal lobe evenly pale grey/cream, paler at edge foot/wall; blotches of black pigmentation on centre of cephalic folds, faintly on foot wall; mantle narrower than width of foot wall, non-translucent, covers exposed inner shell lip, edge thickened, lobed, vertical bands of black pigmentation aligned with shell rib interstices; genital pore indistinct, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two centrally touching cephalic folds; pneumostomal lobe long under the mantle between the right ADMs.

Shell (Figs 31A–I, O, S–U; Table S9). Small sized (max sl mean = 12.56 mm, SD = 2.02 mm, n = 13), circular ovate; height medium to tall; apex offset posterior and weakly left, apical sides straight to weakly convex, shell edge; protoconch direction heterostrophic, initially hooked (n = 4; Fig. 31S–T), shell whorl dextral; growth striae prominent, radial colour banding often present, shell thickness thick; rib count (mean = 33, SD = 0.87, n = 13), primary ribs distinct, white to pale, usually radially evenly spread, fairly straight, broaden to and align with fairly flat faintly scalloped shell edge; ribs may be raised or flat, ; 1–2 interspersed pale white finer secondary ribs, rib interstices darker; paired primary ribs on siphonal ridge, no more prominent than other primary ribs. Interior shell margin varies from pale tan to dark brown; white rays extend from the shell lip to over the shell margin fading to the spatula, align under primary/secondary ribs, spatula varies from pale yellow (Fig. 31E), pale tan (Fig. 31B) to dark chocolate brown (Fig. 31F); siphonal groove distinct, paler than shell margin or spatula; ADM scar distinct, CMS straight, paler than shell lip; thickening of shell lip common, margin becomes whitened (Fig. 31E).

Reproductive system (Figs 32A, C; n = 9). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between BM and RAM; GP small, singular, positioned through foot wall behind right cephalic fold, GA small, prominent; AO very small, short, narrow, blunt, slightly bent centrally, joins to top of GA in conjunction with ED; ED short, broad, joins to back side of GA alongside AO; single short broad blunt flagellum (F1), longer than and same width as ED, join of F1 to ED indistinct, marked by connection of very small white folded EG; AO, GA and ED all muscular white tissue; BD and CD connect closely side-by-side into GA between connections of ED and AO, both ducts narrow smooth featureless, pass together through RAM connecting into MG (BD above CD), BD longer than CD, often loop immediately in front of BC; BC large to medium, spherical, embedded in folds of MG, test translucent; SV embedded on left side of AG; HD short, thick coils, links AG to smaller yellowish granular HG; MG and AG folded, soft white tissue; sides match curvature of inner foot wall on right posterior of coelom; outer edge of MG lobed.

Spermatophore (Figs 32B, D). Broad head with short flagellum (length = 2.47 ± 0.195 mm, n = 3); head section cylindrical, bulbous, centrally bent, rounded tip; test thin, smooth, featureless, translucent encasing a white opaque central core; short tapering section (often looped) merges head to filamentous flagellum; head slightly shorter, wider than translucent flagellum (head length = 1.23 ± 0.45 mm, flagellum length = 1.24 ± 0.34 mm, SPM head ~ 49% of total lenght; head width = 110 ± 13 µm, flagellum width = 11 ± 0 µm, n = 3); up to 9 SPMs tightly coiled in BC of topotypic specimens (AM C.585930).

Comparative remarks. *Siphonaria normalis* (*normalis* group, unit 14) is the sister species of a clade containing *S. fuliginata* and *S. madangensis* **sp. nov.** (Figs 1, 4). These three species are closely related and differ from each other by COI distances of ≥ 5.9% (*S. fuliginata*, unit 80) and ≥ 5.6% (*S. madangensis* **sp. nov.**, unit 88) (Table S8). Two other closely related species are *S. campestra* **sp. nov.** (unit 86, COI distance ≥ 18.6%) and *S. costellata* **sp. nov.** (unit 13, COI distance ≥ 7.8%) (Table S8).

Siphonaria campestra **sp. nov.** differs in having a shell with slightly broader ribs, predominantly primary and few secondary ribs, slightly more scalloped shell edge, darker interior, a smaller AO, shorter ED, and a thicker SPM. *Siphonaria fuliginata* has a much paler, thicker shell, less scalloped edge, a thicker BD, smaller BC, shorter and narrower ED, and a shorter SPM.

Throughout the range of *S. normalis* we found twenty-seven congeners to occur in partial sympatry. *Siphonaria gemina* **sp. nov.** has a smaller shell with stronger raised ribbing and edge scalloping, more prominent siphonal ridge, a larger AO and GA, a shorter, wider BD, and a wider SPM. *Siphonaria mauiensis* **sp. nov.** (sympatric in Hawaii) has a smaller shell with more raised ribbing and weaker edge scalloping, a smaller BC, shorter BD, and a shorter SPM. *Siphonaria nuttallii* (sympatric in Hawaii) has a taller shell with a more central apex, slightly greater raised ribbing, stronger edge scalloping, more prominent and multi ribbed siphonal ridge, a larger AO, smaller BC, broader BD, and a longer SPM. Eight congeners

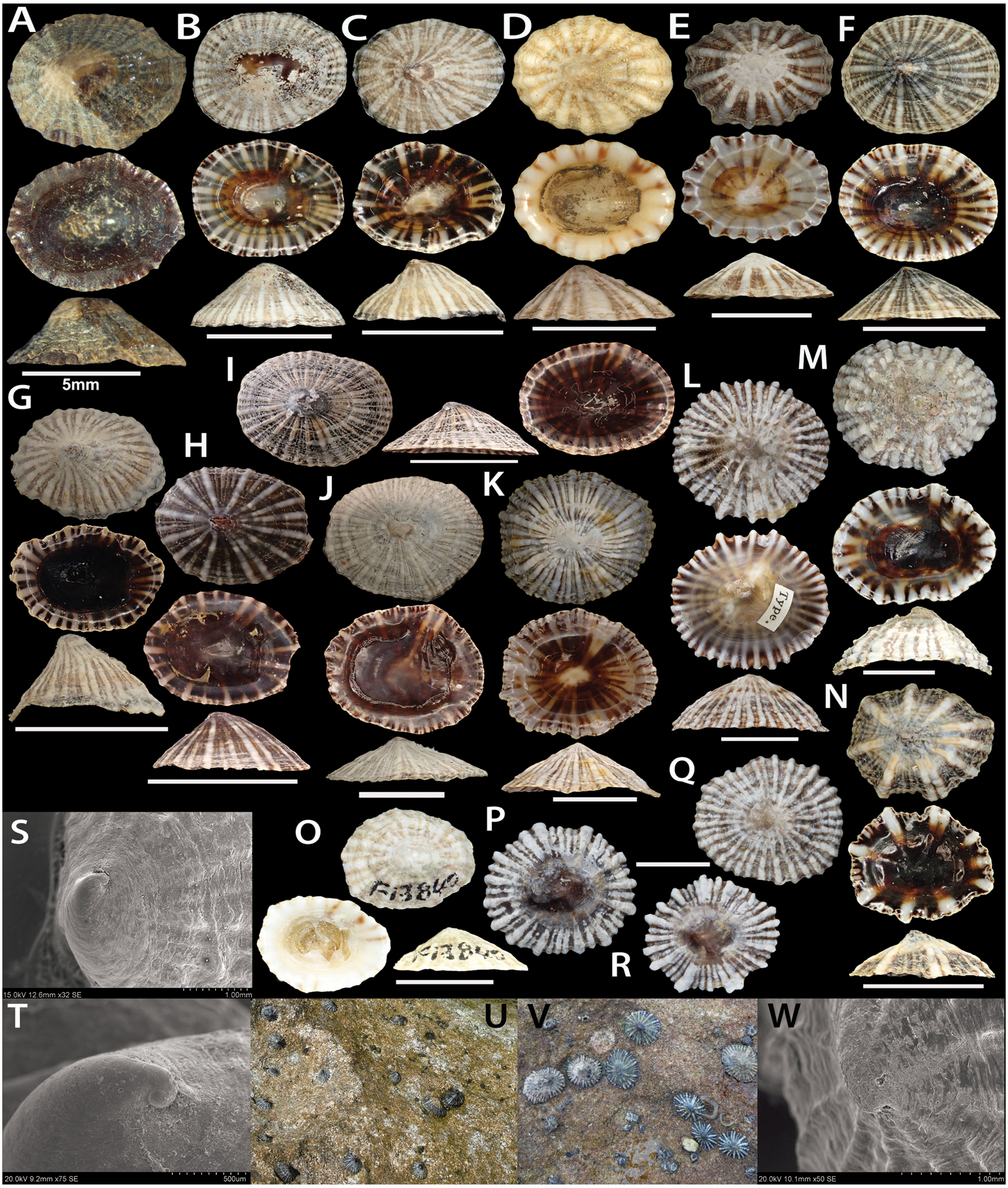

FIGURE 31. Shells of *S. normalis*, *S. radians* and *S. scabra*. **A–I, O, S–U.** *S. normalis*, **A.** Hawaii, syntype USNM 15346. **B.** Maui, TS, AM C.585929 [M296, SK240]. **C.** Oahu, TS, AM C.585930 [SK209]. **D.** Probable holotype of *P. soranus* AM C.103709. **E.** Qld, Townsville, TS of *P. soranus* AM C.585932 [SK075]. **F.** Qld, Cape York Peninsula, AM C.584792 [M180]. **G.** Marquesas, Fatu Hiva, IM-2013-74897 [M570]. **H.** PNG, Riwo waters, IM-2013-15250 [M555]. **I.** PNG, Wonad Is, IM-2013-15280 [M563]. **O.** Probable paratype of *P. soranus* MV F13840, **S.** Protoconch, Maui, AM C.584892 [SK212]. **T.** Protoconch, Qld, Cape York, AM C.585178 [SK195]. **U.** Hawaii, *in situ*. **J–K.** *S. radians*. **J.** Indonesia, Riau Islands, Neotype ZRC.MOL.24912 [M519]. **K.** Malaysia, ZRC.MOL.24894 [M594, SK526]. **L–N, P–R, V–W.** *S. scabra*. **L.** Lectotype NHMUK 1981011/1. **M.** NSW, Sydney Harbour, TS, AM C.585061 [M152]. **N.** AM C.585114 [M154]. **P–R.** Paralectotypes NHMUK 1981011/2-4. **V.** NSW, *in situ*. **W.** Protoconch, AM C.585062 [SK169]. Unlabelled scale bars = 10 mm.

are sympatric in Fiji and NC. For comparison with *S. atra* refer to comparative remarks under that species. *Siphonaria hienghenensis* **sp. nov.** has a larger, taller, paler shell with a more prominent siphonal ridge and centralised apex, a larger AO, shorter ED and a smaller BC. *Siphonaria monticulus* has taller shell with slightly more raised and even ribbing, paler interior, a larger AO and a longer ED. *Siphonaria namukaensis* **sp. nov.** has a paler shell with more central apex, more prominent siphonal ridge, paler golden spatula, a larger AO and a smaller BC. *Siphonaria caledonica* **sp. nov.** has a taller shell with interstice markings, a darker interior, a larger AO and ED, and a smaller BC. *Siphonaria bourailensis* **sp. nov.** has a taller, paler shell with more prominent raised ribbing, stronger edge scalloping, a larger AO, and a smaller BC. *Siphonaria poindimiensis* **sp. nov.** has a taller shell with more prominent raised ribbing, stronger edge scalloping, a larger AO and ED, and a smaller BC. *Siphonaria vudaensis* **sp. nov.** has a larger shell with narrower ribbing, a more prominent and flared siphonal ridge, stronger edge scalloping, a larger AO, and a smaller BC. Three congeners are sympatric in Guam. *Siphonaria guamensis* has a slightly darker shell with finer and raised ribbing, paler margin, and darker spatula, a longer AO and ED, a smaller BC, and a longer SPM. *Siphonaria lirata* has a shell with finer raised ribbing, a larger AO, broader ED, and a smaller BC. *Siphonaria tanguissonensis* **sp. nov.** has a slightly darker shell with finer and raised ribbing, paler margin, and darker spatula, a smaller BC, shorter BD, and longer SPM,

Four congeners are sympatric in PNG. For comparison with *S. javanica* refer to comparative remarks under that species. *Siphonaria madangensis* **sp. nov.** has a smaller shell with more raised ribbing and stronger edge scalloping, a smaller, less prominent AO, smaller ED, larger BC, longer narrower BD, and a very similar but shorter SPM. *Siphonaria recurva* **sp. nov.** has a darker shell with more prominent white ribbing and weaker edge scalloping, a larger AO and BC, and longer ED and F1. *Siphonaria viridis* has a taller shell with dark patterning and distinct dual siphonal ridge, a larger AO, smaller BC, and longer SPM.

Seven congeners occur sympatrically throughout Australia. *Siphonaria costellata* has a browner shell with more raised ribbing, prominent siphonal ridge, a longer BD, and longer SPM. *Siphonaria gemina* **sp. nov.** has a slightly taller darker shell with more raised ribbing, stronger edge scalloping, a smaller BC, and shorter BD. *Siphonaria jiigurruensis* **sp. nov.** has a taller darker shell with more prominent primary ribbing, red-brown patterning, a larger AO, smaller BC, longer and broader ED, and a longer SPM. *Siphonaria oblia* has a far smaller, darker, browner, and more fragile shell with unraised ribbing, apex strongly offset, a smaller AO, BD without distal loop, and larger ED and BC (Jenkins 2018: 278, fig. 3C–D). *Siphonaria opposita* has a larger, lower shell with more prominent and flared siphonal ridge, central apex, stronger edge scalloping, a larger AO and ED. *Siphonaria scabra* has a larger, darker shell, greater raised ribbing, more prominent siphonal ridge, a larger AO, and a longer SPM. *Siphonaria alba* is sympatric in Singapore. It has a larger, darker shell with more prominent siphonal ridge, stronger edge scalloping, a larger AO, longer ED, and a longer SPM.

Siphonaria normalis has a very wide distribution spanning from the northern to the southern Tropical Pacific (Fig. 25). We have not found any discontinuities in the ranges of anatomical, morphological, or mitochondrial variation that may suggest that this species as currently delineated may represent a species complex.

The SPM of *S. normalis* resembles that of *S. radiata* and *S. gemina* **sp. nov.** Hubendick (1946: 30–32, 63) considered *Parellsiphon soranus* from Townsville, N Qld (= *S. normalis*) as of questionable status and possible synonym of *S. acmaeoides* for the 'considerable resemblance' in shell characters. Figured specimens of *S. normalis* in Hubendick (1947b: 2, fig 3b–i, 4b–i) appear to be a mixture of *S. normalis* (figs 3a–d, i) and *S. waikoloaensis* **sp. nov.** (figs 3f–h). The RS figured by Hubendick (1947b: 2, fig 5) closely matches that of *S. waikoloaensis* **sp. nov.** Figured specimens of '*S. normalis*' from Oahu, Hawaii in Hubendick (1947b: 2, fig 3a–I, 4a–i) closely match *S. normalis* rather than *S. mauiensis* **sp. nov.** (finer ribbing, dark interior), *S. nuttallii* (usually paler interior, ribbing different), *S. undans* **sp. nov.** (distinct ribbing) or *S. waikoloaensis* **sp. nov.** (distinct ribbing). While Hubendick (1947b: 2) stated that the specimen depicted in figs 3a, 4a 'except for its size, agrees with *S. nuttalli* [sic *nuttallii*]'. However, it differs from types of *S. nuttallii*. The figured specimen of '*S.* cf *normalis*' in Maes (1967: 154, pl. 14, fig. L, from CKI) is a specimen of *S. gemina* **sp. nov.** The figured specimen of '*S. normalis*' from Lomalagi, Fiji in Cernohorsky (1972: 210, pl. 60, fig. 2) matches *S. normalis* depicted herein. The figured specimen of '*S. normalis*' in Kay (1979: 493, figs 157I–J) is a misidentification of *S. nuttallii.* The figured specimens of 'unit 14' in Dayrat *et al.* (2014: figs 3P, 5Q, 3R, 3S) closely resemble *S. normalis* as delineated herein.

Distribution and habitat. Widespread through tropical Pacific Ocean, including Society Islands, Gambier Islands, Marquesas, Hawaii, Nauru to Guam, American Samoa, Santa Cruz Islands, Solomon Islands, NC, PNG, northern Australia (Cape York through to Broome, Kimberley, WA), and Timor-Leste. In the Indian Ocean recorded from Praslin Island, Seychelles (Ossenbrügger *et al*. 2023). In this study found to be rather common in sheltered positions on exposed rocky shores at upper littoral levels in Australia, Fiji, New Caledonia, Hawaii, and Guam (Fig. 25).

Siphonaria savignyi **Krauss, 1848**

(Figs 14J–L, O)

Siphonaria savignyi Krauss 1848: 61.—Hanley 1858b: 152; Paetel 1873: 117; 1875: 92; 1883: 178; Tomlin 1927: 291; Bouchet & Danrigal 1982: 15; White & Dayrat 2012: 67.

Siphonaria (*Siphonaria*) *savignyi*—Hubendick 1945: 72; 1946: 55, pl. 4, figs 25–29.

Siphonaria (*Siphonaria*) *laciniosa* forma *savignyi*—Morrison 1972: 56–58, 60, 59, figs 3, 4.

Siphonaria kurracheensis—Barash & Danin 1972: 329, fig. 14; 1977: 98 (not *S. kurracheensis* Reeve, 1856).

Siphonaria savignyi Krauss, 1848—Coan & Kabat 2017: 205.

Material examined. *Type material*. Lectotype of *S. savignyi* Krauss, 1848, present designation, type locality unknown, likely Red Sea; collector and date unknown (Savigny collection) (IM 2000-35936, Fig. 14J). Paralectotypes, same data as lectotype (MNHN IM 2000-35935 d, Fig. 14K; MNHN IM 2000-35934 d, Fig. 14L).

Taxonomic remarks. In the original description, Krauss (1848) attributed this name to Philippi. However, Krauss is author of the name, and not Philippi in accordance with Art. 12.2.6 of the Code (see also Bouchet & Danrigal, 1982: 15; Kabat & Coan, 2017: 205). The new name *S. savignyi* has been made available by Krauss (1848) through providing a bibliographic reference to pl. 1, fig. 1 in the work of Savigny (1817). Hubendick (1946: 55) incorrectly attributed the name to an alleged publication by Philippi (1826) entitled "Gasteropodes et Qoquille in Savignyi: Descriptions de l'Egypte". However, this title is that of Savigny's (1817) work and no published work was authored by Philippi under this title (Kabat & Coan, 2017).

Shell (Figs 14J–L; Table S9). Small to medium sized (max sl mean = 41 mm, SD = 2.2 mm, n = 3), ovate; height medium to tall; apex offset weakly posterior and to left, apical sides strongly convex, protoconch direction undetermined; shell whorl dextral; exterior whitish, uneven without prominent radial colour bands, growth striae prominent in bands, shell thickness thick; rib count (mean = 49, SD = 2.9, n = 3); ribs fairly even in width, straight to wavy, ridges rounded narrow, slightly broaden and increasingly raised to shell edge, 8–10 spread prominent whitish primary ribs whitish; siphonal ridge formed by 3–5 primary ribs, flared up at shell edge; few finer secondary ribs, rib interstices darker, edge weakly scalloped and unevenly corrugated; interior shell margin white, short dark brown rays on shell lip, align under rib interstices, margin thickened white, siphonal groove distinct; same colour as mottled reddish to dark brown spatula; ADM scar distinct, darker brown, CMS slightly convex; thickening and whitening of shell lip occurs (Fig. 14J).

Reproductive system and Spermatophore. unknown.

Comparative remarks. Figured shells from Port Fenfick and Gulf of Suez, Red Sea, and the description in Hubendick (1948: 55, pl. 4, 26–29) and figured shells from Israel in Morrison (1972: 60, figs 3–4) exhibit a morphology consistent with the types (Figs 14J–L). No material has been available to study the anatomy and/or mitochondrial phylogenetics of this species.

Distribution and habitat. So far recorded from the Red Sea and the Mediterranean coast of Israel.

Siphonaria radians H. Adams & A. Adams, 1855
(Figs 30H–I, 31J–K)

Siphonaria radiata A. Adams & Reeve 1850: 69, pl. 13, fig. 2a–b (invalid, preoccupied by Blainville, 1826).—Paetel 1889: 429; White & Dayrat 2012: 67.

Siphonaria radians H. Adams & A. Adams 1855 (in 1853–58): 271 (replacement name for *S. radiata* A. Adams & Reeve, 1850 not Blainville, 1826 nor Sowerby I, 1835).—H. Adams & A. Adams 1863: 271; Paetel 1889: 429; Hylleberg & Kilburn 2003: 133; White & Dayrat 2012: 67.

Siphonaria (*Sacculosiphonaria*) *radians*—Hubendick 1946: 43.

Material examined. *Type material.* Neotype of *Siphonaria radians*, present designation, from Natuna Regency, Riau Islands, NE coast of Palau Panjang (NW of Pulau Natuna Besar), Indonesia, South China Sea. 04°15.9'N, 108°12.27'E, Expedition Anambas, ZRC EA-ZJ09; coll. 17 March 2002 (ZRC.MOL.24912 [M519, SK435], Fig. 31J).

Other, non-type material. **Indonesia:** Pulau Panjang, Riau Islands 1°10.215'N, 104°18.905'E ZRC EA ZJ09 (AM C.595976 p [M590, SK512], C.595977 p [M591, SK513]). **Malaysia:** Bak Bak Beach, Kudat, Sabah 07°00′ N, 116°46′ E (AM C.585940 p [SK521]); Tangung Bidara, Malacca 2°17.568'N, 102°5.207'E (ZRC.MOL.24893 p [M595, SK527], ZRC.MOL.24894 p [M594, SK526], Fig. 31K, Pulau Langkawi 6°18′ N, 99°52′ E (AM C.585697 p [SK524]).

Taxonomic remarks. The name *S. radiata* A. Adams & Reeve, 1850 is a junior secondary homonym of *S. radiata* (Blainville, 1826) and a junior objective homonym of *S. radiata* Sowerby I, 1835. It is not invalidated by *S. radiata* Gray (1824), however, which is an unnecessary replacement name (see under *S. sipho*). H. Adams & A. Adams (1855) introduced *S. radians* as a replacement name (Art. 12.2 of the Code). No type material of *S. radiata* A. Adams & Reeve, 1850 could be found in the NHMUK and the types are therefore considered lost. The neotype of *Siphonaria radians* is designated herein to clarify the taxonomic status and the type locality of this taxon (Art. 75.3 of the Code).

External morphology (preserved). Foot sole grey, lighter to foot edge; mantle, footwall, pneumostome and cephalic lobes cream with irregular darker pigmentation markings concentrated over cephalic lobes, mantle thin translucent lobed with white edge band and black marking aligning under rib interstices.

Shell (Figs 31J, K; Table S9). External sculpture and height variable, lower fine ribbed form (Fig. 31J), taller prominent ribbed form (Fig. 31K); small to medium sized (max sl mean = 16.8 mm, SD = 2.1 mm, n = 11), circular ovate, low; apex slightly curved, apex offset slightly to posterior and left, apical sides weakly convex, posterior straight to concave, protoconch direction weakly homostrophic to central (n = 1), shell whorl dextral, shell thin, growth striae prominent, even, unraised; radial colour bands indistinct; rib count (mean = 48, SD = 12.4, n = 11), primary ribs indistinct from secondary ribs; ~ 16 pale brown to off white indistinct primary ribs, ridges weakly raised, rounded; siphonal ridge formed by 3 primary ribs, align with shell lip; shell edge uneven, weakly scalloped and corrugated; 2–3 finer secondary ribs between primary ribs, rib interstices darker. Interior shell margin and spatula dark chocolate brown, centre of spatula and distinct siphonal groove paler, off white to cream rays on shell margin, align under primary/secondary ribs; ADM scar distinct, similar to margin and spatula; CMS convex; whitening or thickening of shell lip not observed.

The neotype (Fig. 31J). Shell (sl = 17.9, sw = 14.2, sh = 5.2 mm) circular ovate, low; apex offset weakly to posterior and left, exterior grey, 68 fine weakly curved ribs; siphonal ridge formed by three adjacent ribs. Interior shell lip chocolate brown and cream under rib ends, dark brown rays on shell lip aligning under rib interstices. RS (Fig. 30H).

Reproductive system (Fig. 30H; n = 5). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity, epiphallic parts positioned between inner side RAM and behind BM; GA medium, with singular GP through foot wall; AO medium sized, broad, bluntly pointed, central bend, joined to upper GA; ED short wide, centrally twisted, joins to outer side of GA; GA, AO, ED all white muscular fibrous tissue; EG large sized, soft whitish tissue, folded, joins at junction of end of ED and extension of single broad long twisted flagellum (F1); BD and CD connect closely in opposite directions into GA between ED junction and GP, CD junction into GA bulbous, both ducts long, smooth, narrow, whitish, featureless, pass closely together outside RAM (BD over CD) and broaden at junction into soft white folded tissues of MG; BD with distal loop and MA; CD connects to large MG/AG complex; BC embedded in MG folds, close to embedded SV; BC small, thin whitish translucent test; HD short, wide, coiled, links ducts in soft white folds of AG to yellowish granulated HG; outer edge of MG lobbed; AG slightly larger than HG.

Spermatophore (Fig. 30I). Thread-like, test thin, comprises a translucent cylindrical body section containing a white gelatinous core, tapers rapidly into a filamentous transparent flagellum (head length = 8.34 ± 1.5 mm, n = 4, ~ 76% of SPM length, head width = 168 µm, ± 33 µm; flagellum width = 19 µm ± 2 µm), head section much thicker than flagellum, head tip bluntly rounded; both sections smooth, featureless; 3 and 4 SPM coiled, embedded in whitish gelatinous mass within 2 BC's.

Comparative remarks. Specimens identified as *S. radians* herein match well the original description and figures of S. *radiata* (A. Adams & Reeve, 1850). *Siphonaria radians* (*atra* group, unit 95) is the sister species of *S. umbra* **sp. nov.** (unit 46). Both species together form a well-differentiated and well-supported subclade (Figs 1, 2). Both species differ from each other by COI genetic of ≥ 21.8% (Table S4). Throughout its range, *S. radians* has been found in sympatry with three congeners. On the Riau Islands it occurs in sympatry with *Siphonaria sipho*; for comparative remarks refer to that species. Two congeners are sympatric at Kudat, Sabah, E. Malaysia. For comparisons with these species refer to comparative remarks under *Siphonaria radiata* and *S. kudatensis* **sp. nov.**, respectively.

Specimens from Malaysia and China Sea match the shell sculpture (wide to fine and wavy ribbing), external (grey/brown) and internal colouration (black and white rays on shell margin, typical for this species. A specimen figured as '*Siphonaria radians*' in Habe & Kosuge (1966: pl. 42, figs 24, 25) is attributed to *S. rucuana*.

Distribution and habitat. Currently known only from Riau Islands, Indonesia and Sabah, E Malaysia (Fig. 25). Found on rocky headlands, at upper and lower littoral levels.

Siphonaria scabra Reeve, 1856

(Figs 31L–N, P–Q, V–W, 32E–F)

Siphonaria scabra Reeve, 1856: pl. 1, species 2 (type locality Port Jackson [Sydney Harbour], Australia).—Hanley 1858b: 152; Angas 1865: 190; Tenison Woods 1878b: 99; Paetel 1883: 178; Whitelegge 1889: 117; Hedley 1917a: 715, pl. 1, fig. 32; 1917b: M95; Galindo 1977: 416; McAlpine 1952: 41; Trew 1983: 7; White & Dayrat 2012: 67.

Siphonaria diemenensis var. *scabra*—Tenison Woods 1878b: 99; Hubendick 1945: 66; 1946: 38, pl. 2, fig. 14.

Material examined. *Type material.* Lectotype of *Siphonaria scabra* Reeve, 1856, present designation, from Port Jackson, [Sydney], Australia (NHMUK 1981011/1, Fig. 31L). Four paralectotypes, same data as lectotype (NHMUK 1981011/2-4, Figs 31P–Q).

Other, non-type material. **Australia, Qld:** Slade Point, Mackay, 21°03.813'S, 149°13.527'E, Q14-1 (AM C.585702 8p, C.585139 d [M214], C.585140 p [M215], C.585141 p [M216]); Wreck Pt, Yeppoon, 23°08.736'S, 150°45.865'E, Q08-4 (AM C.585138 p [M426]); Northwest Island, 23°17.683'S, 151°42.997'E, Q07-3 (AM C.585130p [M078]); Urangan Hervey Bay, 25°17.504'S, 152°54.664'E, Q05-1 (AM C.585342 p, C.585127 p [M403], C.585128 p [M182]); Drury Point Scarborough, 27°12.168'S, 153°06.980'E, Q03-8 (AM C.585748 1 p); **NSW**: Bolton Point Lake Macquarie, 33°0.389'S, 151°36.889'E, NSW08-3 (AM C.585448 12p, AM C.585060 p [SK168], AM C.585062 p [SK169]); Laings Point Sydney Harbour, 33°50.419'S, 151°16.638'E, NSW06-3 (AM C.585898 7p, C.585061 p [M152], C.585114 p [M154]).

Taxonomic remarks. The syntype marked as 'type' (Fig. 31L) is herein designated as the lectotype of *S. scabra* for the stabilisation of the name (Art. 74.1 of the Code). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 31J) and geographic series of additional specimens (Table S1). Several authors treated *S. scabra* as a junior synonym or variety of *S. diemenensis*, which is rejected herein. The record of '*S. scabra*' from SA in Adcock (1893: 11) is probably a misidentification of *S. zelandica* and incorrectly synonymised with *S. luzonica*.

External morphology. Foot sole, foot wall, foot

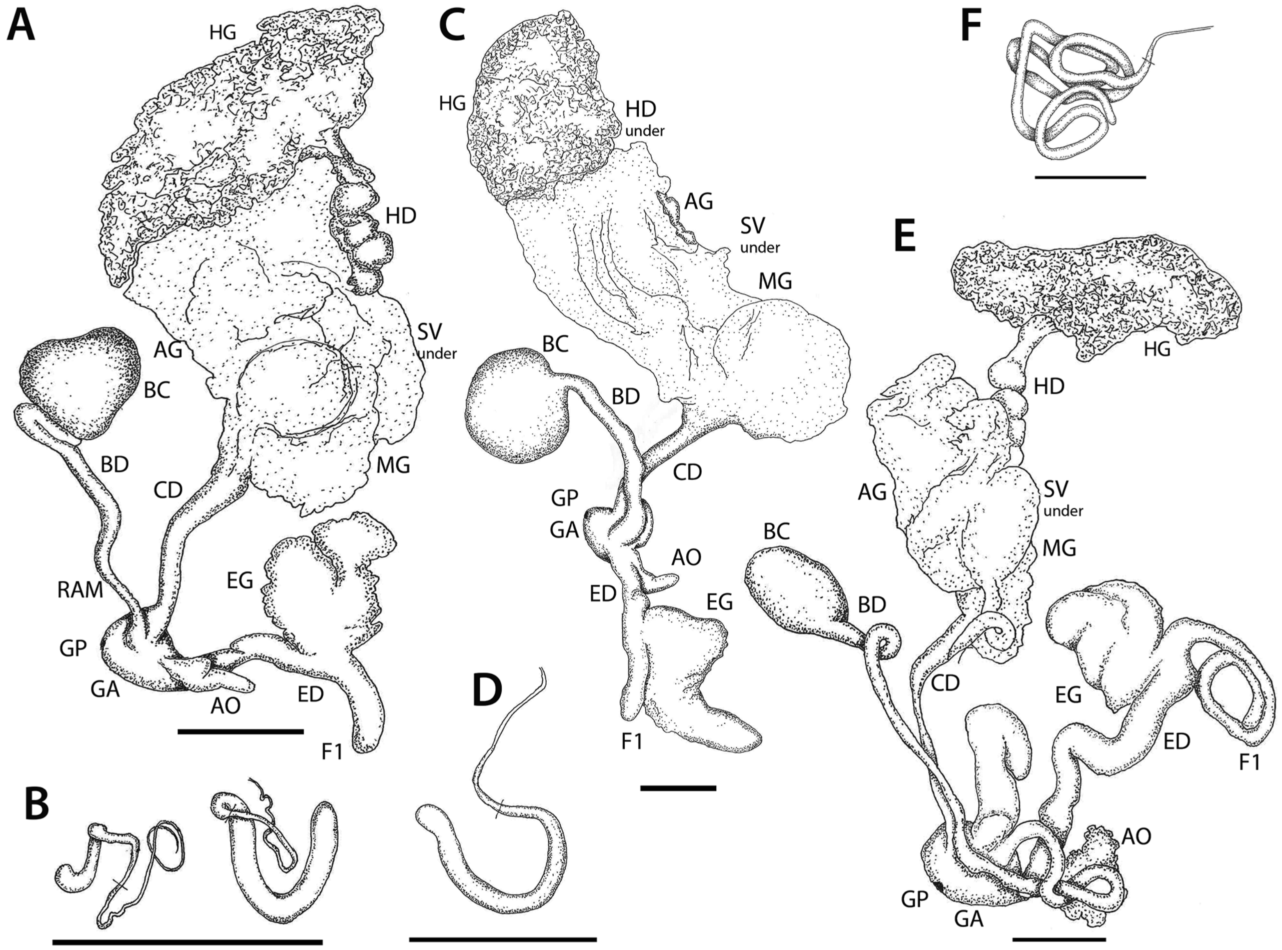

FIGURE 32. Reproductive morphology of *S. normalis* and *S. scabra*. **A–D.** *S. normalis* **A–B.** Hawaii, Oahu, TS, AM C.585930 [SK209]. **C**. Guam, Umatac Bay, AM C.584872 [M346, SK142]. **D**. Hawaii, Maui, TS, AM C.585929 [M296, SK240]. **E–F.** *S. scabra,* NSW, Sydney Harbour, TS, AM C.585114 [M154, SK236]. Scale bars = 1 mm.

edge, mantle and cephalic folds all evenly cream, paler at foot edge; regular vertical black pigmentation bands/stripes on foot wall, short of foot edge; mantle narrow, strongly finely lobed, thickened at edge; pneumostomal lobe narrow, faint black pigmentation, under mantle behind right cephalic fold; closes the pneumostomal and anal openings at the mantle edge; two small black epithelial eye spots centralised on two centrally touching cephalic folds; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold.

Shell (Figs 31L–N, P–Q, V–W; Table S9). Medium sized (max sl mean = 16.1 mm, SD = 3.4 mm, n = 7), elongate ovate; height medium; apex offset sightly posterior and to left, apical sides convex, protoconch direction homostrophic (n = 3; Fig. 31V), shell whorl dextral; exterior sculpture variable, uneven, rough, growth striae layered leaving rib protrusions, uneven; radial colour bands, protoconch dark, central pale, edge with dark rib interstices; shell thick; rib count (mean = 37, SD = 6.8, n = 7), with ten primary ribs (Fig. 31N), pale white to cream, wavy, broad, ridges flat to rounded, shell lip uneven ribs weakly protrude at shell edge; few (1–2) secondary ribs between and of similar width to primary ribs; rib interstices darker, width slightly less than rib width; siphonal ridge not prominent, formed by paired primary ribs. Interior shell margin dark chocolate brown with white rays under primary/secondary ribs extending to spatula, shell edge corrugated by rib ends, siphonal groove distinct; spatula dark chocolate brown, sometimes reddish, mottled to lighter tan; ADM scar distinct, deep, CMS straight.; thickening of shell lip occurs without whitening, infills and reduces lip scalloping; coarse and fine rib as well as prominent primary/secondary rib change (Fig. 31N).

Reproductive system (Fig. 32E; n = 2): Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between BM and RAM; merge of AO and GA indistinct, AO relatively large, elongated, bluntly pointed, twisted and centrally bent (without a prominent MA), slightly larger than GA, thicker than ED; ED relatively long, centrally bent, thick; EG white, folded, elongated; single flagellum F1 on EG, long, twisted, thickish; AO, GA and ED all muscular white tissue; BD and CD with opposing connections to GA between ED, AO and singular GP; BD long, heavily looped on anterior side with prominent MA, much longer than CD of similar thickness, both ducts smooth and pass together through RAM connecting into MG (BD above CD), BC translucent, clear test, relatively large, bulbous, (0 to 1 SPM in BC's of three specimens); HD with prominent brown markings, short, thickened, coiled, links AG to a small, elongated, narrow, brownish/yellow spotted, finely granulated HG, inner edge firmly moulded; MG and AG small, folded, soft white tissue; purple SV embedded on left side of AG, AG larger than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 32F): Body cylindrical, thread-like (length = 10.88 mm, n = 1), test thin, translucent; head section, bluntly rounded, containing a white gelatinous core, tapers to a thin flagellum and tip; both sections smooth, featureless; head shorter, thicker than flagellum (head length = 10.03 mm; 92% of SPM length; flagellum length = 0.85 mm; head width = 93 µm; flagellum width = 13 µm). Single SPM tightly coiled in brown gelatinous mass in BC of topotypic specimen.

Comparative remarks. *Siphonaria scabra* (*atra* group, unit 50) is the sister species of *S. pravitas* **sp. nov.** (unit 51); both species together form a well-differentiated and well-supported sub-clade (Figs 1, 2). They differ from each other by COI distances of ≥ 8.2% (Table S4). *Siphonaria scabra* differs from any other species by COI distances of ≥ 24% (Table S4). Throughout its range, *S. scabra* has been found in sympatry with nine congeners. Five congeners are sympatric in eastern Australia: For comparisons with *S. normalis*, *S. atra*, *S. denticulata* refer to comparative remarks under these species. *Siphonaria opposita* has a lower shell with a dual-ribbed siphonal ridge, a larger pointed AO, larger BC, and a shorter ED. Four species occur in sympatry with *S. scabra* in Sydney Harbour: For comparison with *S. diemenensis* and *S. zelandica* refer to comparative remarks under these species. *Siphonaria funiculata* has a taller shell with a dual ribbed but indistinct siphonal ridge, less raised ribbing and weaker edge scalloping, a shorter ED and AO, larger BC, and a shorter, drop-like SPM.

Siphonaria pravitas **sp. nov.** has a lower shell with stronger raised ribs and edge scalloping, a smaller AO, shorter ED, larger BC, a shorter wider BD with no distal loop, and a shorter SPM. Specimens figured as '*S. diemenensis* var. *scabra*' from 'Port Jackson [Sydney Harbour]) in Hubendick (1946: pl. 2, figs 14–15) are likely specimens of *S. denticulata* based on patterning on shell lip and margin and only possibly of *S. scabra* based on the presence of few secondary and even primary ribs, yet clearly not of *S. diemenensis*.

Distribution and habitat. Endemic to subtropical to temperate east coast of Australia (Fig. 25). In this study found on sheltered rocky shores across upper to mid littoral levels.

Siphonaria funiculata Reeve, 1856

(Figs 33A–H, O–P, S–U, 34A–D)

Siphonaria funiculata Reeve 1856: pl. 2, species 6 (type locality: 'Van Diemen's Land' [Tasmania, Australia]).—Hanley 1858b: 152; Angas 1867: 232; Tenison Woods 1877: 58; 1878b: 99; Whitelegge 1889: 117; Paetel 1889: 428; Henn & Brazier 1894: 179; Tate & May 1901: 419; Pritchard & Gatliff 1903: 220; Hedley 1917b: M96; May 1921: 88; 1923: 87, pl. 41, fig. 3; Iredale 1924: 275; Macpherson & Gabriel 1962: 262, fig. 301; Galindo 1977: 416; Jenkins 1981: 2, pl. 1b; 1983: 29; Quinn 1983: 83; Phillips *et al.* 1984: 79, text-fig.; Short & Potter 1987: 122; Jansen 1995: 90, fig. 377; Davey 1998: 119, top fig.; Grove *et al.* 2006: 60, 2011: 62, pl. 29, fig.14; White & Dayrat 2012: 63; Colgan & da Costa 2013: 74; Dayrat *et al.* 2014: 266, 'unit 8', fig. 3 I–J; Gonzàlez-Wevar *et al.* 2018: 5, fig. 1.

Siphonaria blainvillei Hanley 1858b: 152, 153 (type locality unknown [probably Tasmania, Australia]).—Paetel 1889: 428; Hedley 1915: 752; Jenkins 1981: 2, pl. 1a; Coan & Kabat 2012: 336; Grove *et al.* 2006: 60; White & Dayrat 2012: 61.

Siphonaria lirata—Hanley 1858b: 152; Hedley 1915: 751; Galindo 1977: 416; White & Dayrat 2012: 65; Dayrat *et al.* 2014: 267 (not *S. lirata* Reeve, 1856).

Siphonaria luzonica—Angas 1865: 190 (not *S. luzonica* Reeve, 1856).

Siphonaria laeviuscula—Hutton 1878: 42 (not *S. laeviuscula* Blainville, 1835).

Siphonaria zonata—Tate & May 1901: 419 (not *S. zonata* Tenison Woods, 1878).

Siphonaria virgulata Hedley 1915: 751, pl. 85, figs 96–98 (type locality: Terrigal, Sydney, and Twofold Bay [NSW, Australia]).—Hedley 1917b: M95; Iredale 1924: 276; Hubendick 1943: 4; Macpherson & Chapple 1951: 142; Hubendick 1955: 1, fig 1; Galindo 1977: 416; Crease 1980: 38; Jenkins 1981: 2, pl. 2a–k; Short & Potter 1987: 122; Davey 1998: 119; Grove *et al.* 2006: 60; Chim & Tan 2009: 269; White & Dayrat 2012: 69.

Talisiphon virgulata—Iredale 1940: 442; Iredale & McMichael 1962: 82.

Siphonaria oblivirgulata Hubendick 1943: 2, figs 2, 6 (type locality: Port Jackson, Australien [Australia]).—Grove *et al.* 2006: 60; White & Dayrat 2012: 66.

Siphonaria (*Pachysiphonaria*) *funiculata*—Hubendick 1945: 12, 15, 16, 66, figs 3, 12, 58; 1946: 23, pl. 1, figs 15–17.

Siphonaria (*Benhamina*) *oblivirgulata*—Hubendick 1946: 25, pl. 1, figs 26–29.

Talisiphon funiculata—Cotton 1959: 441.

Talisiphon oblivirgulata—Iredale & McMichael 1962: 82.

Siphonaria (Talisiphon) virgulata—Morrison 1963: 7.

Pachysiphonaria funiculata—Trew 1983: 2.

Pachysiphonaria virgulata—Trew 1983: 2.

Siphonaria diemenensis—Davey 1998: 117 (not *S. diemenensis* Quoy & Gaimard, 1833).

Siphonaria tasmanica—Davey 1998: 118 (not *S. tasmanica* Tenison Woods, 1877).

Material examined. *Type material.* Lectotype of *Siphonaria funiculata* Reeve, 1856, present designation, from Tasmania [Australia] (NHMUK MC.197927/1, Fig. 33A). Three paralectotypes, same data as lectotype (NHMUK MC.197927/2-4).

Holotype of *Siphonaria blainvillei* Hanley, 1858 (NHMUK 1907.10.28.90, Fig. 33D).

Holotype of *Siphonaria virgulata* Hedley, 1915, from

Terrigal [E of Gosford, NSW], Sydney; coll. C. Hedley, 1915 (AM C.39858, Fig. 33C). Twenty paratypes, same data as holotype (AM C.337311).

Holotype of *Siphonaria oblivirgulata* Hubendick, 1945, from Port Jackson [Sydney, Australia]; coll. Eugenie Exp., 1851–1853 (UUZM 1575, Fig. 33E).

Other, non-type material. **Australia: NSW:** Brunswick Heads, 28°32.297'S, 153°33.444'E, NSW12-1 (AM C.585592 4p, C.585068 p [M185]); Cape Byron, 28°38'S, 153°38'E (AM C.311682 5p); Sand Point, N of Ballina, 28°50.66'S, 153°36.45'E (AM C.343608 p); MinniE, WAter, E of Grafton 29°46.6'S, 153°18'E (AM C.343604 p); N of Coffs Harbour, 30°14'S, 153°9'E (AM C.311683 7p); Nambucca Heads, 30°38.5'S, 153°1'E AM (AM C.311681 7p); Fingal Bay nr Port Stephens, 32°44.990'S, 152°10.481',E, NSW09-1 (AM C.585335 p); Catherine Hill Bay, 33°9.3'S, 151°38'E (AM C.343605 3p); S end Catherine Hill Bay, 33°9.5'S, 151°38'E (AM C.311679 6p); Broken Head Terrigal, 33°26.796'S, 151°27.030'E, NSW08-1 (AM C.585665 6p, C.585051 p [M044]); Terrigal The Skillion, 33°27.008'S, 151°27.122'E, NSW08-2 (AM C.585405 10+p, C.585055 p [M223], C.585056 p [M224]). Sydney, Long Reef Collaroy, 33°44.6'S, 151°18.6'E (AM C.343674 5p); S side Long Reef Collaroy, 33°44.7'S, 151°19'E (AM C.343678 3p; AM C.446108 6p); Fairlight, North Harbour, 33°47.986'S, 151°16.837'E, NSW06-1 (AM C.585470 16p); Shelly Beach Headland Manly, 33°48'S, 151°17.5'E (AM C.311680 5p); North Harbour, SE side Reef Bay, 33°48.5'S, 151°16.38'E (AM C.311687 7p). Middle Harbour, Wy-ar-gine Point, 33°49'S, 151°15'E (AM C.311678 10+p); Wy-ar-gine Point, 33°49.159'S, 151°15.195'E, NSW06-5 (AM C.585664 6p, 3d); Edwards Beach Balmoral, 33°49.38'S, 151°15'E (AM C.311890 10+p); Balmoral, 33°49.7'S, 151°15.02'E (AM C.343610 2p), Laings Point Sydney Harbour, 33°50.419'S, 151°16.638'E, NSW06-3 (AM C.585475 17p, C.585035 p [M162, SK035], C.585036 p [M163], C.585037 d [M164]); Tamarama Point, 33°54'S, 151°16'E (AM C.311684 7p; AM C.343615 2p). Bombo Kiama, 34°39.232'S, 150°51.649'E, NSW03-1 (AM C.585455 13p, C.584884 p [SK384], C.585280 p [SK048]); Ulladulla, Wardens Head, 35°21'S, 150°29'E (AM C.311677 7p); Batemans Bay, Batehaven, 35°44'S, 150°12.5'E (AM C.311685 5p); Wimbie Beach, 35°47'S, 150°14'E (AM C.343613 2p); Eurobodalla Shire, Pretty Point SE facing, 35°48.28'S, 150°14'E (AM C.343611 p); Burrewarra Point, 35°50'S, 150°13.5'E (AM C.343606 3p); Mullimburra Point SE facing, 35°59.75'S, 150°9.58'E (AM C.343607 5p); Murunna Point Camel Head, 36°22.720'S, 150°04.766'E, NSW02-1 (AM C.585718 9p, C.585030 p [SK025], C.585332, d [SK026]); Bermagui, 36°25.18'S, 150°3.78'E (AM C.343612 2p); Wapengo Lagoon estuary S side near Bithry Inlet, 36°37.7'S, 150°59'E (AM C.395918 8p); Aslings Beach, N end Twofold Bay, 37°3.1'S, 149°55'E (AM C.148856 p); Oman Point Eden, 37°04.634'S, 149°53.445'E, NSW01-1 (AM C.585629 5p). Twofold Bay, Murrumbulga Pt, 37°4.75'S, 149°53.06'E (AM C.343622 2p, C.343623 p, C.343624 p, AM C.311688 4p); Red Point, 37°6.083'S, 149°57.1'E (AM C.343625 p); Munganno Point, 37°6.2'S, 149°55.48'E (AM C.343616 p, C.311689 4p, C.343617 3p, C.343618 2p, C.343619 3p, C.343621 3p, C.150599 p); Fisheries Beach, 37°6.78'S, 149°55.6'E (AM C.343620 p). Green Cape, 37°15.8'S, 150°3'E (AM C.343614 p, C.311676 5p); Wonboyn Beach, Disaster Bay, 37°16'S, 149°57'E (AM C.343733 2p); Nadgee Fauna Reserve, N of Little River, 37°24'S, 149°57'E (AM C.343735 3p). **Vic:** Bastion Head Mallacoota, 37°34.429'S, 149°45.927'E, V09-1 (AM C.585459 13p); Cape Conran, 37°48.798'S, 148°43.608'E, V08-2 (AM C.585610 4p); Wilsons Promontory, 39°S, 146°22'E (AM C.311674, 3 p); Bear Gully, 38°53.519'S, 145°59.029'E, V07-3 (AM C.585652 5p); Flat Rock, Inverloch, 38°38.877'S, 145°41.638'E, V07-6 (AM C.585573 3p); Blow Hole, Western Port Bay nr. Flinders, 38°29'S, 145°1'E (AM C.311673 2p); Cape Schanck, 38°29.951'S, 144°53.369'E, V06-4 (AM C.585515 p [SK548]); Port Phillip, Portsea, 38°19'S, 144°43'E (AM C.311675 2p); Point Lonsdale (nr Queenscliff), 38°17.276'S, 144°36.977'E, V05-1 (AM C.585514 2p); Roadknight Point, 38°25.707'S, 144°11.102'E, V04-1 (AM C.585457 13p); Loutit Bay Lorne, 38°31.190'S, 143°59.429'E, V03-2 (AM C.585465 15p). **Tas:** Flinders Island, Northeast River, 39°43.8'S, 147°57.6'E (TMAG E54212 2d); Palana Beach, 39°45.6'S, 147°52.8'E (TMAG E54211 d); Port Davies & Cave Beach, 40°0.6'S, 147°52.8'E (TMAG E27150 d; TMAG E27142 4d). Boat Harbour, 40°57'S, 145°38'E (AM C.311672 3p); West Point, 40°57'S, 144°36'E AM (AM C.311668 3p); Little Peggs Beach, 40°51'S, 145°21.6'E (TMAG E41987 d); Rocky Cape: Picnic Beach & rocks to S, 40°52.2'S, 145°28.8'E (TMAG E41989 d); S of Granite Point Bridport, 40°59.739'S, 147°23.468'E, T01-1 (AM C.585251 p [M174]); Bridport: beach, 41°24.6'S, 147°23.4'E (TMAG E41986 d); Bellingham, 41°0.6'S, 147°9.6'E (TMAG E54215 4d); Greens Beach, 41°4.8'S, 146°45'E (TMAG E54216 d). The Gardens, Seatons Cove, 41°12.6'S, 148°16.8'E (TMAG E41988 3d); Swimcart Beach, 41°13.8'S, 148°17.4'E (TMAG E27411 4d, TMAG E54214 5d, TMAG E41975 3d). Beaumaris, Shelly Point, 41°26.4'S, 148°16.8'E (TMAG E41981 d); Steels Beach, 41°28.2'S, 148°16.2'E (TMAG E54217 d); Bicheno, 41°52.837'S, 148°18.525'E, T02-1 (AM C.585693 7p); Bicheno, S end Redbill Beach, 41°53'S, 148°18'E (AM C.311669 2p); Maria Island, Darlington Bay, 42°34.8'S, 148°3.6'E (TMAG E41984 3d); Dodges Ferry, 42°51.083'S, 147°36.981'E, T03-1 (AM C.585462 14p); Park Beach Dodges Ferry, 42°51.716'S, 147°36.665'E, T03-4 (AM C.584883 p [SK138], C.585660 p [M111], C.585262 p [SK139]); Lagoon Bch (near Saltwater River), 42°56.903'S, 147°39.962'E, T03-2 (AM C.585648 5p, C.595922 p [SK551]); Blackmans Bay, 43°0.6'S, 147°19.8'E (TMAG E15879 10+d); Tasman Arch, 43°02.033'S, 147°56.963'E, T03-3 (AM C.585772 12p, C.585258 p [M116]); Huon Point d'Entrecasteaux Channel, 43°17.471'S, 147°05.778'E, T04-1 (AM C.585678 6p, C.585267 p [M106], C.585268 p [M135]); South Bruny Island: Coal Point, 43°19.8'S, 147°19.8'E (TMAG E35240 p); Moss Glen, 43°31.910'S,

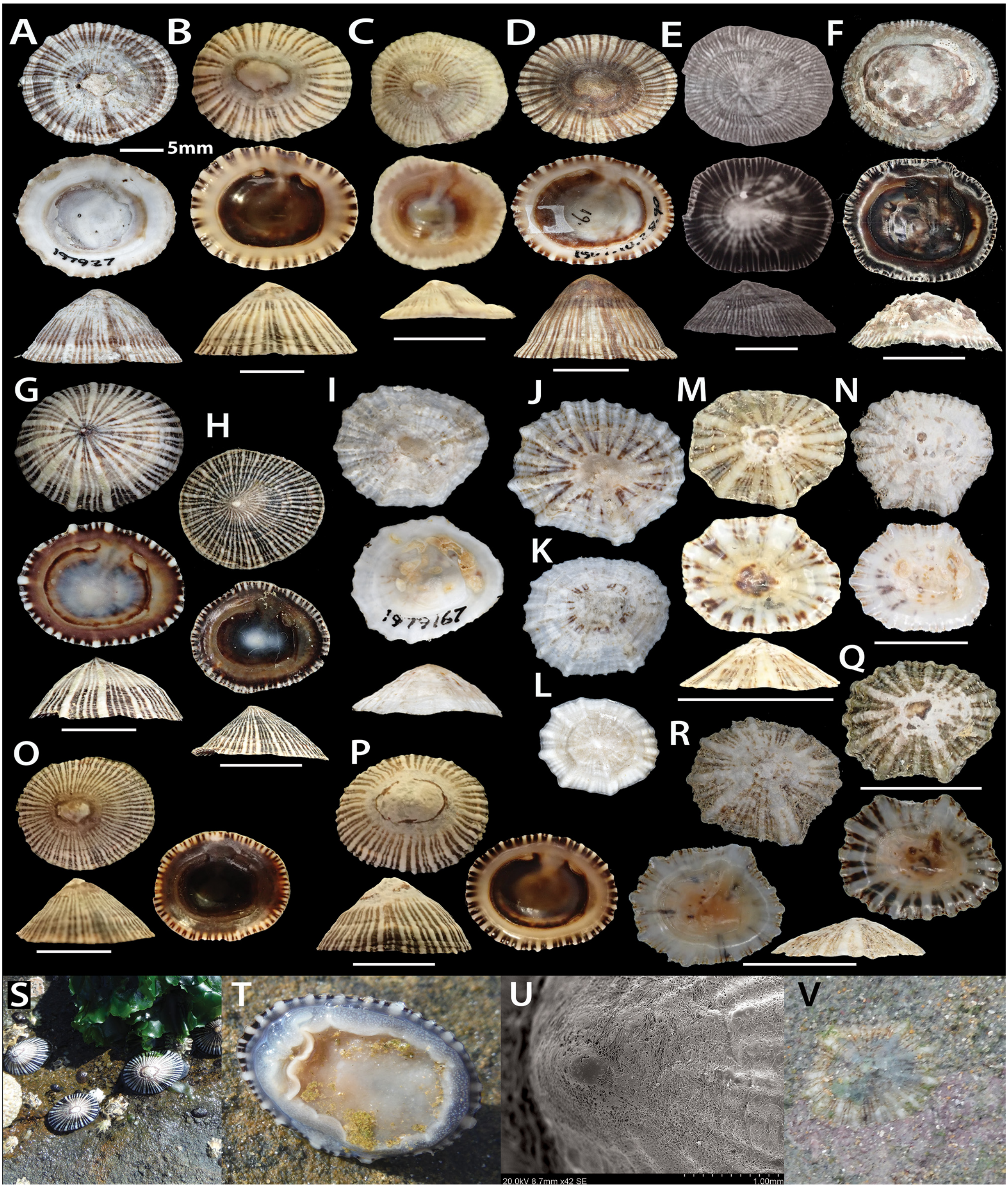

FIGURE 33. Shells of *S. funiculata* and *S. kurracheensis*. **A–H, O–P, S–U.** *S. funiculata*. **A.** Lectotype NHMUK 1979027/1. **B.** Tas, d'Entrecasteaux Channel, TS, AM C.585268 [M135, SK049]. **C**. Holotype of *S. virgulata* AM C.39858. **D.** Holotype of *S. blainvillei* NHMUK 1907.10.28.90, **E.** Holotype of *S. oblivirgulata* UUZM 1575. **F.** NSW, Sydney Harbour, TS of *S. oblivirgulata* AM C.585035 [M162]. **G.** Tas, Dodges Ferry, TS of *S. funiculata* AM C.584883 [SK138]. **H**. NSW, Sydney Harbour, AM C.585068 [M185]. **O.** NSW, Terrigal, TS of S. *virgulata* AM C.585056 [M224]. **P.** Tas, Bridport, AM C.585251 [M174]. **S.** Tas, *in situ*. **T.** Tas, animal, **U.** Protoconch AM C.585332 [SK026]. **I–N, Q–R, V.** *S. kurracheensis*, **I.** Lectotype NHMUK 1979167/1, **J–L.** Paralectotypes NHMUK 1979167/2-4. **M.** Pakistan, Karachi, TS, AM C.585857 [M230, SK192]. **N.** Karachi, TS, WAM S72336 [SK148]. **Q.** AM C.585856 [M229]. **R.** AM C.585849 [M241]. **V.** Karachi, *in situ*. Unlabelled scale bars = 10 mm.

146°53.641’E, T05-1 (AM C.585569 3p); Flensing Rock, 43°34.291’S, 146°54.856’E, T05-2 (AM C.585605 4p). King Island, Little Porky Beach, 39°51’S, 143°51.6’E (TMAG E41980 2d), Naracoopa, foreshore, 39°55.2’S, 144°7.2’E (TMAG E41978 d), Currie Harbour, 39°55.8’S, 143°50.4’E (TMAG E41985 10d), Red Hut Point, 40°6’S, 144°6’E (TMAG E41983 d).

Taxonomic remarks. The lectotype of *S. funiculata* has been referred to as the holotype by Jenkins (1981: 2), an act that qualifies as the designation of the lectotype. The lectotype (Fig. 33A) closely matches the figure in the original description (Reeve, 1856: pl. 2, fig. 6a–b). Reeve (1856: pl. 7, fig. 35a–b) erroneously labelled species 35 (= *S. lirata*) as ‘*S. funiculata*’ (see erratum in the appendix). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes of *S. funiculata* (Fig. 33B), *S. blainvillei* (Fig. 33P), *S. virgulata* (Figs 33H, O), and *S. oblivirgulata* (Fig. 33F) and a geographic series of additional specimens (Table S1).

Tenison Woods (1877: 58) incorrectly treated *S. funiculata* as a variety of *S. diemenensis*. Hutton (1878: 42) treated *S. funiculata* as a synonym of *S. laeviuscula*, but Hubendick (1946: 23) thought that Hutton’s (1878: 42) reference to *S. laeviuscula* was a misidentification of *S. funiculata*. Hedley (1915: 751) described *S. virgulata* indicating that Angas’ (1867: 232) record of ‘*S. funiculata*’ was in fact a misidentification of this new species. This conclusion was subsequently upheld by Hedley (1917b) and Hubendick (1946: 23), the latter also including a record of ‘*S. funiculata*’ by Adam & Leloup (1939: pl. 2, fig. 2a–b) from Pisang Island, PNG. Hedley (1915) and Jenkins (1981: pl. 1, fig. a) observed that *S. blainvillei* (based on one specimen) was a tall and broad ribbed specimen of *S. funiculata*. Hubendick (1946: 23) also treated *S. blainvillei* as a synonym of *S. funiculata*. Several tall specimens of *S. funiculata* have been collected as part of this work with a shell geometry resembling the type specimen of *S. blainvillei* and analyses of these specimens confirm this conclusion (e.g., AM C.585660, AM C.585251). Similarly tall individuals occur in other *Siphonaria* species, such as *S. radiata*, *S. plicata, S. radians, S. sipho* and *S. monticulus*.

Iredale (1924: 275–276) and Jenkins (1981) considered *S. virgulata* as a geographical variant of *S. funiculata*. Hubendick (1947b: 1) incorrectly considered *S. funiculata* Reeve 1856 as a synonym of *S. pisangensis* Hubendick 1947b (type locality Pisang Island, PNG). Grove *et al.* (2006: 60) correctly listed *S. blainvillei, S. virgulata* and *S. oblivirgulata* in the synonymy of *S. funiculata*. No records of *S. funiculata* are available from NZ based on our examinations of museum samples. The description below is based on the redescription in Jenkins (1981), which is expanded here for completeness and consistency.

External morphology (Fig. 33T). Foot sole smooth, greyish yellow centrally, fading to become paler at foot edge; foot wall dark grey with evenly spread white subepithelial pustules becoming more vivid and dense close to the foot sole; genital pore inconspicuous, located on foot wall posterior to right cephalic fold; two small black epithelial eye spots centralised on two thick centrally touching dark grey to blueish cephalic folds, folds fade to a paler cream to yellowish at outer edge, covered with clustered white mucous cells similar (but smaller) to those of the foot wall tissue; fringing whitish mantle around top of foot wall, extends and increasingly transparent to shell edge, mantle edge thickened, lobed with an outer band of cream and brown pigmentation reflecting corrugations and inner colouration of shell lip and ribs; thin whitish pneumostomal lobe part of the mantle, between the right ADMs, closes the pneumostome and anus at the mantle edge.

Shell (Fig. 33A–H, O, P, U; Table S9). Small to medium sized (max sl mean = 23.3 mm, SD = 4.45 mm, n = 30); height medium to tall; shell thickness medium; ovate; apical sides weakly convex, apex often eroded creating a white spot; protoconch direction homostrophic (n = 3; Fig. 33U), shell whorl dextral; apex offset weakly posterior and central; exterior sculpture finely costate with irregularly spaced radial ribs and growth striae; ribbing flat, broad with rib widths at shell lip ranging from 0.39 to 1.89 mm (mean = 0.82 mm, SD = 0.02 mm, n = 30), white axial ribs, often bistriate, chocolate coloured interstices, narrow and curve adapically; number of ribs variable, rib count (range 28–94; mean = 63, SD = 10.5, n = 60); siphonal ridge is weakly visible with fine, clustered, brown radial striae above a slight fold in the marginal lip; interior is polished and purplish brown with a white to blue spatula (colouration extends into the shallow siphonal groove) fading to a chocolate brown zone above the brown ADM impression and tan margin; marginal lip is shallowly scalloped with alternating chocolate brown and white radial markings, restricted to the lip margin and reflecting the exterior ribbing; ADM impression is horseshoe-shaped with a thin, lightly convex, anterior attachment area and a bare siphonal groove flanked by broad, ovate muscle impressions. Juvenile specimens have fine radial ribs, a dark brown interior and exterior (often obvious around the apex of adult specimens), with a white spatula.

Reproductive system (Figs 34A, B, D; n = 3). Epiphallic parts fill the region between RAM and BM, ED, GA, AO, EG white, smoothly rounded, possessing thick fibrous layers of tissue, ED larger than EG, often elongated; F1 very stubby, inconspicuous; GA large, bulbous, opening below the mantle on the side of the foot, behind right cephalic fold, anterior to pneumostome; AO very large, sack-like, joins GA; ED very short thick, joins to side of GA, EG larger than AO or GA; BD and CD enter GA very close together and AO, both pass through RAM (BD above CD) are of similar length (although BD may be shorter); HG at posterior right quarter of coelom over the foot muscle tissue; HG usually yellow, granulated, linked by thin duct to the pinkish white, lobed, coiled HD, which in turn links to CD; SV partly lobed, uncoiled, pink to white, connected via thin duct alongside the AG to CD; AG/MG complex yellow to white, folded, lobed, closely attached to HG; SV embedded in folds; BC ovate, brown, patterned, tissue often expanded and stretched or collapsed and wrinkled; test thin, enclosing granulated, brown gelatinous mass.

Spermatophore (Fig. 34C). Elongated drop shaped, test thin, smooth, featureless, translucent (length = 1.12 mm, n = 1), head spherical; flagellum very short; both sections smooth, featureless; head much larger than flagellum (head length = 0.93 mm, head ~83 % length of SPM, head width = 0.79 mm, flagellum width = 0.103 mm, n = 1); single SPM found in one BC (AM C.584848). SPM matches SPM depicted in Jenkins (1983: fig. 3f).

Radula and jaw (figured in Jenkins 1983: 10, pl. 3a–h). Radula with a central tooth and longitudinally variable number of inner, mid and outer lateral teeth in longitudinal rows. Mean dentition formula 43:1:43 (SD = 7.9, n = 17) with around 120 transverse rows (SD = 14.9). These rows are parallel and slightly curved (anteriorly convex) Jenkins (1981: 9, pl.3a–h). Of the 43 half row laterals, 7 (SD = 4.2) are inner, 17 (SD = 7.6) mid and 18 (SD = 3.1) outer lateral teeth, respectively. The total number of lateral teeth appears related to the length of the shell (max. 54:1:54, shell length = 22.0 mm, mean 43:1:43, shell length = 18.1 mm, min 34:1:34, shell length = 15.1mm). However, the numbers of inner, mid and outer lateral teeth vary independently of animal dimensions and distributions. All teeth are bluntly concave posteriorly. The central tooth is narrow and weakly bicuspidate (often pointed) with a lower profile than the flanking laterals. The base is broad with adjacent central teeth. Mid and inner lateral teeth interlock with posteriorly and anteriorly aligned laterals. Outer laterals do not interlock between transverse rows. The space between rows increases to the ribbon edges associated with a gradual decrease in tooth size (Jenkins 1981: 10, pl.3c, g). The space varies between individuals (Jenkins, 1981: 10, pl.3d, h) as well as posterior and anterior areas of the ribbon. All lateral teeth are broad based and bicuspidate on the mesocone with a longer inner cusp. Outer lateral teeth are often multicuspidate. Increasing side denticle numbers, less elongated shape and increasingly stunted mesocones are transverse row features less accentuated from the central to the outer lateral teeth. Inner lateral teeth are elongated without flanking endo and ecto cones (inner and outer side denticles respectively). The more numerous outer lateral teeth have both ecto and endo cones while the mid laterals possess only an ectocone. The angle of separation from the mesocone of these side denticles is widely variable. Both side cones curve either towards or away from the mesocone (Jenkins, 1981: 10, pl.3 g, h). The length and width of the separation cleft is also widely variable, both generally increase towards the ribbon edge (Jenkins, 1981: 10, pl.3c, d mid half ribbon area, pl.3g, h ribbon edge). Aberrant outer lateral teeth are often present on both sides of the ribbon appearing as fused teeth with double mesocones. Not all individuals have inner lateral teeth, most have increased numbers of mid laterals. The number is independent of the number of lateral teeth, for example, of two radulae with 54 half row laterals, one had no inner laterals while the other had 18. The same variability was noted for radulae with fewer numbers of lateral teeth. Inner laterals do not possess endo or ectocones.

Comparative remarks. *Siphonaria funiculata* (*lateralis* group, unit 8) is the sister species of *S. lessonii*, both together representing the sister lineage of *S. tasmanica* (Figs 1, 4). *Siphonaria funiculata* differs from *S. lessonii* by COI distances of ≥ 12% and from *S. tasmanica* by ≥ 8.5% (Table S8). Throughout its range, *S. funiculata* has been found in sympatry with nine congeners. For comparisons with *S. diemenensis*, *S. denticulata*, *S. scabra*, and *S. zelandica* refer to comparative remarks under these species. *Siphonaria emergens* has a much smaller, paler, orange-brown shell with less prominent ribbing, stronger edge scalloping and a strongly offset apex. *Siphonaria pravitas* **sp. nov.** has much paler brown shell with a more prominent siphonal ridge, raised ribbing, a darker spatula, a smaller AO, and a narrower, thread-like SPM. *Siphonaria stowae* has a much smaller, paler, yellowish cream shell with less prominent ribbing, stronger edge scalloping, a strongly offset apex, a smaller AO and BC, a shorter ED, and a narrower, thread-like SPM. *Siphonaria jeanae* has a smaller, grey-blue shell with slightly more raised brown ribbing, purplish spatula, an indistinct AO, narrower BD, and a more bulbous SPM. *Siphonaria tasmanica* has a grey-blue shell with a less distinct siphonal ridge, fainter ribbing, a smaller AO and BC.

A record of *S. funiculata* from NZ (Hutton, 1873: 55) has been attributed subsequently to *S. australis* (Jenkins, 1983: 13). Based on similarity in reproductive anatomy (i.e., closeness of the duct joint, smallness of the genital atrium and greatly swollen epiphallus duct), Hubendick (1946: 23) assigned *S. funiculata* to *Pachysiphonaria*. The RS shown herein (Figs 34A, B, D) correspond well with illustrations of the RS figures of *S. funiculata* elsewhere (e.g., Hubendick 1945: figs 3, 12; 1946: fig. 5, as '*S. virgulata*'; 1955: figs 1–2, as '*S. virgulata*'; Jenkins, 1983: figs 3a–c). The mean radula dentition formula observed herein is consistent with the 39:1:39 count given by Hubendick (1946: 23). A specimen figured as '*S. funiculata*' from Lakshadweep, India by Ravinesh & Biju Kumar (2015: 38) is a misidentification of an unidentified species. Specimens depicted as '*S. funiculata*' from Kelsi Coast, India in Vakani & Rahul Kundu (2021: 134, figs 2d, 3d) are misidentifications and are likely specimens of *S. incerta* **sp. nov.**

Distribution and habitat. Endemic to eastern and southeastern coasts of Australia, from Brunswick Heads, northern NSW, south to west of Lorne, Vic, including Tas (Fig. 25). In this study found to be common in sheltered places, such as crevices and vertical faces, on exposed rocky shores, upper to mid littoral levels, often associated with barnacles (Fig. 33S).

Siphonaria kurracheensis Reeve, 1856

(Figs 33I–N, Q–R, V, 34E–G)

Siphonaria kurracheensis Reeve 1856: pl. 5, species 20 (type locality: Kurrachee, Scinde [Karachi, Pakistan]).—Hanley 1858b: 152; Issel 1869: 320; Fischer 1870: 167; Paetel 1873: 117; Fischer 1883 (in 1880–1887): Index, pl. 11, fig. 25 (ventral only); Paetel 1883: 178; 1889: 428; Melvill & Standen 1901:

457; Melville & Abercrombie 1893: 24; Hubendick 1946: 54, pl. 2, figs 36, 39, 40; Berry 1977: 210; Anon 1980: 11; Trew 1983: 6; Jones 1986: 130, pl. 23; White & Dayrat 2012: 64.

Siphonaria cochleariformis—Cooke 1886a: 133 (not *S. cochleariformis* Reeve, 1856).

Siphonaria luzonica—Cooke 1886a: 133 (not *S. luzonica* Reeve, 1856).

Siphonaria natalensis—Cooke 1886a: 133 (not *S. natalensis* Krauss, 1848).

Siphonaria siquijorensis—Cooke 1886a: 133 (not *S. siquijorensis* Reeve, 1856).

Siphonaria kurrachensis Cooke 1886a: 133; 1886b: 383; Galindo 1977: 416 (incorrect subsequent spelling of *kurracheensis*).

Siphonaria diemenensis—Smythe 1982: 80 (not *S diemenensis* Quoy & Gaimard, 1833).

Siphonaria savignyi—Dayrat *et al.* 2014: 261, 'unit 28', fig. 5 E, F (not *S. savignyi* Krauss, 1848).

Material examined. *Type material.* Lectotype of *Siphonaria kurracheensis* Reeve, 1856, present designation, from Kurrachee [Karachi], Scinde, [Pakistan] (NHMUK 1979167/1, Fig. 33I). Three paralectotypes, same data as lectotype (NHMUK 1979167/2-4, Fig. 33J–L).

Other, non-type material. **Pakistan:** Karachi, Bubiji Beach, 24°53'N, 67°01'E (WAM S72336 p, WAM S74134 p [SK148]); French Beach, 24°50.367'N, 66°49.387'E PA01-1 (AM C.585741 4p, C.585848 p [M240], C.585849 p [M241], C.585850 p [M484], C.585852 p [M485, SK304]); Clifton Beach, 24°45.500'N, 67°05.968'E PA02-1 (AM C.585107 p [SK008], C.585744 p [SK045], C.585856 p [M229], C.585857 p [M230],C.585858 p [M231]).

Taxonomic remarks. The largest syntype with clearest external sculpture (Fig. 33I) is herein designated as the lectotype of *S. kurracheensis* for the stabilisation of the name (Art. 74.1 of the Code). The shell figure in Reeve's (1856) original description provides a ventral view only. Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 33N, M, Q) and geographic series of additional specimens (Table S1). We do not accept Hubendick's (1946) extended concept of *S. kurracheensis*, which included several extralimital nominal taxa (e.g., *S. belcheri, S. depressa, S. luzonica*, *S. savignyi*, *S. siquijorensis* and *S. zebra*), all of which represent distinct species. Therefore, the accepted distribution of this species is much smaller than previously stated.

Morrison (1972: 56–58) synonymized *S. kurracheensis* with *S. laciniosa* based on similarity in shell form and a 'common reproductive development'. This synonymy is rejected herein based on examination of types and topotypes. The species identified as '*S. kurracheensis*' in WA by various authors is shown herein to be morphologically and genetically distinct and is described as a new species, *Siphonaria restis* **sp. nov.** (unit **54**) below.

External morphology. External parts evenly pale cream without black pigmentation apart from faint shading at centre of cephalic folds; mantle weakly lobed, translucent, narrower than foot wall, covers exposed inner shell lip; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold; single small black epithelial eye spots centralised on two centrally touching cephalic folds; pneumostomal lobe under the mantle, unpigmented, between the right anterior and right posterior ADMs.

Shell (Fig. 33I–N, Q, R; Table S9). Small sized (max sl mean = 11.5 mm, SD = 1.7 mm, n = 7), ovate, height low to medium; shell thickness thin to medium, apex offset weakly posterior and left, apical sides weakly convex, protoconch direction undetermined, shell whorl dextral; growth striae indistinct; rib count (mean = 42, SD = 4, n = 7), primary ribs pale white, fairly straight, unraised, flat, ridge rounded; secondary ribs even whitish; ribs increasingly widen to shell lip; more primary than secondary ribs; rib interstices very narrow brown, marking on side of primary ribs; siphonal ridge low prominent; shell lip uneven, weakly scalloped, corrugated by primary ribs. Interior mottled red brown blotches on margin; spatula golden to pale brown/whitish; clearly demarked from margin by siphonal groove similar colour paler fairly prominent; irregular narrow brown rays from shell lip to spatula; brown interstices show through shell lip; ADM scar indistinct, CMS convex. Smaller and tall specimens with thicker shells, tend to show dark brown rays on shell margin. Thickening of shell margin and variability in shell height occurs in larger specimens in this species.

Reproductive system (Figs 34E, F; n = 3). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned between BM and to side of RAM; AO medium, broad, tip bluntly hooked, merges with MA, joins to upper end of small GA; ED very short, centrally twisted, bent, joins to side of GA; EG folded may be large; single wide looped flagellum F1 joins as an extension of broader ED; AO, GA and ED all muscular white tissue; BD and CD with opposing connections (bulbous at CD) into GA between ED, AO and GP; BD longer and narrower than CD with a prominent distal loop, top of loop attached via a long MA to inner foot wall in front of BM; both BD and CD smooth, similar thickness and pass together through RAM connecting into folds of MG (BD above CD), BC small, translucent test and bulbous drop shaped; HD brownish, narrow coils, links AG to a small elongated narrow brownish granulated HG; dark SV embedded within AG/MG; MG and AG small folded soft white tissue, similar size, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 34G). Thread-like, test thin, translucent (length = 7.2 mm, n = 1, AL = 9 mm); head section cylindrical, centrally coiled, rounded tip; test thin, smooth, featureless, translucent, contains a white core, tapers into flagellum; head longer, wider than translucent flagellum (head length = 5.5 mm, ~ 76 % of total length, head width = 172 µm, flagellum width = 17 µm, n = 1); SPM tightly coiled in yellowish gel in BC of one specimen.

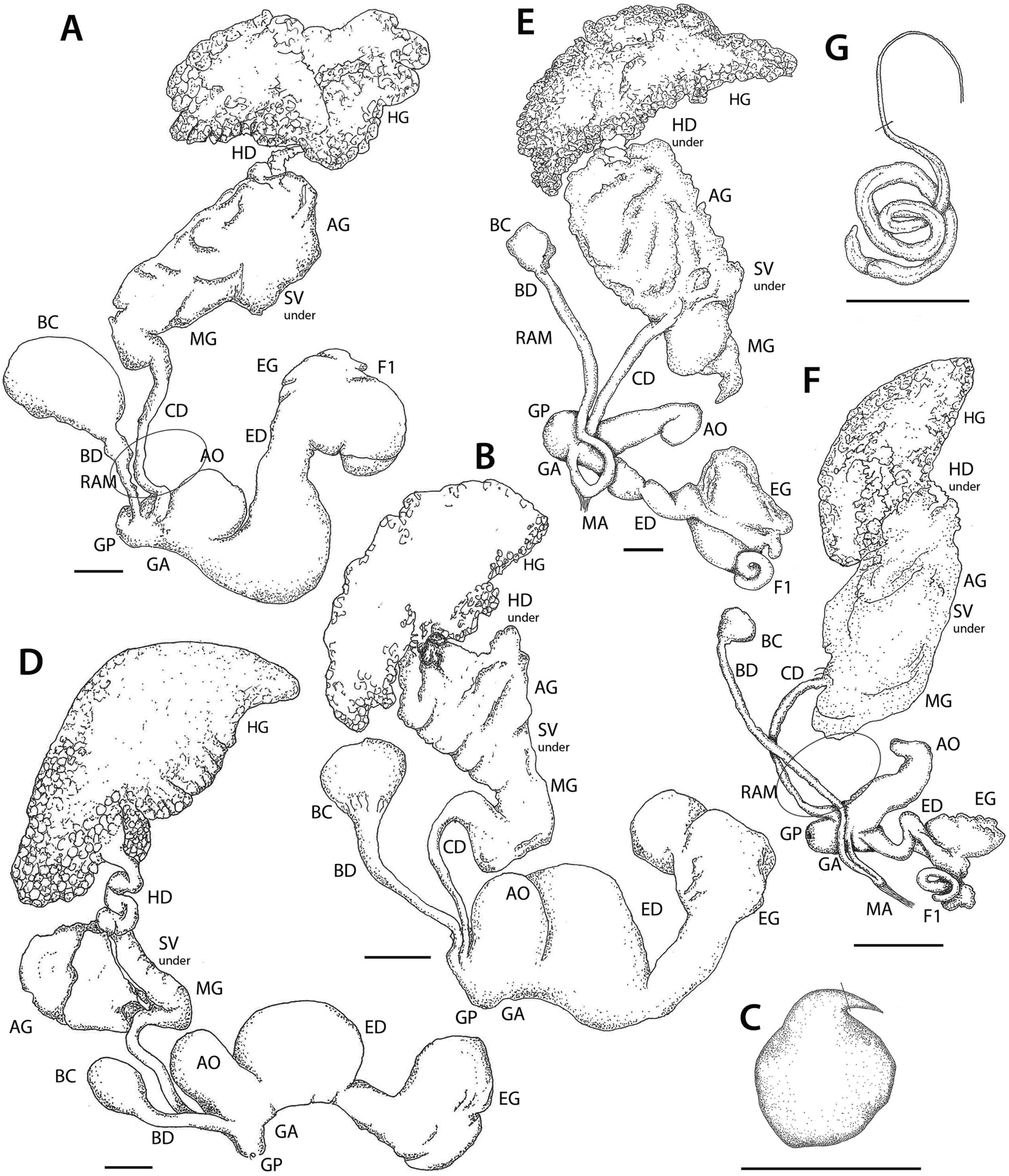

FIGURE 34. Reproductive morphology of *S. funiculata* and *S. kurracheensis*. **A–D.** *S. funiculata*. **A.** Tas, d'Entrecasteaux Channel, TS, AM C.585268 [M135, SK049]. **B–C.** NSW, Kiama, **B.** AM C.585280 [SK048]. **C.** AM C.584884 [SK384]. **D.** NSW, Sydney Harbour, TS of *S. obvirgulata* AM C.585035 [M162, SK035]. **E–G.** *S. kurracheensis*, Pakistan, Karachi, TS. **E.** WAM S74134 [SK148]. **F.** AM C.585857 [M230, SK192]. **G.** WAM S72336 [SK516]. Scale bars = 1 mm.

Comparative remarks. In our mitochondrial phylogeny (Figs 1–4), *S. kurracheensis* (atra group, unit 28) forms a clade with *S. alternata* from the Caribbean and Gulf of Mexico as well as *S. striata* **sp. nov.** from Madagascar (Figs 1, 2). These species differ from *S. kurracheensis* by COI distances of ≥ 7.1% (*S. alternata*, unit 29) and ≥ 8.6% (*S. striata* **sp. nov.**, unit 74) (Table S5). For a comparison with *S. striata* **sp. nov.** refer to comparative remarks under that species. *Siphonaria kurracheensis* occurs in sympatry with four congeners in Karachi, Pakistan. *Siphonaria asghar* has weaker, finer edge scalloping, less prominent siphonal groove, darker interior, a smaller AO, a shorter, wider DB, and a larger BC. *Siphonaria belcheri* has a darker exterior and interior, a larger, wider AO, a longer, narrower BD, and a larger F1. *Siphonaria perexigua* **sp. nov.** has a smaller, taller shell with less raised ribbing, a smaller AO, larger BC, and longer, wider ED. For comparison with *Siphonaria crenata* refer to comparative remarks under that species. Shell sculpture and geometry of *S. kurracheensis* resembles that of *S. zelandica* (flat, fine ribs); however, this resemblance is convergent since both species are not closely related with each other. Both species have non-overlapping distributions.

A record of '*S. kurracheensis*' from SA in Adcock (1893: 11, in synonymy of *S. luzonica*) is based on a misidentification of *S. zelandica*. A record of '*S. kurracheensis*' from the Suez Canal in Moazzo (1939: 280, fig. 2) is a misidentification of *S. belcheri* (also noticed by Hubendick 1946: 54), the shell closely resembles the weakly ribbed paralectotype of *S. belcheri*. SPM and RS of '*S. kurracheensis*' and '*S. kurracheensis* var. *siquiorensis*' depicted in Hubendick (1945: figs 51–52) are here attributed to *S. japonica* and probably *S. javanica*, respectively. Hubendick (1946: 54) treated five taxa as varieties of *S. kurracheensis* (i.e., *S. savignyi*, *S. luzonica*, *S. zebra*, *S. belcheri, S. depressa* and *S. siquijorensis*). None of these treatments are accepted herein and these taxa are all removed from the concept of *S. kurracheensis* as delineated herein. Hence, the distribution of *S. kurracheensis* outlined in Hubendick (1946: 54), which includes locations well beyond Karachi and Persian Gulf (i.e., Java Sea, Philippines, Qld, and Port Jackson), is also disputed.

The SPM depicted herein differs from that of '*S. kurracheensis*' figured in Hubendick (1945: 31, fig. 51) and reproduced by Berry (1977: fig. 19) by being longer and without barbs on flagellum. A specimen figured as *S. kurracheensis* from the Suez Canal (Barash & Danin 1972: fig. 14) is *S. savignyi*. Dayrat *et al.* (2014: 261, fig. 5 E) misidentified unit **28** as *S. savignyi*; it is in fact *S. kurracheensis* based on the clustering with sequences of that species. Similarly, they misidentified unit **27** as *S. kurracheensis*, but the correct identification is *S. belcheri*. Specimens figured as '*S. kurracheensis*' from Mubarak Village, Karachi (Bosch *et al.* 1995: fig. 863; Ali *et al.* 2011: fig. 1B) and from Dwarka Coast, Gujarat (Vakani & Rahul Kundu 2021: figs 2d, 3d) are misidentifications and are likely specimens of *S. crenata* based on size, ribbing and extension of siphonal ridge.

Distribution and habitat. Recorded from Muscat, Gulf of Oman, Karachi, Pakistan and Gujarat, India (Fig. 25). In the present study found in sheltered positions on exposed rocky intertidal marine shores, upper to mid littoral level.

Siphonaria bifurcata Reeve, 1856

(Figs 35A–F, O–P, S, 36A–C)

Siphonaria bifurcata Reeve, 1856: pl. 5, species 21 [not species 22]. Type locality: 'Port Jackson, Australia' [in error for Philippines, see remarks].—Trew 1983: 3; Jenkins 1983: 5, 28; White & Dayrat 2012: 61.

Siphonaria bifasciata Galindo 1977: 416 (invalid; misspelling of *S. bifurcata*).

Material examined. *Type material.* Lectotype of *Siphonaria bifurcata* Reeve, 1856, present designation, from 'Philippine Islands' (NHMUK 1979169/1, Fig. 35A). Three paralectotypes, same data as lectotype (NHMUK 1979169/2-4, Figs 35B–D).

Other, non-type material. **Philippines:** NW Polillo Is, E Quezon, Bolunga District, nr Panukalan, 14°59'N, 121°49'E (WAM S74096 p [SK073], WAM S74098 p [SK410, protoconch H8], WAM S113801 p [SK411], WAM S74097 p [SK412]); Cebu, Mactan Point, 10°20.014'N, 124°02.723'E, PHS04-2 (AM C.585118 p [M414, SK097]).

Taxonomic remarks. The largest syntype (Fig. 35A) is herein designated as the lectotype of *S. bifurcata* for the stabilisation of the name (Art. 74.1 of the Code). This specimen corresponds well with the specimen erroneously figured by Reeve (1856, pl. 3, fig. 21) as '*S. zebra*'. Inspection of the types of *S. zebra* reveal that this is a nominal species from eastern Australia, which is here synonymized with *S. zelandica*. Correspondingly, the types of *S. bifurcata* are not of an Australian species but are conspecific with freshly collected specimens from the Philippines. Therefore, we conclude that the original descriptions of these two species have accidentally been mixed up: The text of the description for species 21 (labelled as '*S. zebra*') applies to the shell depicted in figure 22 and is based on the type material originally labelled as '*S. bifurcata*' from the Philippines. In turn, the description of species 22 (labelled as '*S. bifurcata*') applies to figure 21, which corresponds well with the type material of *S. zebra* from eastern Australia (= *S. zelandica*; Jenkins, 1983: 28; White & Dayrat, 2012: 61). Hence, the description of '*S. zebra*' (including the type locality but excluding the figure) is herein attributed to *S. bifurcata* based on the types. Correspondingly, the description of '*S. bifurcata*' (including type locality but excluding the figure) is herein attributed to *S. zebra* also based on the types.

The concept of *S. bifurcata* in Hubendick (1946: 46) is confused. He appears not to have examined the types and must have been misled by the above-mentioned mix-up of descriptions in Reeve (1856). Hubendick (1946) mentioned 'specimens examined' from Port Jackson [Sydney], which is outside the known distribution of *S. bifurcata*. The shells figured by Hubendick (1946: pl. 2, figs 9–13) and the description of Hubendick (1946: 14, fig. 13) are herein attributed to *S. denticulata* and *S. zelandica*, respectively. Our delineation of *S. bifurcata* is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Figs 35E, F) and geographic series of additional specimens (Table S1).

External morphology (Fig. 35O). External parts evenly pale cream without black pigmentation apart from faint shading at centre of cephalic folds; mantle lobed, translucent; single small black epithelial eye spots centralised on two centrally touching cephalic folds; pneumostomal lobe under the mantle, unpigmented, between the right anterior and right posterior ADMs.

Shell (Figs 35A–F, S; Table S9). Medium sized (max sl mean = 15.8 mm, SD = 4.4 mm, n = 2), elongate ovate; height low to medium; apex offset posterior and left, apical sides convex, protoconch direction weakly heterostrophic (n = 1; Fig. 35S) shell whorl dextral; growth striae indistinct, irregular growth may create rib irregularities and offsets; shell thick, externally white; rib count (mean = 43, SD = 5, n = 2), ~11 primary ribs white, fairly straight but may be bent, raised, rounded ridge, most prominent with paired ribs forming siphonal ridge and prominent protrusion at right quarter; primary ribs broaden to and protrude beyond shell lip to strongly unevenly scallop and corrugate the edge; finer secondary ribs fill gaps between primary ribs, rib interstices narrow. Interior outer shell margin white with pale brown markings aligning under rib interstices, interior pink in one specimen (Fig. 35E); siphonal groove distinct, appears notched/raised, same colour as shell edge, points to right anterior; spatula mottled brown underlying white; ADM scar distinct, CMS straight, golden/brown; thickening of shell lip apparent, infills and reduces lip scalloping, spatula becomes whitened.

Reproductive system (Fig. 36A, C; n = 3). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned over and looped/folded in front of BM and to side of RAM; AO large, elongated, bluntly pointed (embeds into MG), centrally bent, often with MA, joins to top of indistinct GA; ED relatively short, broad, slightly twisted; EG small, folded; at join of ED and EG a single long, narrow, twisted flagellum F1 joins as an extension of ED; AO, GA and ED all muscular white tissue; BD and CD junctions into GA (bulbous at CD) opposing between ED, AO and GP; BD longer than CD with a prominent distal loop, top of loop attached via a long MA to inner foot wall in front of BM, both ducts smooth, similar thickness, pass together through RAM (BD above CD), CD connects to midsized bulbous translucent test BC, CD connecting into folds of MG; HD brownish small coiled, links AG to elongated narrow brownish coarsely granulated HG; MG and AG similar sized, folded soft white tissue, dark SV embedded within AG/MG, AG and HG sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 36B). Thread-like, test thin, translucent (length = 6.78 mm, n = 1, AL = 15 mm); head cylindrical, broad, tip bluntly rounded, tapers into long flagellum; flagellum attached to inside of BC; both sections smooth, featureless; head longer and thicker than flagellum (head length = 4.79 mm, ~ 71% of total length, head width = 103 µm, flagellum width = 17 µm, n = 1); SPM tightly coiled in light brown gelatinous mass in one BC (WAM S74097).

Comparative remarks. *Siphonaria bifurcata* (*atra* group, unit 45) forms a well-differentiated subclade within the mitochondrial tree and is the sister clade of a subclade containing *S. umbra* **sp. nov.** and *S. radians* (Figs 1, 2). *Siphonaria bifurcata* is well-differentiated from any other species by COI distances of ≥ 29% (Table S4). This species has been found in Cebu, Philippines in sympatry with four congeners. For comparison with *S. sipho* refer to comparative remarks under that species. *Siphonaria alba* has a lower shell with a more scalloped edge, a narrower AO, larger BC, smaller GA, and a shorter F1. *Siphonaria sirius* (unit 31), has a more central shell apex and scalloped edge, darker external and internal colour, and a paler spatula. *Siphonaria caubianensis* **sp. nov.** has a slightly taller shell with wider primary ribs, a more strongly scalloped edge, darker external and internal colour, paler spatula, a narrower AO, strongly twisted ED, and bursal loop. The RS of *S. bifurcata* resembles that of several other species, such as *S. denticulata*, *S. javanica*, *S. poindimiensis* **sp. nov.**, *S. viridis*, and *S. tanguissonensis* **sp. nov.** According to the phylogenetic tree (Fig. 1), none of these species is closely related to *S. bifurcata*. The shell of *S. bifurcata* resembles that of other species in the *laciniosa* and *atra* groups, such as *S. sipho*, *S. alba*, and *S. atra* in that it exhibits variations of a thickened white shell lip. Several authors have been misled by the mix-up of text labels and figures in Reeve's (1856) description and confused this species with *S. zebra*. Consequently, *S. bifurcata* was repeatedly listed as a junior synonym of *S. zelandica*, which it is not. Figures of '*S. bifurcata*' from 'Port Jackson' [Sydney] in Hubendick (1946: pl. 2, figs 9–13) are herein attributed to *S. zelandica*. The RS figure of '*Ductosiphonaria bifurcata*' in McAlpine (1952: 42) is also of *S. zelandica*. The SPM of '*S. bifurcata*' from 'Port Jackson' depicted in Hubendick (1946: fig. 19) and reproduced in Berry (1977: fig. 19) closely matches that of *S. denticulate* but not of *S. zelandica*.

Distribution and habitat. Philippines, recorded from Mactan (Cebu), Quezon, and Siquijor islands (Fig. 37). In the present study found in sheltered places on moderately exposed rocky shores, lower littoral level.

Siphonaria fuliginata Reeve, 1856

(Figs 35G–I, Q, 36D–E)

Siphonaria fuliginata Reeve 1856: pl. 7, species 34 (without type locality).—Paetel 1883: 178; 1889: 428; Hanley 1858b: 152; Hubendick 1946: 67; Galindo 1977: 416; Trew 1983: 7; White & Dayrat 2012: 63 (as '*nomen dubium*').

Material examined. *Type material.* Holotype of *Siphonaria fuliginata* Reeve, 1856 (NHMUK MC.1981002, Fig. 35G).

Other, non-type material. **Rodrigues:** Rivière Banane, N coast, 19°11.25'S, 63°22.866'E RG01-1 (AM C.585896 6p, C.585190 p [M428, SK331], C.585191 p [M429, SK332], C.585194 p [SK369]; Anse Quiter, SW coast, 19°46.183'S, 63°22.866'E, RG02-1 (AM C.585874 p [M430, SK134]).

Taxonomic remarks. No type locality has been given in the original description of Reeve (1856). For its unknown origins, this taxon has subsequently been

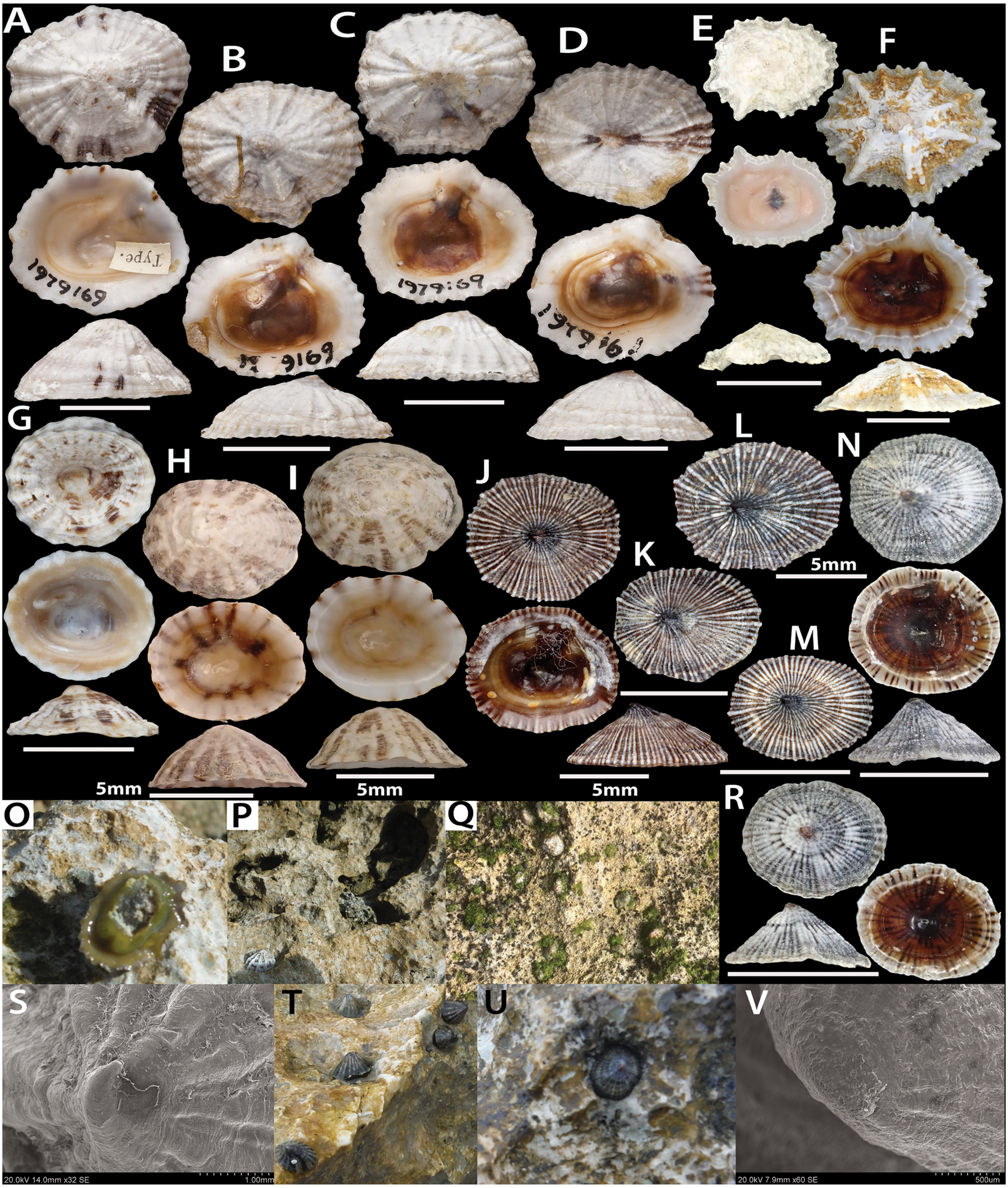

FIGURE 35. Shells of *S. bifurcata*, *S. fuliginata* and *S. lirata*. **A–F, O–P, S.** *S. bifurcata*. **A.** Lectotype NHMUK 1979169/1. **B–D.** Paralectotypes NHMUK 1979169/2-4. **E.** Philippines, Cebu, TS, AM C.585118 [M414, SK097]. **F.** Philippines, Polillo Is, TS, WAM S74096 [SK073]. **O.** Animal & **P.** Cebu, *in situ*. **S.** Protoconch, WAM S74098 [SK410]. **G–I, Q.** *S. fuliginata*. **G.** Holotype NHMUK 1981002. **H.** Rodrigues, AM C.585194 [SK369]. **I.** Rodrigues, AM C.585874 [M430, SK134]. **Q.** Rodrigues, *in situ*. **J–N, R, T–V.** *S. lirata*. **J.** Lectotype NHMUK 1979028/1. **K–M.** Paralectotypes NHMUK 1979028/2-4. **N, R.** Guam, Apra. **N.** AM C.585832 [M448, SK242]. **R.** AM C.585192 [SK252]. **T–U.** Guam, *in situ*. **V.** Protoconch, AM C.585833 [M449]. Unlabelled scale bars = 10 mm.

considered as a *nomen dubium* by White & Dayrat (2012). However, examining freshly collected from Rodrigues revealed a shell form that closely resembled the features of the holotype. We therefore infer that these samples and the type of *S. fuliginata* are conspecific. Here, we provide a detailed redescription of *S. fuliginata* based on samples from Rodrigues to remove the uncertainty about the identity of this species.

External morphology. Foot wall, mantle, cephalic folds and pneumostomal lobe all evenly pale cream in colour; dark pigmentation markings absent, foot sole darker cream, foot edge paler; Mantle translucent, narrower than foot wall, lobed with a thickened edge, pneumostome wide between right ADMs and within mantle.

Shell (Figs 35G–I; Table S9). Small sized (max sl mean = 9.7 mm, SD = 2.9 mm, n = 3), ovate, height medium to low, apex weakly offset central and left, apical sides convex, protoconch direction undetermined, shell whorl dextral growth lines distinct; rib count (mean = 27, SD = 1.7, n = 3), raised, whitish, straight, rib width increases to shell lip; rib interstices paler, may have irregular red/brown markings; ~ 9 primary ribs, extend from apex to shell edge, similar secondary ribs between primary ribs; paired primary ribs over siphonal ridge; shell lip weakly scalloped, corrugated aligning with rib ends; interior colouration of margin rays match underside of white primary ribs and brown rib interstices, inner margin often brown from inner margin to the golden (often mottled blue) coloured spatula (Fig. 35H); ADM impression and siphonal groove distinct, paler than shell margin colouring, cephalic scar convex; thickening and whitening of shell lip/margin not observed; some shells may be display dark brown exterior and interior (AM C.585191).

Reproductive system (Fig. 36D; n = 3). Positioned within coelom under the respiratory cavity, epiphallic parts positioned between RAM and over back of BM close. ED joins at underside of small GA, AO short, bluntly pointed, smaller than GA, joins through underside of ED; ED thick, elongated, centrally twisted, broader at EG; single broad curled stubby flagellum F1, appears as extension of ED at connection with EG; AO, GA and ED all muscular white tissue; EG broad, relatedly large, soft white folded tissue; BD and CD connect in parallel to GA at top and side of GA respectively; BD without distal loop or MA, slightly longer and thinner than CD, both ducts smooth and pass together between RAM and inner foot wall connecting into thick layered folds of MG (BD over CD), bursal loop in BD immediately in front of BC; BC relatively large, spherical, embedded along with part of BD in AG/MG; SV embedded in AG under BC; HD short, narrow, straight, links large AG to a much smaller yellowish granulated HG, AG and MG folded, inner edge MG lobed, both soft white tissue, with outer sides curved reflecting the close positioning to curvature of inner foot wall at right posterior quarter of coelom, MG flattened against inner foot sole.

Spermatophore (Fig. 36E). Bulbous, test thin, translucent (length = 1.43 mm, n = 1, AL = 6.5 mm); head cylindrical, broad, tip bluntly rounded, containing a white gelatinous core, tapers into short flagellum; both sections smooth, featureless; head longer and thicker than flagellum (head length = 1.03 mm, ~ 89% of total length, head width = 138 μm, flagellum width = 35 μm, n = 1); 2 SPM tightly coiled in cream gelatinous mass in one BC (Fig. 36E).

Comparative remarks. *Siphonaria fuliginata* (*normalis* group, unit 80) is closely related to *S. normalis* (unit 14) and *S. madangensis* (unit 88) (Figs 1, 4). It differs from these two species by COI distances of ≥ 5.9% (*S. normalis*) and ≥ 4.4% (*S. madangensis*), respectively (Table S8). From the next more closely related species, *S. costellata*, it differs by COI distances of ≥ 6.5%. The close phylogenetic relationships with *S. normalis*, *S. madangensis*, and *S. costellata* are reflected in shared similarities in shell characters (thickened white shell lip variations) and the RS (broad epiphallic parts). However, *S. normalis* has a darker, more finely ribbed shell, a longer, narrower BD, larger BC, and a longer SPM. *Siphonaria madangensis* **sp. nov.** has a darker shell with a more central apex and prominent siphonal ridge, a smaller to indistinct AO, BD without a bursal loop, and a more bulbous SPM. *Siphonaria costellata* **sp. nov.** has a larger, taller, more brownish (less grey) shell, with a more central apex, a smaller AO, and wider BD without a bursal loop. *Siphonaria fuliginata* has been found in sympatry with *Siphonaria rodriguensis* **sp. nov.** on Rodrigues Is, which has a smaller, taller, darker shell with pale parallel-marked primary ribs, a longer wider BD, larger BC and AG, and longer, narrower SPM.

Distribution and habitat. Known only from Rodrigues, Indian Ocean (Fig. 37). In the present study found in sheltered positions on moderately exposed rocky shores, mid littoral level, amongst barnacles (Fig. 35Q).

Siphonaria lirata Reeve, 1856

(Figs 35J–N, R, T–V, 36F–H)

Siphonaria lirata Reeve 1856: pl. 7, species 35 (type locality unknown). Hanley 1858b: 152; Hedley 1915: 751; Cernohorsky 1972: 210; Galindo 1977: 416; Trew 1983: 8; White & Dayrat 2012: 65; Dayrat *et al.* 2014: 267.

Material examined. *Type material.* Lectotype of *Siphonaria lirata* Reeve, 1856, present designation, without locality (NHMUK MC.1979028/1, Fig. 35J). Three paralectotypes, same data as lectotype (NHMUK MC.1979028/2-4, Figs 35K–M).

Other, non-type material. **Guam:** Pago Bay, below UoG Marine Lab, 13°25.645'N, 144°47.927'E, GM04-1 (AM C.585890 3p, C.584885 p [SK251]); Coast W of Piti Bay, Apra, 13°27.879'N, 144°40.762'E, GM03-1 (AM C.585889 10+p, C.585192 p [SK252], C.585832 p [M448, SK242], C.585833 p [M449, SK162]).

Taxonomic remarks. The largest syntype (Fig. 35J) is herein designated as the lectotype of *S. lirata* for the stabilisation of the name (Art. 74.1 of the Code). Reeve (1856: Erratum) clarified a mistake in labelling pl. 7, fig. 35: The correct name is *S. lirata* and not *S. fuliginata*. No

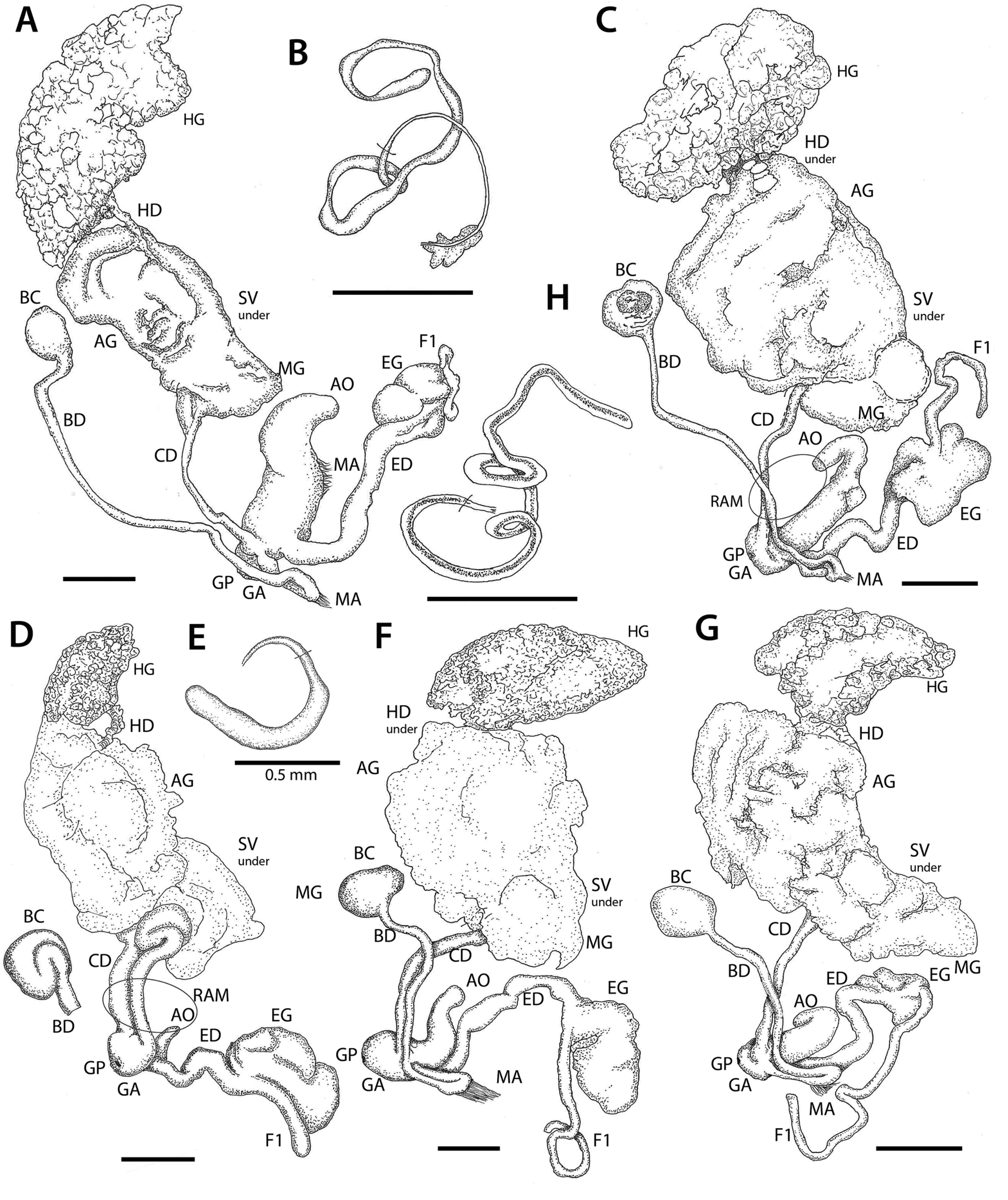

FIGURE 36. Reproductive morphology of *S. bifurcata*, *S. fuliginata* and *S. lirata*. **A**–**C.** *S. bifurcata*. **A.** Philippines, Polillo Is, TS, WAM S74096 [SK073]. **B.** Polillo Is, TS, WAM S74097 [SK412]. **C**. Cebu, TS, AM C.585118 [M414, SK097]. **D**–**E.** *S. fuliginata,* Rodrigues. **D.** AM C.585874 [M430, SK134]. **E.** AM C.585194 [SK369]. **F**–**H.** *S. lirata,* Guam, Apra. **F.** AM C.585832 [M448, SK242]. **G**–**H**. AM C.585833 [M449, SK162]. Scale bars = 1 mm.

type locality has been given in the original description of Reeve (1856). However, examining freshly collected from Guam revealed a shell form that closely resembled the features of the syntypes. Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected specimens from Guam (Fig. 35N) and geographic series of additional specimens (Table S1).

Pilsbry (1920b: 379) and Cernohorsky (1972: 210) incorrectly considered *S. lirata* as a synonym of

S. normalis. Both Hubendick (1946: 23) and Jenkins (1981: 2) incorrectly treated *S. lirata* as a synonym of *S. funiculata*.

External morphology. Exterior evenly grey, paler grey to cream at foot edge and inner foot wall, foot sole darker grey; irregular black blotches of pigmentation on foot wall, pneumostomal lobe and concentrated over front of cephalic folds; mantle translucent, covers shell mantle, wider at anterior, outer edge thickened, weakly lobed with black bands of pigmentation aligning with rib interstices; pneumostomal lobe small, under mantle between the right anterior and right posterior ADMs, closes the pneumostomal and anal openings at the mantle edge; two small black epithelial eye spots centralised on centrally touching cephalic folds; genital pore inconspicuous, located on foot wall to right anterior of right cephalic lobe.

Shell (Figs 35J–N, V; Table S9). Small sized (max sl mean = 9.6 mm, SD = 0.6 mm, n = 3), ovate, height medium; apex offset posterior and to left; apical sides convex, posterior concave to straight; protoconch direction heterostrophic (n = 2; Fig. 35V), area black colouration, shell whorl dextral; growth striae weak; shell thickness thin; colouration uneven with some radial banding; rib count (mean = 66.7, SD = 7.3, n = 3); slightly raised, pale white, fairly straight, faintly protrude beyond shell lip; predominantly primary ribs, finer secondary ribs interspersed, develop between primary ribs with shell growth, rib interstices darker; siphonal ridge formed by paired primary ribs, protrudes past shell edge, otherwise indistinct. Interior evenly dark brown to black from margin to spatula, paler on shell lip aligning under rib ends, siphonal groove clear; ADM scar indistinct, CMS weakly convex; No evidence of growth variations in shell thickness or shell margin colouration was observed.

Reproductive system (Figs 36F,G; n = 2). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned over and looped/folded in front of BM and to side of RAM; AO large, elongated, bluntly pointed (embeds into MG), centrally bent with MA, merges with indistinct GA; ED relatively short, slightly twisted, thick with side appendage; EG relatively large, folded, elongated and pointed; single short narrow bent flagellum F1 on EG; AO, GA and ED all muscular white tissue; BD and CD opposing connections (bulbous at CD) into GA between ED, AO and GP; BD longer and narrower than CD with a prominent distal loop, top of loop attached via a short MA to inner foot wall in front of BM, both ducts smooth and pass together through RAM connecting into folds of MG (BD above CD), BC translucent test, midsized and bulbous; HD brownish long coiled links AG to a small elongated narrow brownish finely granulated HG; MG and AG small folded soft white tissue; dark SV embedded within AG, AG larger than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 36H). Thread-like, test thin, translucent; head cylindrical, very narrow, tip bluntly rounded, containing a white gelatinous core; taper region into the filamentous transparent flagellum is extended; both sections smooth, featureless; head longer and much thicker than flagellum (head length = 5.09 mm, n = 1, head width = 66.6 µm, flagellum width = 13 µm, flagellum incomplete); 1 SPM tightly coiled in a white gelatinous mass in one BC (Fig. 36H).

Comparative remarks. *Siphonaria lirata* (*plicata* group, unit 58) is the sister species of *S. tanguissonensis* **sp. nov.**, also from Guam (Figs 1, 3). Both species differ from each other by COI distances of ≥ 11.6% (Table S7). *Siphonaria lirata* differs from *S. monticulus* by COI distances of ≥ 15% and from other species by ≥ 21% (Table S7). *Siphonaria lirata* has been found in sympatry with three congeners in Guam. For comparison with *S. guamensis* and *S. normalis* refer to comparative remarks under these species. *Siphonaria tanguissonensis* **sp. nov.** has a lower, darker shell with a paler, golden brown/tan interior, a smaller AO, and larger ED. Species with similar shell forms are *S. mauiensis* **sp. nov.**, *S. normalis*), *S. exulum*, and *S. incerta*. Previous records of '*S. lirata*' from southern Australia are based on misidentifications of *S. funiculata*, which has a somewhat similar shell.

Distribution and habitat. Endemic to Guam (Fig. 37). In the present study found on rock platforms and boulder areas on exposed rocky shores, mid to upper littoral levels (Fig. 35T).

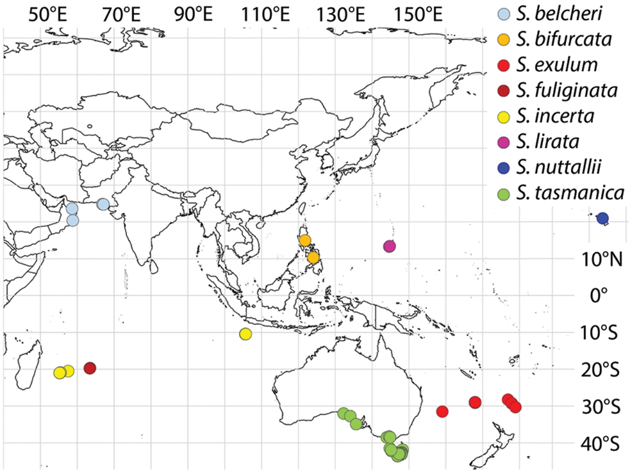

FIGURE 37. Known occurrence records of *S. bifurcata*, *S. fuliginata*, *S. lirata*, *S. exulum*, *S. belcheri*, *S. nuttallii*, *S. incerta* and *S. tasmanica*

***Siphonaria carbo* Hanley, 1858**
(Figs 38A–E, 39A–B)

Siphonaria carbo Hanley 1858a: 24 (type locality unknown).—Hanley 1858b: 151; Paetel 1889: 428; Kilburn & Rippey 1982: 134; Chambers & McQuaid 1994a: 264; Bosch *et al.* 1995: fig. 860; Coan & Kabat 2012: 336; White & Dayrat 2012: 61.

Siphonaria nigerrima Smith 1903: 356, pl. 15, figs 4, 5 (type locality: Umhlali, Natal (Burnup) [South Africa]).—Hubendick 1947: 162, fig. 2; Trew 1983: 3; Chambers & McQuaid 1994a: 265, fig. 1M; Teske *et al.* 2007: 223, 225, fig. 2; 2011: 5026; White & Dayrat 2012: 66.

Siphonaria tenuicostulata Smith 1903: 356, pl. 15, figs 14, 15 (type locality: Umhlali, Natal (Burnup) [South Africa]).—Hubendick 1947: 161, fig. 1; Kilburn & Rippey 1982: 134; Allanson 1958: 166; Trew 1983: 4; Chambers & McQuaid 1994a: 265, fig. 1N; Teske *et al.* 2007: 223, 225, fig. 2; 2011: 5028, White & Dayrat 2012: 68.

Siphonaria anneae Tomlin 1944: 92–93 (type locality Umpangazilali [South Africa]).—Allanson 1963: 70; Chambers & McQuaid 1994a: 265, fig. 1H, I, 3C; Teske *et al.* 2007: 223, 225, fig. 2; 2011: 5028, White & Dayrat 2012: 61.

Siphonaria (*Patellopsis*) *nigerrima*—Hubendick 1945: 70; Chambers & McQuaid 1994b: 418; Chambers *et al.* 1996: 3; 1998: 51.

Siphonaria (*Patellopsis*) *tenuicostulata*—Hubendick 1945: 70; 1946: 35, pl. 6, figs 18–19; Chambers & McQuaid 1994b: 418; Chambers *et al.* 1996: 3; 1998: 51.

Siphonaria (*Patellopsis*) *carbo*—Hubendick 1946: 35, pl. 6, figs 16–17; Allanson 1958: 150, 167, 170, fig. 14.

Siphonaria (*Patellopsis*) *dayi* Allanson 1958: 169, pl. 1b, 2b, figs 5, 16 (type locality: Inhaca Island, Delagoa Bay [South Africa]).—Chambers & McQuaid 1994a: 265, fig. 1L; 1994b: 418; Chambers *et al.* 1996: 3; 1998: 51.

Siphonaria (*Patellopsis*) *anneae*—Allanson 1958: 150, 166, pl. 1b, 2b, fig. 3, 13; Chambers & McQuaid 1994b: 418; Chambers *et al.* 1996: 3; 1998: 51.

Siphonaria dayi—Teske *et al.* 2007: 223, 225, fig. 2; 2011: 5028, White & Dayrat 2012: 62.

Material examined. *Type material.* Holotype of *Siphonaria carbo* Hanley, 1858; coll. Cuming (NHMUK 1981009, Fig. 38A).

Lectotype of *Siphonaria nigerrima* Smith, 1903, present designation, from Umhlali, KwaZulu-Natal, South Africa; donated J H. Ponsonby (NHMUK 1903.9.9.15, Fig. 38B). Two paralectotypes, same data as lectotype (NHMUK 1903.9.9.16–17).

Eight syntypes of *Siphonaria tenuicostulata* Smith, 1903 from Umhlali, KwaZulu-Natal, South Africa; donated J H. Ponsonby (NHMUK 1903.9.9.7 (Fig. 38C, largest syntype)–14).

Other, non-type material. **Mozambique:** Inhaca, Ponta do Farol, 25°58.2'S, 32°59.4'E MM6 (MNHN IM-2019-1489 29p, MNHN IM-2019-16164 p [M586], MNHN IM-2019-16165 p [M587]).

Taxonomic remarks. Hubendick (1946: 35) treated *S. nigerrima* as a synonym of *S. carbo* Hanley, 1858. Which was confirmed later in the taxonomic revision of Teske *et al*. (2007) based on comparative morphology and mitochondrial phylogenetics. They added the species *S. anneae* and *S. tenuicostulata* to the synonymy of this species, which is also accepted herein. The largest syntype of *S. nigerrima* is herein designated as the lectotype (Fig. 38B) for the stabilisation of the name (Art. 74.1 of the Code). This type specimens matches the typical characteristics of *S. carbo* (Fig. 38A) in size, shape, height, colour (Fig. 38B). Our analysis of topotypical specimens of *S. nigerrima* confirms its status as a synonym of *S. carbo*. Previously, Chambers & McQuaid (1994a: 264) incorrectly stated that *S. carbo* was described from the Caribbean and 'does not occur on South African shores'. This observation is not accepted herein. Based on examinations of topotypic samples matching the morphological characteristics of *S. dayi* (Fig. 38D, E), this taxon is also placed in the synonymy of *S. carbo*.

External morphology (preserved). Foot sole grey, paler to foot edge; mantle translucent, pigmentation absent on foot wall, mantle edge, pneumostome; faint pigmentation over centre of cephalic folds.

Shell (Figs 38A–E; Table S9). Small to medium sized (max sl mean = 12.5 mm, SD = 6.0 mm, n = 5), circular ovate, height tall; apex offset central, apical sides convex, protoconch direction weakly homostrophic to central (n = 1), shell whorl dextral; exterior dark metallic brown/grey, often pale brown; primary ribs with 0–2 finer in between secondary ribs, interstices similar colour, growth striae prominent; radial colour bands distinct, darker at apex and shell margin; rib count (mean = 48, SD = 7.8, n = 5), majority primary ribs, ridges weakly raised, rounded; siphonal ridge indistinct, formed by paired primary ribs, primary ribs broaden weakly, project weakly beyond shell lip (especially siphonal ridge) to scallop and corrugate shell edge. Interior of shell evenly dark brown to grey (Fig. 38A–B), may also display off-white rays on shell margin align under primary/secondary ribs, extending to spatula (Fig 38C); siphonal groove distinct, shallow, often paler than margin; ADM scar clear, similar to margin and spatula; CMS convex; whitening and thickening of shell lip not observed.

Reproductive system (Fig. 39A; n = 1). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts between RAM and extending over BM; GA large, AO indistinct and appears part of GA, singular prominent GP, ED short, centrally bent; ED enters at upper end of GA, AO, GA and ED all muscular white tissue; EG very large, elongated, folded, soft white tissue; single thick elongated blunt flagellum F1 appears as extension of ED at EG join; BD and CD connect closely together into GA close to ED junction, both ducts smooth, featureless, wide, slightly bent, pass together between inner foot wall and outer side of RAM (BD over CD) connecting into MG/AG; BC large, bulbous, white opaque test, embedded along with part of BD in soft white folds of MG; HD short, wide, unpigmented, heavily lobed, links soft white folded AG to smaller yellowish granular HG; SV embedded in AG close to BC.

Spermatophore (Fig. 39B). Broad head with short flagellum (length = 1.29 mm, n = 1); head section bulbous but flattened, test thin, smooth, featureless; tapering section merges head to flagellum; head longer, wider than flagellum (head length = 0.77 mm, n = 1; flagellum length; 0.53 mm, ~ 59% of SMP length; head width = 362 µm, flagellum width = 149 µm); 2 SPMs held in cream gelatinous mass in BC of one specimen [M587].

Radula. Dentition formula 36:1:36 (Hubendick 1947: 162 as '*S. nigerrima*'), 36:1:36 (Hubendick 1946: 35 as '*S. carbo*') and 40:1:40 (Hubendick 1946: 35, 1947: 162 as '*S. tenuicostulata*')._

Comparative remarks. Collectively, the works of Allanson (1958), Chambers & McQuaid, (1994a: 264) and Teske *et al.* (2007, 2011: 5025) clarified the taxonomy of South African *Siphonaria* species, which is followed herein except that *S. dayi* is treated as a junior synonym of *S. carbo*. Our study does not include analyses of the South African species *S. concinna*, *S. oculus* and *S. serrata*; refer to Teske *et al.* (2007, 2011) for comparisons. We found that *S. carbo* (*pectinata* group, unit 94) is the sister species of *S. itampoloensis* **sp. nov.** in our phylogenetic tree (Figs 1, 4). Both species together form the sister lineage of *S. asghar*. *Siphonaria carbo* differs from *S. itampoloensis* by COI distances of ≥ 5.1% and from *S. asghar* by distances of ≥ 11.1% (Table S8). *Siphonaria carbo* differs from *S. itampoloensis* by having a darker, lower shell with finer ribbing, a wider BD, larger EG, and a larger, elongate BC. *Siphonaria carbo* has been found in sympatry with two congeners in Mozambique. For comparisons with *S. capensis* and *S. plana* refer to comparative remarks under these species. The shape of the SPM of *S. carbo* closely resembles that of other species, such as *S. funiculata*, *S. zelandica*, *S. acmaeoides*, *S. lateralis*, and *S. tasmanica*. However, *Siphonaria carbo* has a smaller ED/EG and broader CD/BD's than these species. The RS of '*S. tenuicostulata'* (= *S. carbo*) figured in Hubendick (1945: 21, fig. 22) corresponds well with the typical anatomy of this species except for details of the CD/BD/GP/GA junction, which Hubendick (1946: fig. 20) showed to be wider and with the ducts more separated. Hubendick (1947: 161) considered the RS of '*S. tenuicostulata*' (fig. 1) and '*S. nigerrima*' (fig. 2, epiphallic parts absent), from Umhlali Natal, to be a 'closely related' species 'only showing differences in small details'. Hubendick (1947) figured a RS matching that of *S. carbo* shown here (Fig. 39A) more closely than any other species. Allanson (1958: 167) stated that the distal genitalia of *S. anneae* were 'Exactly similar to *S. teniucostulata*' referring to '*S. tenuicostulata*' from Oman figured in Bosch (1982: 141; 1991: 75). However, these figures are incorrectly assigned to *S. tenuicostulata* (= *S. carbo*) because this location is well outside the known distribution of this species.

Distribution and habitat. Recorded from tropical and subtropical coasts of southeastern Africa (Fig. 25). Found on exposed rocky shores across mid to upper littoral levels.

Siphonaria exulum Hanley, 1858
(Figs 38F–T, 39E–H)

Siphonaria exulum Hanley 1858a: 25 (type locality: Norfolk Island).—Paetel 1889: 428; Coan & Kabat 2012: 336; White & Dayrat 2012: 63.

Siphonaria exulorum Hanley 1858b: 152 (invalid; unjustified emendation of *S. exulum*).—Paetel 1889: 428; Suter 1909b: 258; Oliver 1915: 547; Trew 1983: 5; White & Dayrat 2012: 63.

Siphonaria corrugata—Brazier 1888: 1001 (not *S. corrugata* Reeve, 1856).

Siphonaria lirata—Brazier 1888: 1001 (not *S. lirata* Reeve, 1856).

Ellsiphon (?) *exulorum*—Iredale 1940: 438.

Siphonaria diemenensis—Iredale 1910: 71 (not *S. diemenensis* Quoy & Gaimard, 1833).

Siphonaria atra—Iredale 1910: 71 (not *S. atra* Quoy & Gaimard, 1833).

Siphonaria raoulensis Oliver 1915: 545, pl. 12, fig. 40, 40a (type locality: Sunday Island [Raoul Island], Kermadec Islands, NZ).—Brook 1998: 232; Wood & Gardner 2007: 160; White & Dayrat 2012: 67; Duffy & Ahyong 2015: 67.

Siphonaria cheesemani Oliver 1915: 545, pl. 12, fig. 41, 41a (type locality: Sunday Island [Raoul Island], Kermadec Islands).—Jenkins 1983: 29; Brook 1998: 232; Wood & Gardner 2007: 161; White & Dayrat 2012: 61.

Siphonaria macauleyensis Oliver 1915: 545, pl. 12, fig. 42, 42a (type locality: Macauley Island, Kermadec Islands).—Brook 1998: 232; Wood & Gardner 2007: 161; White & Dayrat 2012: 65.

Siphonaria macauleyensis perplexa Oliver 1915: 545, pl. 12, fig. 43, 43a (type locality: Fleetwood Bluff, Sunday Island [Raoul Island], Kermadec Islands).—Brook 1998: 232; Wood & Gardner 2007: 161; White & Dayrat 2012: 61.

Siphonaria amphibia Oliver 1915: 545, pl. 12, fig. 44 (type locality: Sunday Island [Raoul Island], Kermadec Islands).—Brook 1998: 232; Wood & Gardner 2007: 161; White & Dayrat 2012: 61.

Parellsiphon innocuus Iredale 1940: 439, fig. 9, 10 (type locality: Norfolk Island).—Hubendick 1946: 49; Jenkins 1983: 29; White & Dayrat 2012: 64.

Siphonaria (*Ductosiphonaria*) *diemenensis* var. *exulum*—Hubendick 1946: 38–39.

Siphonaria (*Ductosiphonaria*) *diemenensis* var. *perplexa*—Hubendick 1946: 38–39.

Siphonaria normalis—Paul 1980: 14 (not *S. normalis* Gould, 1846).

Material examined. *Type material.* Holotype of *Siphonaria exulum* Hanley, 1858a from Norfolk Is [Australia] (NHMUK 1900.3.19.27, Fig. 38F).

Holotype of *Siphonaria raoulensis* Oliver, 1915 from Rocks between tide marks, Sunday Island, Kermadec Islands, [NZ] (CM M.3666, Fig. 38I). Four paratypes, Raoul Is; coll. W.R.B. Oliver (AM C.40293).

Holotype of *Siphonaria cheesemani* Oliver, 1915 from Sunday Island, Kermadec Islands, [NZ]; coll. W.R.B. Oliver (CM M.3660, Fig. 38J). Four paratypes, Raoul Is; coll. W.R.B. Oliver (AM C.40294).

Holotype of *Siphonaria macauleyensis* Oliver, 1915 from Macauley Island, Kermadec Islands, [NZ]; coll. W.R.B. Oliver 1908 (CM M.3663, Fig. 38K).

Holotype of *Siphonaria macauleyensis perplexa* Oliver, 1915 from Sunday Island, Kermadec Islands, [NZ]; coll. W.R.B. Oliver, 1908 (CM M.3661, Fig. 38L). Two paratypes, Raoul Is; coll. 1908, W.R.B. Oliver (AM C.40300).

Holotype of *Siphonaria amphibia* Oliver, 1915 from Fleetwood Bluff, Sunday Island, Kermadec Islands, [NZ]; coll. W.R.B. Oliver 1908 (CM M.3665, Fig. 38M). Two probable paratypes, Raoul Is; coll. W.R.B. Oliver (AM C.40299).

Syntype of *Parellsiphon innocuus* Iredale, 1940 from Norfolk Is; coll. 1910 (AM C.103708, Fig. 38N).

Other, non-type material. **NZ, Kermadec Islands:** Raoul Island, Fishing Rock landing, 29°14.55'S,

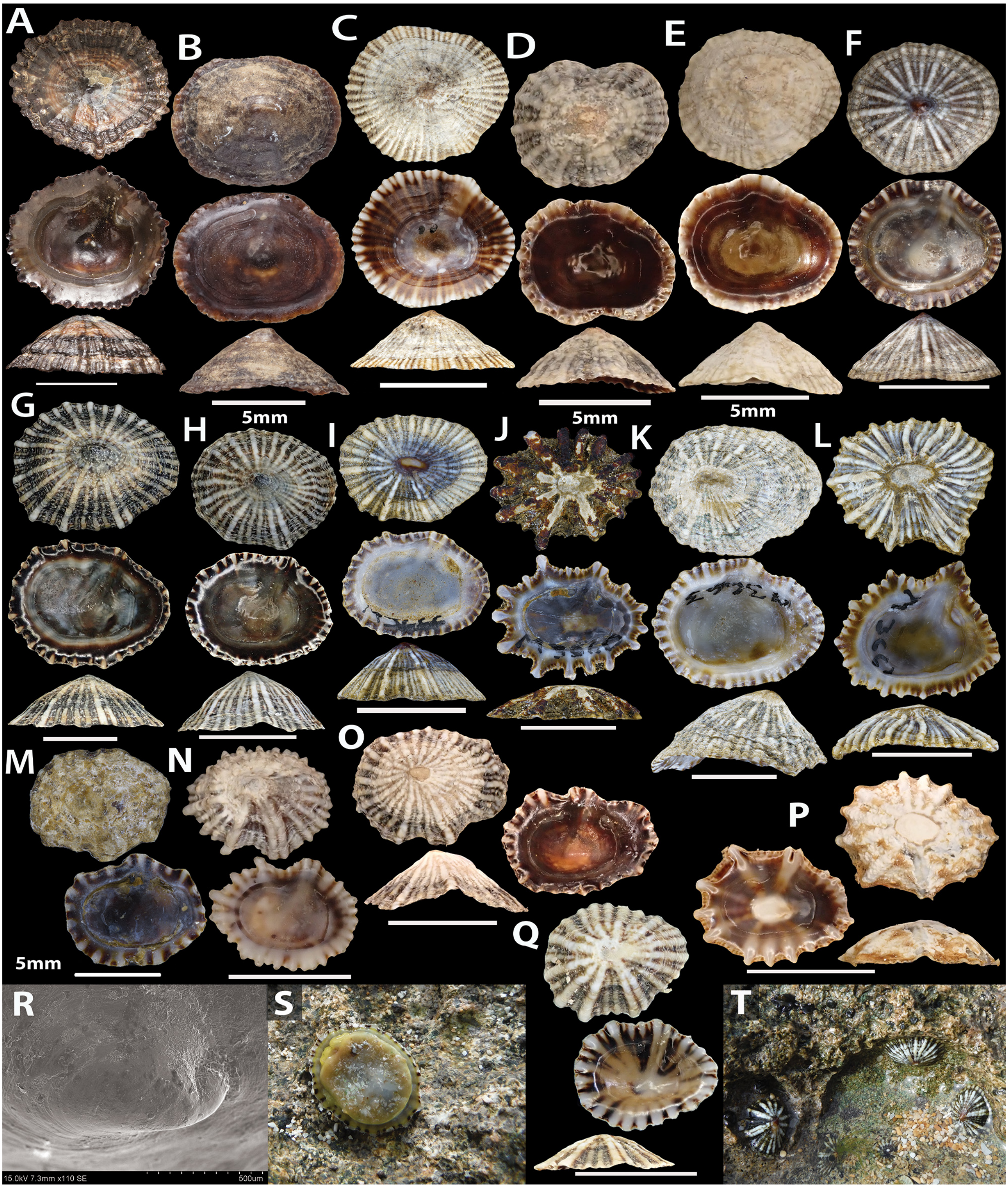

FIGURE 38. Shells of *S. carbo* and *S. exulum*. **A–E.** *S. carbo*. **A.** Holotype NHMUK 1981009. **B.** Lectotype of *S. nigerrima* NHMUK 1903.9.9.15. **C.** Largest syntype of *S. tenuicostulata* NHMUK 1903.9.9.7. **D–E.** Mozambique, Inhaca. **D.** IM 2019-16165 [M587]. **E.** MNHN IM 2019-16164 [M586]. **F–T.** *S. exulum*, **F.** Holotype NHMUK 1900.3.19.27. **G**. NI, TS, AM C.585026 [M220]. **H**. NI, TS, AM C.585025 [SK041]. **I.** Holotype of *S. raoulensis* CM M.3666. **J.** Holotype of *S. cheesemani* CM M.3660. **K.** Holotype of *S. macauleyensis* CM M.3663. **L.** Holotype of *S. macauleyensis perplexa* CM M.3661. **M.** Holotype of *S. amphibia* CM M.3665. **N**. Syntype of *Parellsiphon innocuus* AM C.103708. **O.** Kermadec Is, Raoul Is, TS, AM C.475847 [M513]. **P.** Kermadec Is, South Meyer Is, TS, AM C.475848 [M512]. **Q**. NI, TS of *S. innocuus* AM C.585020 [M217]. **R**. Protoconch, AM C.585029 [SK010]. **S.** NI, animal. **T.** NI, *in situ*. Unlabelled scale bars = 10 mm.

177°54.22'W (AM C.608196 p [SK418 protoconch I5], C.595914 p [SK419 protoconch G12]); Boat Cove, 29°16.783'S, 177°53.65'W K2011-102 (AM C.475847 p [M513], 29°16.666'S, 177°53.717'W K2011-29-1 (AM C.475481 d); south side of Te Konui Pt, 29°18.53'S, 177°53.75'W. (AM C.475477 d, C.475479 d, C.475480 d). South Meyer Island, 29°14.817'S, 177°52.817'W (AM C.475848 p [M512]). **Australia, NI:** Anson Bay, NW side of NI, Stn D3/2 rock pools, 29°00'S, 167°55'E (AM C.595968 p); Anson Bay, 29°00.550'S, 167°55.332'E NFI04-1 (AM C.585378 10p, C.585024 p [M219], C.585025 p [SK041]); Duncombe Bay, N side of NI, 29°00'02.5'S, 67°55'48.8'E (AM C.595965 10+p, C.595946 p [SK005]); Cascade Bay, 29°01.206'S, 167°58.174'E NFI05-1 (AM C.585551 26p, C.585026 p [M220], C.585027 d [R001], C.585028 d [R002], C.585029 p [SK010]); Ball Bay, 29°02'S, 167°59'E (AM C.595964 10+p); Ball Bay 29°02.844'S, 167°59.044'E NFI01-1 (AM C.585526 20+p); Creswell Bay 29°03.478'S, 167°56.547'E NFI03-1 (AM C.585400 10+p, C.585023 p [M221]); Slaughter Bay 29°03.511'S, 167°57.416'E NFI02-1 (AM C.585581 30p, C.585020 p [M217], C.585021 p [M218],C.585022 p [SK009]); Emily Bay, S side NI 29°03'36.0'S 167°57'40.5'E (AM C.595967 p); Point Hunter Reserve, E side of cemetery 29°03'S, 167°58'E (AM C.595966 10+p, C.595944 p [SK042]) ; Point Hunter 29°03.629'S, 167°58.045'E NFI02-2 (AM C.585681 7p, C.595947 p [SK006]); Phillip Island 29°06.9'S, 167°56.88'E (AM C.585944 15p). **LHI:** Signal Point 31°31.501'S, 159°03.578'E LHI2017Apr04-099 (AM C.546717 5p, C.595945 p [SK052]); On marine debris Old Settlement, LHI, 31°31.18'S, 159°03.45'E (AM C.582859 8p, C.585945 p [M467, SK234]).

Taxonomic remarks. The original description of *S. exulum* gives measurements for a single specimen, the holotype. The holotype is the only type specimen known to exist (J. Ablett, pers. comm. NHM). No type has originally been designated in the description of *P. innocuus*. The type specimen in Iredale (1940: 441, pl. 34, figs 9–10) is therefore considered as a syntype (Fig. 38N). No other type specimens are known. Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes of *S. exulum* (Figs 38G), *P. innocuus* (Fig. 38Q), *S. raoulensis* (Fig. 38O), *S. cheesemani* (Fig. 38P), *S. macauleyensis* and *S. macauleyensis perplexa* (Fig. 38O) and geographic series of additional specimens (Table S1). These analyses confirm the synonymy of *P. innocuous*, *S. raoulensis*, *S. amphibia*, *S. cheesemani*, *S. macauleyensis* and *S. macauleyensis perplexa*. *Siphonaria amphibia*, *S. cheesemani, S. macauleyensis* and *S. macauleyensis perplexa* had previously been synonymised with *S. raoulensis* by Wood & Gardiner (2007) based on molecular phylogenetic evidence. However, the relevant sequences are not available on Genbank (accessed 28 April 2021) precluding their use in this review.

Records of '*S. corrugata*' and '*S. lirata*' from Norfolk Island in Brazier (1888, 1001) are misidentifications attributed herein to *S. exulum*. Paetel (1889: 428) listed both *S. exulum* and its emendation *S. exulorum* as accepted species. Suter (1907: 265) misidentified specimens of this species from the Kermadec Islands as *S. diemenensis.* Oliver (1915: 545) described several species from the Kermadec, which he considered to be distinct although 'difficult to separate'. All these species are synonyms of *S. exulum*. Iredale (1940, 438) apparently not being aware of Hanley's description, incorrectly attributed the name *exulorum* to Suter and tentatively placed it in *Ellsiphon*. Hubendick (1946: 36, 38, 63) incorrectly treated *S. cheesemani* as a synonym of '*S. cookiana*' (= *S. propria*); *S. raoulensis*, *S. macauleyensis* and *S. perplexa* as synonyms or varieties of *S. diemenensis*; and *S. amphibia* as a synonym of *S. acmaeoides*. However, he listed no specimens from the Kermadecs under 'specimens examined'. Furthermore, Hubendick (1946: 38) also listed *S. exulum* and *S. exulorum* ('Error for *exulum*') as varieties of *S. diemenensis* Quoy & Gaimard, 1833, which is not accepted herein. Morrison (1972: 56–58) treated '*Parellsiphon innocuous*' (sic *innocuus*) as a synonym of *S. laciniosa* based on similarity in shell form and 'common reproductive development'. This synonymy is not supported by examination of type specimens and morpho-anatomy. Trew (1983: 5) treated *S. exulorum* (= *exulum*) as a synonym of '*Pachysiphonaria diemenensis*'. Grove (2006: 60) also synonymized *S. exulum* with *S. diemenensis*, but the specimen figured by Grove (2017) as '*S. exulum* is actually an individual of *S. diemenensis*. Brook (1998: 232) stated that 'there is only one morphologically variable species of *Siphonaria*, namely *S. raoulensis,* at the northern Kermadec Islands'. The correct name for this species is *S. exulum*, however.

External morphology (Fig. 38S). Foot sole smooth, evenly dark yellow to centrally greyish; foot wall narrow dark yellow with evenly spread white subepithelial pustules becoming more vivid and dense close to the foot sole and around pneumostomal lobe; fringing mantle narrow, yellowish translucent, extends to shell edge, outer edge lobed, strongly banded yellow, reflects the profile shell lip and ribs; pneumostomal lobe paler and within mantle between the right anterior and right posterior ADMs, closes the pneumostomal and anal openings at the mantle edge; two small black epithelial eye spots centralised on two thick centrally touching dark yellow cephalic folds that darken to their outer edge, covered with white mucous cells similar (but smaller) to those of the foot wall tissue; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold.

Shell (Figs 38K–M, R–T; Table S9). Small to medium sized (max sl mean = 14.4 mm, SD = 2.2 mm, n = 24); ovate, thin, height tall to flattened ('*exulum*', '*raoulensis'* and '*macauleyensis*' forms, Figs 38H, K–O) to flat ('*cheesemani*' form, Fig. 38P); dark and pale shell forms variable, exterior uneven; apex fairly central and weakly offset to posterior; apical sides evenly convex; apex weakly hooked, protoconch direction homostrophic (n = 4; Fig. 38R), shell whorl dextral; rib count (mean 39, SD = 7, n = 24) slightly raised to strongly raised, primary ribs grey to white, fairly straight, very prominent in some individuals; few secondary ribs, develop between primary ribs to a similar size at shell margin, rib interstices dark brown to black; paired touching primary ribs over indistinct siphonal ridge; growth striae distinct, 2–3 discontinuous bands of brown radial shading, protoconch area dark brown; shell edge uneven, scalloped by weakly extending ribs; interior mottled brown to evenly dark brown, apart from short cream markings on shell lip aligning with primary ribs; spatula pale brown to blue/white, pale shell form has golden brown spatula. Siphonal groove shallow, ADM scar variably distinct, CMS convex. Translucent thickening of internal shell occurs, infills and reduces scalloping of lip, spatula becomes whitened (prominent in pale shell forms; '*innocuus*'; Fig. 38Q, P).

Reproductive system (Figs 39E, G, H; n = 3). Single GP located in foot wall on right posterior side of right cephalic fold; opens internally into a relatively small GA positioned between right dorsal of BM and RAM; elongated horn-shaped AO present protrudes as an extension of GA, a short wide whitish muscular tissued ED joins side of GA; a singular short thin blunt hooked cream-coloured flagellum F1 protrudes from the join between the ED and lobed blunt whitish EG; the long, narrow thickened whitish CD and thin smooth unlooped BD (BD thinner and dorsal to CD) together pass through the RAM to enter the GA close to GP (BD closest), posterior to entry of AO and ED; at the end of BD is a relatively small spherical brownish BC, test thin, loosely embedded in dorsal of AG, SV elongated, deeply embedded; CD (spermoviduct) joins soft white folds of MG and AG; HD thickened distinctly coiled and striated, connects AG to the yellowish granulated crescent shaped HG. The HG is positioned in right posterior of coelom under pallial cavity, to which the AG is distal and positioned under the digestive gland.

Spermatophore (Fig. 39F). Thread-like (length = 8.66 mm, n = 1), translucent, test thin; head section, bluntly rounded, body cylindrical, containing a white gelatinous mass, tapers along the transparent flagellum to a very thin tip; both sections smooth, featureless; head shorter, thinner than flagellum (head length = 3.37 mm; flagellum length = 5.32 mm; ~ 39% of SPM length; head width = 71 µm; flagellum width = 21 µm). Single SPM coiled embedded in brown gelatinous mass in one BC (LHI, AM C.546717 [SK052]).

Comparative remarks. *Siphonaria exulum* (*atra* group, unit 47) is the sister species of a subclade containing four species, *S. scabra*, *S. pravitas* **sp. nov.**, *S. bourailensis* **sp. nov.**, and *S. ouassensis* **sp. nov.** All five species together form Clade B in the siphonariid tree (Figs 1, 2). *Siphonaria exulum* differs from other species by COI distances of ≥ 18.9% (Table S4). *Siphonaria exulum* has been found in sympatry with *S. lentula* on LHI, which has a shell with more prominent raised ribs, scalloped edge, and siphonal ridge with a flared end, darker interior, BD with distal loop, and SPM with a bulbous head. *Siphonaria pravitas* **sp. nov.** has more prominent and raised ribs on siphonal ridge, greater edge scalloping, darker interior, a shorter wider BD without a distal loop, a larger BC and a shorter SPM. *Siphonaria exulum* is the only known species in the Kermadec Islands. *Siphonaria ouasseensis* has a lower, paler, less evenly ribbed shell, a smaller, narrower AO, a more elongate and narrower CD, and a smaller BC, and *S. bourailensis* has a lower, less evenly and broader ribbed shell, more prominent siphonal ridge, a larger, broader AO, a more elongate and narrower CD, a larger HD, and a shorter SPM.

We found that the RS structures of specimens from NI correspond reasonably well with those of specimens from the Kermadec Islands especially in size and shape of the epiphallic parts, AO and HD (hermaphroditic parts may vary) (Figs 39E, G, H). Conchologically, the most similar species are *S. mauiensis* **sp. nov.** (Hawaii), *S. griffithsorum* **sp. nov.** (Mauritius), and *S. tongatapuensis* **sp. nov.** (Tonga).

Distribution and habitat. Known exclusively from Kermadec Islands, NI and LHI (Fig. 37). In this study, found to be common in sheltered rocky surfaces (e.g., crevices, hollows, pits) on exposed rocky shores, often in vertical positions, upper to mid littoral level; home scars apparent (Fig. 38T). Also found attached to shells of *Scutellastra kermadecensis* (Pilsbry, 1894) on Kermadec Islands (see Oliver, 1915: 547) and marine debris at LHI.

Siphonaria belcheri Hanley, 1858

(Figs 39C–D, 40A–J, R)

Siphonaria belcheri Hanley 1858b: 153 ('probably taken in the Indian seas' [Indian Ocean]).—Paetel 1883: 178; 1889: 428; Hubendick 1947a: 163; Bosch *et al.* 1995: 185, fig. 859; Ali *et al.* 2011: 1086, fig. 1B; Coan & Kabat 2012: 336; White & Dayrat 2012; 61; Vakani *et al.* 2021: 134, fig. 2a.

Siphonaria (*Patellopsis*) *belcheri*—Hubendick 1945: 70; 1946, 34, pl. 2, fig. 5–8; Knox 1955: 88.

Siphonaria kurracheensis—Moazzo 1939: 7, 280, fig. 2; Dayrat *et al.* 2014: 268, 'unit 27', fig. 5 D (not *S. kurracheensis* Reeve, 1856).

Material examined. *Type material.* Lectotype of *Siphonaria belcheri* Hanley, 1858, present designation (NHMUK 1900.3.19.29, Fig. 40A). Six paralectotypes, same data as lectotype (NHMUK 1900.3.19.28, 30–34, Figs 40B–G).

Other, non-type material. **Pakistan:** Karachi, Clifton Beach 24°45.500'N, 67°05.968'E, PA02-1 (AM C.585449 10p, C.585102 p [M227], C.585103 p [M228], C.585106 p [SK147], C.585500 p [SK146], C.595930 p [SK533]); French Beach, 24°50.367'N, 66°49.387'E, PA01-1 (AM C.585382 10p, C.585100 p [M237], C.585101 p [M238]), 24°50.345'N, 66°49.244'E, PA01-2 (AM C.585669 6p).

Taxonomic remarks. The largest syntype is herein designated as the lectotype of *S. belcheri* (Fig. 40A) for the stabilisation of the name (Art. 74.1 of the Code). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes ('Indian Ocean', from Pakistan; Figs 40H, J) and geographic series of additional specimens (Table S1).

External morphology. Foot wall, mantle and pneumostomal lobe evenly grey, foot sole darker grey; edge of foot sole/wall, cephalic folds and foot wall mantle join fade to pale cream; mantle translucent, wider than foot wall, elongated at anterior, edge thickened lobed whitish with black bands aligning to rib interstices; pneumostome within mantle, between right and posterior ADMs.

Shell (Figs 40A–J; Table S9). Small sized (max sl mean = 12.08 mm, SD = 1.38 mm, n = 3), circular ovate; height medium; exterior maybe uneven, apex offset weakly to posterior and left, apical sides weakly concave, protoconch direction heterostrophic (n = 1), curls below apex to posterior, shell whorl dextral; growth striae prominent, shell thickness thick; rib count (mean = 33, SD = 3.3, n = 3), primary ribs pale white, fairly straight, ridge raised, rounded, may broaden significantly to shell lip, rib interstices; shell lip to scalloped and weakly corrugated; finer irregular secondary ribs fill gap between primary ribs, rib interstices brown; paired primary ribs form siphonal ridge. Interior shell margin golden brown with irregular mottled dark brown, shell lip white with brown rays under rib interstices variably extending over margin or to spatula, centre of spatula dark brown often orange; siphonal groove distinct, same colour as shell edge; ADM scar indistinct, CMS straight; thickening of shell lip occurs in more mature specimens, in-fills and reduces lip scalloping.

Reproductive system (Fig. 39C; n = 2). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts positioned between BM and RAM. GA small, with singular GP through foot wall; AO large broad bluntly pointed, joined to upper GA; ED elongated narrow thickened, slightly centrally bent, joins to lower side of GA; GA, AO, ED all white muscular fibrous tissue; EG large, soft whitish tissue, folded, joins ED; single wide flagellum (F1), shorter but similar width to ED, appears as an extension of ED. BD and CD connect in opposing directions into GA between ED join and GP, both ducts narrow long straight smooth whitish, pass together through RAM (BD over thicker CD) into soft white folded tissues of MG, BC embedded in folds close to embedded blackish SV; BD long narrow with prominent distal loop and MA to inner anterior foot wall; CD long, wider than BD; BC relatively small bulbous, thin whitish translucent test (yellowish gelatinous mass in BC); MG/AG complex relatively large; HD short narrow coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; AG/MG larger than HG, sides match curvature of inner foot wall.

Spermatophore (Fig. 39D). Broad head with short flagellum, coiled (length = 0.57 ± 0.09 mm, n = 2); head section cylindrical, bulbous, elongate, rounded tip; test smooth, featureless, translucent encasing a white opaque central core; tapering section merges head to flagellum; head longer, wider than translucent flagellum (head length = 0.51 ± 0.07 mm, ~ 90% of SPM length, head width = 47 ± 9 µm; flagellum width = 6 ± 0 µm, n = 2); 2 SPM coiled in one BC (AM C.595930).

Radula. Dentition formula 12:1:12 (Hubendick 1946: 38).

Comparative remarks. *Siphonaria belcheri* (*atra* group, unit 27) is the sister species of *S. madagascariensis* in our mitochondrial tree (Figs 1, 2). It differs from other species by COI distances of ≥ 20% (Table S%).

We found *S. belcheri* in sympatry with four congeners in Oman and Karachi, Pakistan. *Siphonaria asghar* has a lower shell with uneven ribbing, weaker edge scalloping, a larger BC, and a smaller, indistinct AO. *Siphonaria perexigua* **sp. nov.** has a lower shell with broader, more raised ribs, weaker edge scalloping, a shorter, bulbous, blunt AO, longer, wider ED and BD, and a larger BC. For comparisons with *S. kurracheensis* and *S. crenata* refer to comparative remarks under these species.

The RS structure of *S. atra* and *S. bifurcata* resemble that of *S. belcheri*; however, these species differ in shell morphology and are genetically highly distinct. Figures of '*S. belcheri*' in Hubendick (1946: 90, pl. 2, figs 5–8, from 'Persian Gulf'), are specimens of *S. belcheri*. However, the RS figured and described in Hubendick (1946: 10, fig. 7) differs from that shown herein in details of epiphallic parts, omitting AO, F1, distal loop in BD and opposing connections of BD and CD. Hubendick's RS figure and description matches that of *S. carbo*, which Hubendick (1946: 35) indicated was 'of the same type'. Figured specimen of '*S. kurracheensis*' in Moazzo (1939: 7, 280 fig. 2 closely resembles *S. belcheri* (in particular the weakly ribbed paralectotype; Fig. 39G). Figured specimen of 'unit 27, *S. kurracheensis'* from Masirah Is, Oman in Dayrat *et al.* (2014: 263, fig. 5D) matches the coarser ribbed form of *S. belcheri* rather than the narrower/finer ribbed *S. kurracheensis*.

Distribution and habitat. Coasts of the Arabian Sea, recorded from Masirah Island, Oman, Karachi, Pakistan, and India (Fig. 37). In the present study found in sheltered positions on exposed rocky shores, upper to mid littoral level (Fig. 40R).

Siphonaria nuttallii Hanley, 1858

(Figs 39I–J, 40K–N, S, U–V)

Siphonaria nuttallii Hanley 1858b: 153 (type locality: 'littora insularum sandvicensium' [coast of the Hawaiian Islands]).—Paetel 1875: 92; Coan & Kabat 2012: 336; White & Dayrat 2012: 66; Dayrat *et al.* 2014: 266.

Siphonaria nuttalli—Paetel 1873: 117; 1883: 178; 1889: 429; Pilsbry 1920b: 379; Christiaens 1980a: 79 (incorrect subsequent spelling of *nuttallii*).

Siphonaria normalis forma *chirura* Pilsbry 1920b: 380, fig. 15 (type locality: Hawaii).—Edmondson 1946: 188, fig. 102b.

Siphonaria (*Siphonaria*) *nuttalli*—Hubendick 1945: 73; 1946: 17, 50, 51–52, 63, pl. 4, fig. 1–4 (incorrect subsequent spelling of *nuttallii*).

Siphonaria chirura—Baker 1964: 159; White & Dayrat 2012: 61.

Siphonaria normalis—Kay 1979: 493, figs 157I–J.

Material examined. *Type material.* Lectotype of *Siphonaria nuttallii* Hanley, 1858b, present designation, from Hawaii (NHMUK 20120166/1, Fig. 40K). Four paralectotypes, same data as lectotype (NHMUK 20120166/2-5, Fig. 40N).

Three syntypes of *Siphonaria normalis* forma *chirura*

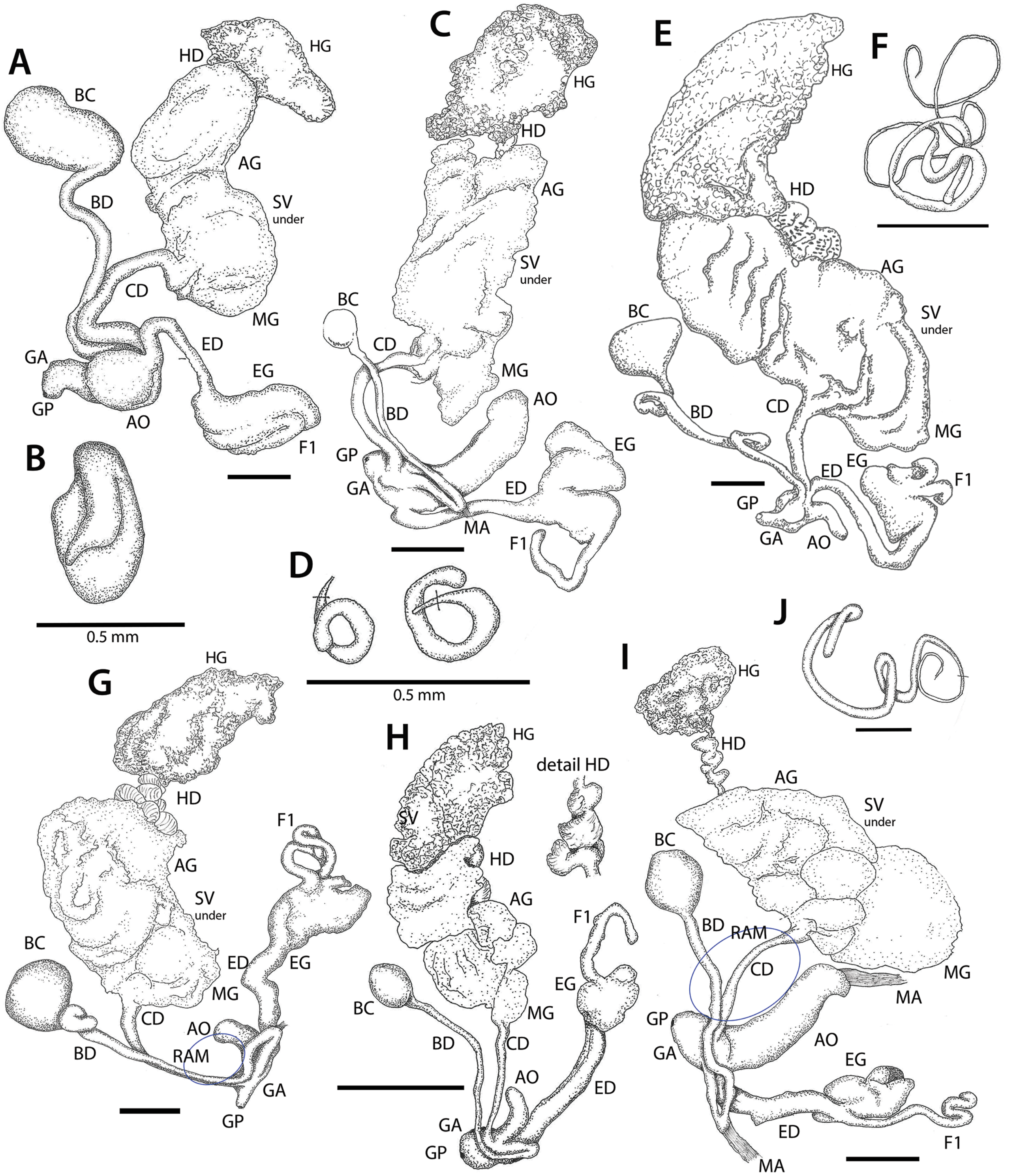

FIGURE 39. Reproductive morphology of *S. carbo*, *S. belcheri*, *S. exulum* and *S. nuttallii*. **A–B.** *S. carbo*, Mozambique, MNHN IM 2019-16165 [M587]. **C–D.** *S. belcheri*, Pakistan, Karachi. **C.** AM C.585500 [SK146]. **D.** AM C.595930 [SK533]. **E–H.** *S. exulum*. **E.** NI, TS, AM C.585025 [SK041]. **F.** LHI, AM C.546717 [SK052]. **G–H.** Kermadec Is, Raoul Is, TS of *S. raoulensis*. **G.** AM C.475847 [M513]. **H.** AM C.475848 [M512]. **I–J.** *S. nuttallii,* Hawaii, Maui, TS. **I.** AM C.584898 [SK211]. **J.** AM C.584895 [M471, SK273]. Unlabelled scale bars = 1 mm.

Pilsbry, 1921 from Kahoolawe, Hawaii [USA]; coll. H. A. Pilsbry, 1913 (ANSP 281800a; 'lectotype', refer Taxonomic remarks).

Other, non-type material. **Hawaii; Maui:** Ho'okipa Beach, 20°56.029'N, 156°21.411'W HA03-4 (AM C.585444 11p, C.585661 3p form *chirura*, C.584894 p [M470, protoconch G7], C.584895 p [M471, SK273, form *chirura*], C.584896 p [M472, SK079], C.584897 p [M486, SK305, form *chirura*], C.584898 p [SK211]).

Taxonomic remarks. The largest syntype of *S.*

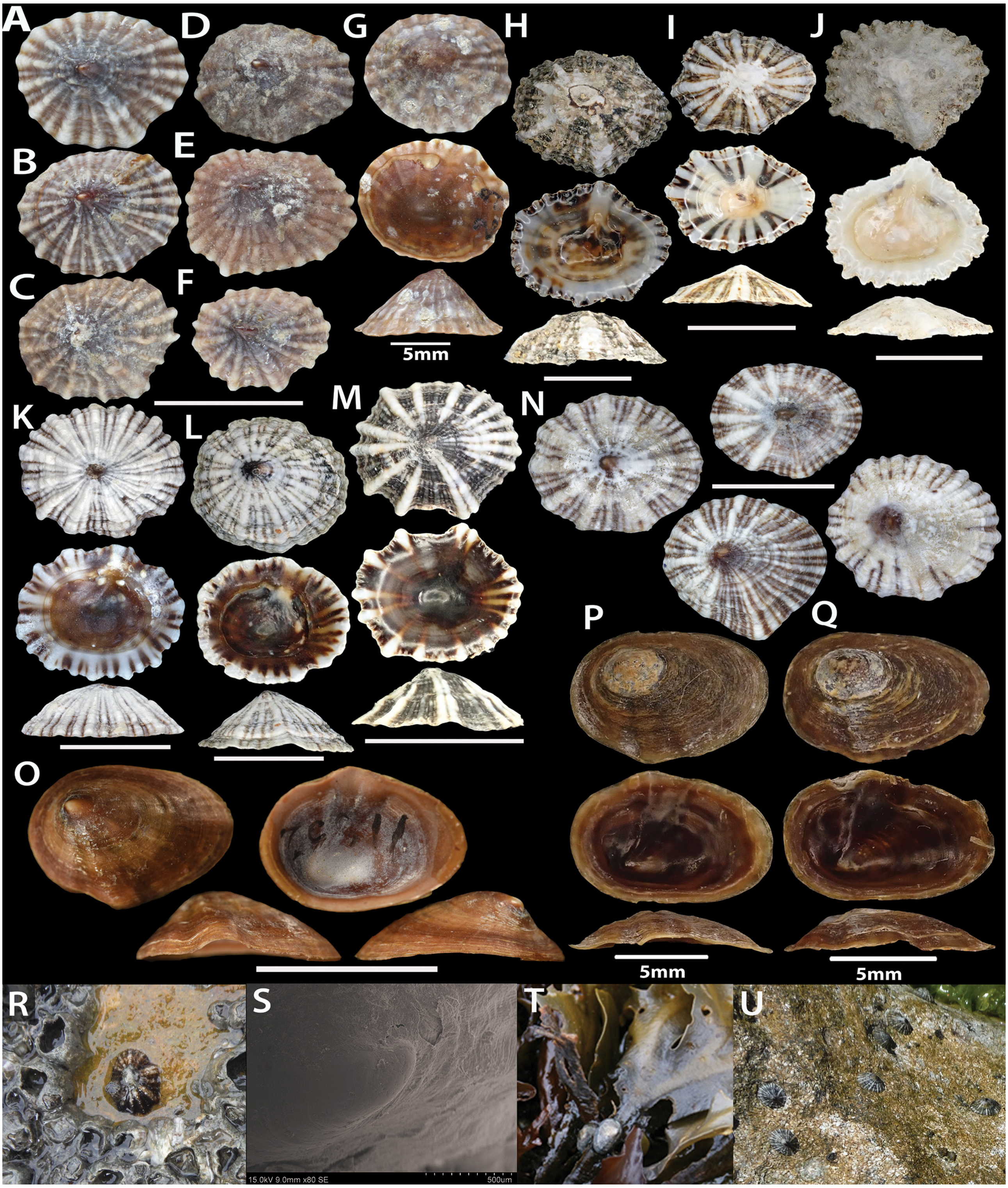

FIGURE 40. Shells of *S. belcheri*, *S. nuttallii* and *S. thersites*. **A–J, R.** *S. belcheri*. **A.** Lectotype NHMUK 1900.3.19.29. **B–G**. Paralectotypes NHMUK 1900.3.19.30-34. **G.** NHMUK 1900.3.19.28. **H**. Pakistan, Karachi, AM C.585102 [M227]. **I**. Karachi, AM C.585500 [SK146]. **J**. Karachi, AM C.585101 [M238]. **R.** Karachi, *in situ*. **K–N, S, U–V.** *S. nuttallii*. **K**. Lectotype NHMUK 20120166/1. **L**. Hawaii, Maui, TS, AM C.584898 [SK211]. **M.** TS of *S. chirura* AM C.584895 [M471, SK273]. **N**. Paralectotypes NHMUK 20120166. **S.** Protoconch, AM C.584894 [M470]. **U**. Maui, *in situ*. **O–Q, T.** *S. thersites,* **O.** Holotype USNM 11852. **P–Q.** Alaska, Cook Inlet. **P.** CBG 11BIOAK-0592 [SK553]. **Q.** 11BIOAK-0589 [SK554]. **T.** Washington, Neeah Bay, TS, *in situ*. Unlabelled scale bars = 10 mm.

nuttallii is herein designated as the lectotype (Fig. 40K) for the stabilisation of the name (Art. 74.1 of the Code). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 40L) and *S. normalis* var. *chirura* (Fig. 40M) and geographic series of additional specimens (Table S1). We establish *S. normalis* var. *chirura* as a new junior synonym. The designation of lectotype for *S. chirura* by Baker (1964: 159 'ANSP TSD now: 281800a') is invalid as it is not based on a syntype (Art. 74.1 of the Code). The specimen is badly worn. Pilsbry (1920b: 379) and Cernohorsky (1972: 210) erroneously treated *S. nuttallii* as a synonym of *S. normalis*.

External morphology. Foot sole, foot wall, mantle, cephalic folds, pneumostomal lobe evenly grey/green, paler to foot edge; irregular black blotches of pigmentation on foot wall and concentrated over centre cephalic folds; mantle thin, translucent narrower than foot wall, covers exposed inner shell lip, wider at anterior, mantle edge thickened, dark edge band, weakly lobed with even black pigmentation rays aligned with underside of shell rib interstices; genital pore indistinct; small black epithelial eye spot centralised on each of centrally touching cephalic folds; pneumostomal lobe long broad under mantle between the right anterior and right posterior ADMs.

Shell (Figs 40K–N, S; Table S9). Small sized (max sl mean = 12.7 mm, SD = 1.9 mm, n = 9), circular ovate; height medium; apex offset weakly posterior and laterally central, apical sides convex to straight; protoconch direction homostrophic to central (n = 3; Fig. 40S), shell whorl dextral; growth striae prominent in bands, shell thickness thick; rib count (mean = 42, SD = 2, n = 9); exterior uneven with faint radial banding; primary ribs pale tan, fairly straight to wavy, broaden and weakly raised to shell edge, ridges and ends rounded, protrude beyond shell edge; edge finely scalloped and unevenly corrugated; 2–5 finer secondary ribs between primary ribs, rib interstices darker brown with white patches; siphonal ridge formed by paired primary ribs; Interior shell margin white rays under primary ribs, dark brown rays under rib interstices, rays extend from shell lip over shell margin fading to spatula; siphonal groove indistinct, paler than shell margin; spatula mottled dark brown to white; ADM scar distinct, dark brown, CMS convex; no thickening or whitening of shell lip observed.

Reproductive system (Fig. 39I; n = 4). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between BM and RAM; GP small, singular, positioned through foot wall behind right cephalic fold, GA small, prominent; AO large, elongate, broad, bluntly pointed, slightly bent centrally, joins to top of GA in conjunction with relatively short, strongly twisted, very broad ED; EG large white folded, single long narrow looped flagellum F1 appears as an extension of ED at join with EG; AO, GA and ED all muscular white tissue; BD and CD connect closely in opposite directions into GA between connections of ED and AO, both ducts narrow smooth featureless, pass together through RAM connecting into MG, BD above and longer than CD, with distal loop and MA to inner foot wall; BC medium in size, spherical, embedded in folds of MG, test translucent; SV embedded in AG; HD reasonably long, thick coils, brown markings, links AG to smaller yellowish granular HG; MG and AG folded soft white tissue; sides match curvature of inner foot wall on right posterior of coelom; outer edge of MG lobed.

Spermatophore (Fig. 39J). Body cylindrical, thread-like (length = 6.7 mm, n = 1), test thin, translucent; head tip tapered bluntly rounded, section containing a white gelatinous core, tapers to a thin flagellum and tip; both sections smooth, featureless; head longer, thicker than flagellum (head length = 5.1 mm; 76% of SPM length; flagellum length = 1.6 mm; head width = 95 µm; flagellum width = 16 µm), 2 SPM tightly coiled in white gelatinous mass in one BC [M471].

Comparative remarks. *Siphonaria nuttallii* (*plicata* group, unit 85; Figs 1, 2) differs from other species by COI distances of ≥ 20% (Table S7). *Siphonaria nuttallii* occurs in sympatry with *S. normalis* at Big Island, Hawaii; refer to comparative remarks under that species. *Siphonaria nuttallii* has a similar shell morphology like other members of the *plicata* group, such as *S. mauiensis* **sp. nov.** (also occurring on Maui, but not found in immediate sympatry), *S. plicata*, *S. tongatapuensis* **sp. nov.** (both from Tonga), *S. monticulus* (from Lifou), *S. namukaensis* **sp. nov.** (Fiji and NC) and *S. poindimiensis* **sp. nov.** However, all these species are genetically well-differentiated. Specimens figured by Hubendick (1946: 91, pl. 4, figs 1–4) as *S. nuttallii* and *S. chirura* by Edmondson (1946: 188, figs 102b) are consistent with typical characteristics of *S. nuttallii* as defined herein and are within the known distribution of this species. Specimens figured as '*S. normalis'* in Kay (1979: 493, figs 157I, J) from Hawaii are likely of *S. nuttallii* for closely resembling the types (Figs 40K–N).

Distribution and habitat. Only known from Maui, Hawaii (Fig. 37), found on moderately exposed rocky shores in sheltered positions, mid littoral level (Fig. 40U).

Siphonaria incerta Deshayes, 1863

(Figs 41A–C, 42H–L, O, Q, T–U)

Siphonaria incerta Deshayes 1863: 81, pl. 7, figs 16–17 (type locality: Réunion).—Lienard 1877: 59; Martens 1880: 310; Paetel 1889: 428; Dautzenberg 1932: 10; Morrison 1972: 56; Michel 1974: 243; Trew 1983: 5; White & Dayrat 2012: 64.

Siphonaria parcicostata Deshayes 1863: 81, pl. 7, figs 18–19 (type locality: Réunion).—Lienard 1877: 59; Paetel 1889: 429; Dautzenberg 1932: 10; Hubendick 1945: 29; 1947a: 163; 1947b: 3; Michel 1974: 243; Trew 1983: 6; White & Dayrat 2012: 66.

Siphonaria (*Siphonaria*) *parcicostata*—Hubendick 1946: 46, pl. 3, figs 113–15.

Siphonaria sp. #335—Wells *et al.* 1990: 76, pl. 73.

Siphonaria sp. 2—Wells & Slack-Smith 2000: 113; Tan & Low 2014: 367.

Material examined. *Type material.* Neotype of *Siphonaria incerta* Deshayes, 1863, present designation, from Cap de la Houssaye, Saint Paul, Réunion (Art. 76.1 of the Code) (NMHN IM-2000-35954 [M263], Fig. 42H).

Other, non-type material. **Réunion.** TS (AM C.585204 [M260], Fig. 42I), Saint Denis, 20°53.108'S, 55°28.577'E, RU01-1 (AM C.585906 p [M259, SK276]); Cap de la Houssaye Saint Paul, 21°01.086'S, 55°14.115'E, RU02-1 (AM C.585204 p [M260], C.585205 p [M261], C.585206 p [M262], C.5859061 p [M261]). **Mauritius:** Isle de la Passe, 20°24'S, 57°46.133'E (WAM S72341 3p); Souillac, 20°31.467'S, 57°31.582'E, MRU01-2 (AM C.585975 6p, C.584967 p [M258]); Souillac, 20°31.519'S, 57°31.633'E, MRU01-1 (AM C.585974 17p, C.584964 p [M253], C.584965 p [M255]). **Australia, CI:** E side Smith Point, Flying Fish Cove, 10°25.749'S, 105°39.957'E, CI01-2 (AM C.584701 7p, C.584840 p [M320], C.584841 p [M321], C.584842 p [M322], C.585203 p [SK068]; WAM S74099 3p); West White Beach, 10°27.748'S, 105°34.934'E, CI01-3 (AM C.5847021 4p, C.584843 [M309], C.584844 p [M310]; WAM S74100 3p); Ethel Beach, 10°27.827'S, 105°42.497'E, CI02-1 (AM C.584847 p [M302], C.584848 p [M303], C.584889 p [SK081]; WAM S74101 5p).

Taxonomic remarks. The type locality of *S. incerta* and *S. parcicostata* can be deduced from the title of article that contains the descriptions (= Réunion). The type specimens of both taxa are missing (V. Hero MNHN, pers comm.). Two original hand-drawn coloured figures of shells in Deshayes (1863: *S. incerta* (figs 16, 17) and *S. parcicostata* (figs 18, 19) provide the only indication of species identity. The neotype of *S. incerta* (Fig. 42H) is designated herein to clarify the taxonomic status of this taxon (Art. 75.3.1 of the Code). Shell differences between the original figures of *S. incerta* and *S. parcicostata* are insignificant and within the observed range of variation of *S. incerta* (Fig. 42H, I–L, O; see also Dautzenberg, 1932: 10). Therefore, *S. parcicostata* is herein treated as a junior synonym of *S. incerta* by First Reviewer's Choice. Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly preserved specimens from Réunion, Mauritius, and Christmas Islands, including the neotype of *S. incerta* (Fig. 42H, Table S1).

Hubendick (1946: 47) considered *S. incerta* Deshayes1863 as a possible synonym of *S. laciniosa* (Linne, 1758) without having examined from Réunion or other Mascarene Islands. Morrison (1972: 56–58) treated *S. incerta* as a synonym of *S. laciniosa* based on similarity in shell form and 'common reproductive development'. This synonymy is not supported by our examinations.

External morphology (Fig. 42T). Foot sole, foot edge, foot wall, mantle, cephalic folds and pneumostomal lobe all evenly pale yellow to white in colour without any darker pigmentation markings. Mantle translucent, as wide as foot wall, strongly lobed with a thickened intense yellow to white banded edge; mantle lobes large, align with undulations of primary shell ribs, foot wall and pneumostome pustulose, pneumostome wide, between right anterior and posterior ADMs and within mantle; some individuals with dark brown shell rib interstices and interstice aligned dark pigmentation in mantle.

Shell (Figs 42H–L, O, U; Table S9). Small to medium sized (max sl mean = 13.5 mm, SD = 2.4 mm, n = 15), ovate, flattened, height medium to tall; apex offset posterior and centre, apical sides convex, posterior side straight to weakly concave; protoconch direction heterostrophic to central (n = 3; Fig. 42U), shell whorl dextral; growth lines indistinct; rib count (mean = 30.7, SD = 6.9, n = 15), raised, whitish, weakly wavy, width increases strongly to shell lip; rib interstices black to dark brown; 12–14 prominent primary ribs, extend up to 1 mm beyond shell edge, rib extremities weakly up turned; 1–2 finer secondary ribs may occur between primary ribs; paired primary ribs over siphonal ridge; shell lip uneven, scalloped aligning with protruding ribs; interior colouration matches white primary ribs and dark brown rib interstices, from shell lip to over shell margin to the chocolate to golden coloured spatula; ADM scar impression distinct, same as shell margin colouring, cephalic scar convex; thickening of shell occurs, white layering thickens and covers colouration of shell margin, spatula coated white.

The neotype (Fig 42H). Shell (sl = 11.5, sw = 9.1, sh = 3.9 mm) circular ovate; thin, apex offset weakly to posterior and left, ~18 whitish primary ribs, with 0–3 in between secondary ribs, rib interstices dark, siphonal ridge formed by adjacent dual primary ribs. Interior evenly dark brown, white rays on shell lip under ribs; RS (Fig. 41A) and SPM (Fig. 41B). Neotype specimen grouped within unit **72** (*S. incerta*).

Reproductive system (Figs 41A, C; n = 4). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between BM and RAM. Join of AO and GA distinct, AO larger than GA, elongated, bluntly pointed, slightly folded, thicker than ED; ED relatively short and narrow, EG elongated, bluntly pointed with a single very long, bent, twisted, thin flagellum F1, flagellum often lays on top of the BM; AO, GA and ED all muscular white tissue; BD and CD jointly connected to GA between ED, AO and GP; BD slightly longer and thinner than CD with a prominent loop over GA, both ducts smooth and pass together through RAM connecting into MG (BD over CD), BC small and bulbous, HD short thickened coiled, links AG to a small elongated narrow yellowish granulated HG; MG and AG small, folded, soft white tissue; SV embedded on left side of AG, AG larger than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 41C). Long thread-like; head section (head length = 6.06 mm, head width = 80 µm, n = 1) cylindrical, bulbous, rounded tip, tapers to flagellum; test thin, smooth, featureless, translucent encasing a white opaque central core; a short tapering section merges head to filamentous flagellum; head section wider than translucent flagellum (incomplete); 2 SPMs tightly coiled in brown gelatinous mass in bursa of the neotype.

Comparative remarks. *Siphonaria incerta* (*atra* group, unit 72) is the sister species of *S. recurva* (plus an unidentified *Siphonaria* from Tuituila Island) in our phylogenetic tree (Figs 1, 2). Both species differ from each other by COI distances of ≥ 16.7%. From other species it differs by distances of ≥ 25% (Table S3). Throughout its range, we found seven congeners with partly sympatric occurrences. Five congeners are sympatric on CI: *Siphonaria alba* has a larger, lower, heavier shell with less raised ribs and a weaker scalloped shell edge, a smaller AO and BC, and a longer ED. *Siphonaria christmasensis* **sp. nov.** has a smaller, lower, darker shell with weaker ribbing and scalloped shell edge, dark spatula, and smaller AO and BC. *Siphonaria delicata* **sp. nov.** has a taller and brown/grey shell, with weaker ribbing and scalloped shell edge, and a larger BC. *Siphonaria tenebrae* **sp. nov.** has a lower shell with a less prominent siphonal ridge, stronger scalloped shell edge, and smaller AO and BC. *Siphonaria umbra* **sp. nov.** has a lower, paler shell with less raised ribbing, a weaker scalloped shell edge, darker spatula, a larger BC, and a shorter SPM. Two species are sympatric at Mauritius: For comparison with *S. plana* refer to comparative remarks under his species. *Siphonaria griffithsorum* **sp. nov.** has a smaller shell with less prominent siphonal ridge, even ribbing and weaker scalloped shell edge, and larger AO, ED and BC. Specimens from Mauritius and Port Natal figured as '*S. parcicostata*' in Hubendick (1946: 91, pl. 3, fig. 13–15) correspond well with features typical of *S. incerta* (Figs 42H–L). However, their identity remains uncertain.

Distribution and habitat. Known only from Réunion and CI (Fig. 37); found in sheltered positions on moderately exposed and exposed rocky shores, mid littoral level (Fig. 42Q).

Siphonaria thersites Carpenter, 1864

(Figs 40O–Q, T, 41D–G)

Siphonaria thersites Carpenter 1864b: 561, 627, 647, 676, 684 (type locality: Neeah Bay [Washington, USA]).—Carpenter 1864c: 425; Paetel 1883: 178; 1889: 429; Yonge 1960: 111; Abbott 1974: 335, 4113; Galindo 1977: 416; Nagy 1984: 1, figs 1–9; White & Dayrat 2012: 68.

Siphonaria (*Liriola*) *thersites*—Dall 1870: 33, pl. 4, 8a–b, 1926: 26; Oldroyd 1927: 57; Thiele 1931: 427; Hubendick 1945: 64, fig. 1; 1946: 19, fig. 3, pl. 5, figs 35–38; Palmer 1958: 258; Morrison 1963: 7.

Liriola thersites—Dall 1921: 66; Trew 1983.

Material examined. *Type material.* Holotype of *S. thersites* from 'Neeah Bay, Washington, West Coast, North America'; coll. Swan, J. G. (USNM 11852; Fig. 40O).

Paratype, same data as holotype (MCZ 275190).

Other, non-type material. **USA, Alaska:** Cook Inlet, Camel Rock Camel Rock, 59°26.68'N, 151°43.02'W (CBG 11BIOAK-0589 p [SK554], 11BIOAK-0592 p [SK553], 11BIOAK-0593 p). **Canada, British Columbia:** Houston Stewart Channel, Kunghit Island, 53°0'N -132°0'W (RBCM 80283 d).

Taxonomic remarks. Carpenter (1864b: 423) donated the types to the Smithsonian Institution (i.e., USNM). Palmer's (1958: 258) statements regarding missing type and potential lectotype specimens are incorrect and explicitly not based on examination of the holotype. *Siphonaria thersites* is the type species of *Liriola* Dall, 1870, by original designation.

External morphology. Animal not fully enclosed by shell, foot sole pale grey, foot wall, foot edge, mantle and cephalic folds all darker grey, paler at foot edge; foot wall pustulose, without darker markings; mantle narrow with dark grey edge band, half as wide as foot wall; two small indistinct black epithelial eye spots centralised on two centrally touching cephalic folds, pneumostomal lobe thick, under mantle behind right cephalic fold; closes the pneumostomal and anal openings at the mantle edge.

Shell (Figs 40O–Q; Table S9). small sized (max sl mean = 10.6 mm, SD = 1.7 mm, n = 9), elongate ovate, apex offset strongly posterior and left, apical sides strongly convex, height low, protoconch below apex, close to posterior edge; protoconch direction homostrophic (n = 2), shell whorl dextral; exterior uneven, radially ribbed, reddish brown, growth striae prominent in shaded radial bands, shell thin, lip even fragile, periostracum freely extending; rib count (mean = 36, SD = 3.2, n = 9), ribs weak to indistinct, primary ribs flatly rounded, not protruding beyond shell lip; often interspersed finer secondary ribs, rib interstices darker; siphonal ridge clear, bulged, extends beyond shell edge, formed by paired primary ribs. Interior glossy, shell margin dark brown to tan, lip paler with white markings aligned under ribs, siphonal groove distinct, shallow, same colour as margin; spatula mottled tan, uneven darker markings; ADM scar distinct, CMS convex; thickening of shell lip not observed.

Reproductive system (Figs 41D, F, G; n = 3). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between BM and elongated RAM; AO indistinct, appears as a bulge under medium sized GA, ED short wide, joins to side of GA, singular prominent GP; EG large bulbous soft, flagellum (F1) indistinct to absent; BD indistinct, very narrow, enclosed in ventral tissue of wider whitish CD from BC to GA (Fig. 41F–G); both ducts are of similar length, emerge from folds of MA, together pass between foot wall and outside of RAM, and join into side of GA; GA, ED and BD all muscular white tissue; BC small deflated flattened whitish or expanded (5 SPM in a single BC), positioned under MG/AG; MG and AG small, heavily folded, soft white tissue; yellowish SV embedded on left side of AG, AG larger than HG; HD short, thickened, uncoiled and unlobed, links AG to a small, elongated, brownish/yellow, finely granulated HG.

Spermatophore (Fig. 41E). Body cylindrical, thread-like (length = 14.6 mm, n = 1, 118% of AL), test thin, translucent; head section long even, bluntly rounded, tapers to a thin flagellum and tip; both sections smooth, featureless; head longer, thicker than flagellum (head length = 11.8 mm; 81% of SPM length; flagellum length = 2.8 mm; head width = 150 µm; flagellum width = 14 µm).

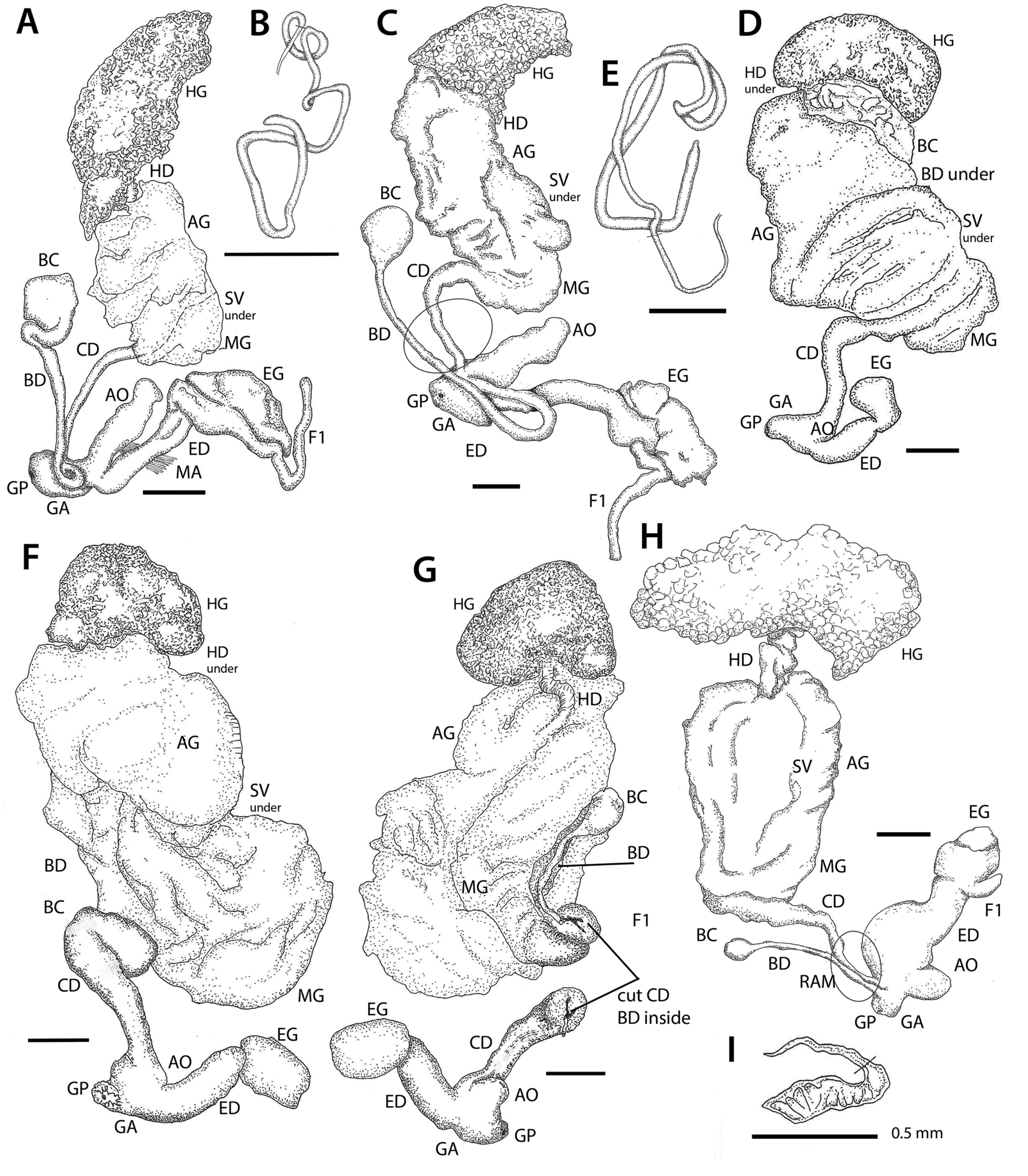

FIGURE 41. Reproductive morphology of *S. incerta*, *S. thersites* and *S. tasmanica*. **A–C.** *S. incerta.* **A–B.** Réunion, Saint Paul, neotype MNHN IM-2000-35954 [M263, SK276]. **C.** CI, AM C.584889 [SK081]. **D–G.** *S. thersites*, Alaska, Cook Inlet. **D–E.** BIOUG 11BIOAK-0592 [SK553]. **F.** Dorsal view. **G.** Ventral view. BIOUG 11BIOAK-0589 [SK554]. **H–I.** Tas, TS of *S. tasmanica*. **H**. AM C.585255 [SK020]. **I.** SPM, AM C.585512 [SK080]. Unlabelled scale bars = 1 mm.

Radula. Dentition formula 22:1:22 or 7.3.3.9:1:9.3.3.7 (Dall, 1870: 33), 24:1:24 (Hubendick 1946: 20).

Comparative remarks. *Siphonaria thersites* (unit 42) is the sister species of all other *Siphonaria* species included herein (Fig. 1). It differs from other species by COI distances of ≥ 15.6%. It is not known to occur in sympatry with any other congener. As the only species found in Alaska, it has not been mistaken with other species in previous taxonomic literature. Contrary to Hubendick (1945: 15, fig. 1; 1946: 8, figs 1, 3), a BC is present and the genital pore (GP) is monoaulic (Fig. 41D, F). Hence, the general layout of the reproductive anatomy of *S. thersites* corresponds well with that of other *Siphonaria* species.

Distribution and habitat. Endemic to northern hemisphere temperate zone from Kurile Islands, Russia, to west coast of Alaska, USA, British Columbia, Canada and Washington USA (Fig. 45). Found on sheltered rocky shores at lower littoral level often on *Fucus* rockweed (Fig. 40T).

Siphonaria tasmanica Tenison Woods, 1877

(Figs 41H–I, 42A–G, M–N, P, R–S)

Siphonaria denticulata var. *tasmanica* Tenison Woods 1877: 54 (type locality: Tasmania).—Verco 1907: 105; Hardy 1915: 62.

Siphonaria zonata Tenison Woods 1878b: 99 (type locality: Tasmania).—Pritchard & Gatliff 1903: Verco 1907: 105; Hardy 1915; 23; Hedley 1915: 752; May 1921: 89; May 1923: 87; Galindo 1977: 416; Grove *et al.* 2006: 61; White & Dayrat 2012: 69.

Siphonaria tasmanica—Iredale 1924: 276; Cotton & Godfrey 1932: 154; Macpherson & Chapple 1951: 142; Macpherson & Gabriel 1962: 262, fig. 300; Galindo 1977: 416; Jenkins 1981: 2; 1983: 29; Quinn 1983: 81; Jenkins 1984: 3; Phillips *et al*. 1984: 79; Grove *et al.* 2006: 61; Chim & Tan 2009: 269; Grove 2011: 62, pl. 29, fig. 15; White & Dayrat 2012: 68; Colgan & da Costa 2013: 74.

Talisiphon tasmanicus nereis Iredale 1940: 442 (type locality: Port Fairy, Vic, [Australia]).—White & Dayrat 2012: 66.

Talisiphon tasmanicus turritus Iredale 1940: 442 (type locality: Macquarie Harbour [Tas, Australia]).

Siphonaria (*Pachysiphonaria*) *tasmanica*—Hubendick 1945: 66; 1946: 22, pl. 1, fig. 12–14.

Pachysiphonaria tasmanica—Trew 1983: 2.

Liriola (*Pachysiphonaria*) *tasmanica*—Ludbrook & Gowlett-Holmes 1989: 612, fig. 11.

Siphonaria nereis—Grove *et al.* 2006: 61.

Siphonaria turritus—Grove *et al.* 2006: 61.

Talisiphon tasmanica turritus—White & Dayrat 2012: 69.

Material examined. *Type material.* Neotype of *Siphonaria tasmanica* Tenison Woods, 1877, present designation, from Tasman Arch, Tasmania (Art. 76.1 of the Code); coll. B.W. Jenkins, T03-3, 27 March 2018 (AM C.585259, Fig. 42A [M114], condition Art. 75.3.7 of the code).

Seven syntypes of *Siphonaria zonata* Tenison Woods, 1877 from S Tasmanian coast; coll. J.E. Tenison Woods, 1877 (MV F686, Figs 42B–C, M–N; AM C.103723, 2d).

More than twenty syntypes of *Talisiphon tasmanicus nereis* Iredale, 1940 from Port Fairy, Vic, [Australia] coll. R. Bell, 1918–1919 (AM C.108499, Figs 42D, E).

Holotype (measurements in text) of *Talisiphon tasmanicus turritus* Iredale, 1940 from Macquarie Harbour, Tas; coll. A.F. Basset Hull, 1922 (AM C.595951, Fig. 42F). Thirteen paratypes, same data as holotype (AM C.53828; labelled ‘syntypes’).

Other, non-type material. **Australia, Vic:** Cape Schanck, 38°29.951’S, 144°53.369’E, V06-4 (AM C.585458 13p); Point Lonsdale (nr Queenscliff), 38°17.276’S, 144°36.977’E, V05-1 (AM C.585730 p [M120]). **Tas:** Lagoon River: mouth, 41°29.4’S, 144°49.2’E (TMAG E.41995 2d); Bicheno, Redbill Beach, 41°51.6’S, 148°17.4’E (TMAG E.42002 p, d); Maria Island, Howells Point & Painted Cliffs, 42°35.796’S, 148°2.886’E (TMAG E.42001 p, d); Maria Island, Trigonia Corner, 42°41.196’S, 148°4.404’E (TMAG E.41993 d, p); Marion Bay, northern beaches 42°45.048’S, 147°53.592’E (TMAG E.42004 d, p); Park Beach Dodges Ferry, 42°51.716’S, 147°36.665’E, T03-4 (AM C.585429 10+p, C.585266 p [SK549 protoconch D6]); Carlton Beach, Spectacle Island, 42°52.044’S, 147°36.024’E (TMAG E.41994 d, p); Taroona, Dixons Beach, 42°56.358’S, 147°21.414’E (TMAG E.41999 d, p); Lagoon Bch (near Saltwater River), 42°56.903’S, 147°39.962’E, T03-2 (AM C.585659 4p, C.585876 d); Taroona Beach; 42°57’S, 147°21’E (TMAG E03651 3p); 42°57.18’S, 147°21’E (TMAG E.42006 4d, 4p): Kingston Beach, 42°58.8’S, 147°19.2’E (TMAG E.02013 p); Eaglehawk Neck, eastern side, 43°0.444’S, 147°56.082’E (TMAG E.42003 d, p), (TMAG E.01659 2p); Blackmans Bay 43°0.6’S, 147°19.8’E (TMAG E.41998, 3 d / 3 p), (TMAG E.15880 10p); Calverts Beach & Goats Bluff, 43°1.65’S, 147°29.07’E (TMAG E.42005 3d, 3p); South Arm–Hope Beach, southern end, 43°1.8’S, 147°27.6’E (TMAG E.01245 3p); Tasman Arch, 43°02.033’S, 147°56.963’E, T03-3 (AM C.585728 9p, C.585255 p [SK020], C.585259 p [M114]); Tinderbox Beach, 43°3.6’S, 147°19.8’E (TMAG E.05224 p); North Bruny Island, Dennes Point, 43°3.87’S, 147°21.066’E (TMAG E.42000 4p, 4d); Nubeena, Parsons Bay, 43°6’S, 147°6’E (TMAG E.05996 2p); Nubeena, White Beach, 43°7.2’S, 147°43.8’E (TMAG E.06015 p); Fortescue Bay, 43°8.4’S, 147°57.6’E (TMAG E.05580 6p); Port Arthur, 43°9’S, 147°52.2’E (TMAG E.05550 4p); Three Hut Point d’Entrecasteaux Channel, 43°16.195’S, 147°14.414’E, T04-3 (AM C.595913 2p); South Bruny Island: Simpsons Bay, 43°17.4’S, 147°18.6’E (TMAG E.04867 4p), Cloudy Beaches–eastern beach, 43°26.352’S, 147°14.202’E (TMAG E.41996 20d, 20p), (TMAG E.25061 d); Peaches Point, 43°34.122’S, 146°55.037’E, T05-3 (AM C.585606 4p); Flensing Rock, 43°34.291’S, 146°54.856’E, T05-2 (AM C.585460 13p, C.585512 p [SK080], C.585877 p [M119]); Cockle Creek Bay, 43°34.8’S, 146°53.4’E (TMAG E.32706 d); Pancake Bay, 43°34.673’S, 146°55.293’E, T05-5 (AM C.585715 8p); Trial Harbour, 41°55.758’S, 145°10.434’E (TMAG E.41997 5d, 5p); Lucas Point, Pilot Bay, Macquarie Harbour, 42°12.241’S, 145°12.005’E, T06-1 (AM C.585483 18p; C.585538 20+p, C.585878 p [M171], C.585879 p [M172]). **SA:** Fishery Bay Cape Wiles, 34°55.107’S, 135°41.086’E, SA05-1 (AM C.585689 7p); Haleys Beach Gibson Peninsula, 32°45.084’S, 134°05.490’E, SA03-4 (AM C.585467 20+p); Wandrilla Beach, nr Cape Nuyts, 32°01.894’S, 132°16.052’E, SA01-1 (AM C.585705 10+p, C.585208 p [SK019]).

Taxonomic remarks. The type locality was not explicitly stated in the original designation of *S. tasmanica* but is evident from the title of the work (“on Tasmanian Patellidae”). Originally, Tenison Woods (1877: 45) described *S. tasmanica* as a variety of *S. denticulata*. Subsequently, Tenison Woods (1878b: 99) described the same taxon again as *S. zonata* without mentioning the earlier introduced name *S. diemenensis* var. *tasmanica*. No original types of *S. tasmanica* are known to exist and we could not locate any in the collection of the AM. The neotype of *S. tasmanica* (Fig. 42A) is designated herein to clarify the taxonomic status of this taxon (Art. 75.3.1 of the Code). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes and geographic series of additional specimens (Table S1). These analyses confirm the synonymy of *S. zonata* (Fig. 42B–C, M–N) and establish *Talisiphon tasmanicus nereis* and *T. tasmanicus turritus* (Fig. 42D–F) as new synonyms. The name '*Siphonaria zonata* ('Schub. et Wagn')' in Deshayes (1843: 31, pl. 62, fig. 17–18) is misapplication for *Patella zonata* Schubert & Wagner, 1829. The figured specimens in Schubert & Wagner (1829) and Deshayes (1843) differ from one another, neither showing a species of *Siphonaria*. Christiaens (1975: 91) listed *Patella zonata* as a synonym of *Scurria scurria* (Lesson, 1830), Lottiidae. Iredale (1924: 276) was the first to recognize the synonymy of *S. zonata* and *S. tasmanica* transferring the species to *Talisiphon*. Tate & May (1901: 419) incorrectly considered *S. zonata* as a synonym of *S. funiculata*.

External morphology (Fig. 42S). Foot sole and foot wall evenly dark grey, paler at foot/wall edge; foot wall and mantle blue-green-grey; fringing mantle narrow, unlobed, translucent, covers exposed inner shell lip; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two centrally touching cephalic folds; pneumostomal lobe small, thin, part of the mantle, between the right anterior and right posterior ADMs, closes the pneumostome at the mantle edge.

Shell (Figs 42A–G, M–N, P, R; Table S9). small to medium sized (max sl mean = 13.8 mm, SD = 2.4 mm, n = 12), height tall; apex offset weakly to posterior and left, often eroded and appearing as a white spot, apical sides convex; protoconch direction homostrophic (n = 2; Fig. 42R), shell whorl dextral; growth striae indistinct; rib count (mean = 48.3, SD = 9.6, n = 11), primary ribs fairly straight, unraised, flattened, broad, few secondary ribs; rib interstices distinct dark brown narrow lines extending to shell lip. Exterior shell colouration very distinct and unlike any other siphonariid; 3 prominent colour bands align with shell growth dividing shell height unevenly into thirds; top band upper half of shell dark brown, mid band widest and pale blue, bottom band greenish blue, limited to shell margin (Figs 42A, G). Internal colouration banded and variable; spatula blueish or cream/white, shell lip markings white aligned under primary ribs, reddish brown aligned under rib interstices; siphonal groove same colour as spatula, ADM scar dark brown, shell margins immediately above and below are paler; CMS straight. Shell thickening not observed. Shell height may be variable; e.g. lower in *S. t. turritus* (Fig. 42G) and taller in *S. blainvillei* (Fig. 42F) forms.

The neotype (Fig. 42A). Shell medium sized (sl = 17.5, sw = 14.3, sh = 8 mm), circular ovate, tall; medium thickness, apex offset strongly to posterior and weakly to left, ~52 mainly primary ribs, few secondary ribs, interior dark brown, spatula and shallow siphonal groove white to bluish; taller and slightly darker interior shell form of *S. tasmanica*. Neotype specimen grouped within unit **76** (*S. tasmanica*).

Reproductive system (Figs 41H; n = 2). Positioned against inside of foot wall and over foot sole on the right posterior quarter within coelom, under the respiratory cavity. GA, EG and ED positioned in coelom between BM and RAM. GA very large, smoothly bulbous, with singular GP; AO absent; ED very short, broad, curved, unfolded, joins to side of GA; GA and ED white muscular fibrous tissue; EG soft whitish, slightly folded, smaller than GA; flagellum absent; BD and CD relatively short (BD longer), slightly curved, smooth, featureless, connect to GA together, pass together through RAM (BD over CD), CD connecting into MG/AG; BC small, elongated, bulbous, thin test, embedded in lower folds of MG/AG; HD short, narrow, coiled, links smallish AG to a large elongated yellowish granulated HD; MG/AG complex small, soft white tissue folds, enveloping SV close to embedded BC, AG larger than HG, HG side reflects curvature of inner foot wall. AL= 13.52 mm.

Spermatophore (Fig. 41I). Length very short compared to other congenors; broad head with short flagellum (length = 1.03 mm, n = 1); head section cylindrical, bulbous, rounded tip (head length = 0.64 mm, ~62% of SPM length; head width = 159 µm; flagellum width = 34 µm), contains whitish core, test thin, translucent encasing a white opaque coiled core; flagellum transparent, tapering to a thread-like end; both sections uneven, featureless; 1 SPM in brown gelatinous mass of one BC [SK080].

Radula. (Fig. 83M–P) Mean dentition formula 43:1:43 (SD = 4.8) with 115 (SD = 26.6), mean transverse rows 115 (SD = 26.6, n = 5); single central rachidian tooth flanked squarely by 43 half row laterals, 0–4 are inner (Figs 83M–N), 14–20 mid and 15 outer laterals (Fig. 83O); central tooth relatively long (half basal length) with narrow unicuspid mesocone; inner laterals (without endo or ectocones) may occur, mesocones of inner and mid laterals single pointed, mid laterals with broad pointed ectocone protruding at an acute angle halfway along the tooth's length; outer laterals typically with a weakly bicuspidate 'chisel' shaped mesocone flanked by small, pointed single ecto and endocones, angle of separation of each cone from the mesocone varies (Fig. 83O).

Comparative remarks. *Siphonaria tasmanica* (*lateralis* group, unit 76) is most closely related to *S. lessonii* from the Southern Ocean (not revised herein, see Güller *et al.* (2015: 81), *S. funiculata* and *S. obliquata* (Figs 1, 4). It differs from *S. lessonii* by COI distances of ≥ 9.4% and from *S. funiculata* of ≥ 8.5% (Table S8). Throughout its range, *S. tasmanica* has been found in sympatry with five congeners in southeastern Australia. For comparisons with *S. diemenensis*, *S. funiculata*, and *S. zelandica* refer to comparative remarks under these species. *Siphonaria jeanae* has a lower, grey-blue shell with more prominent

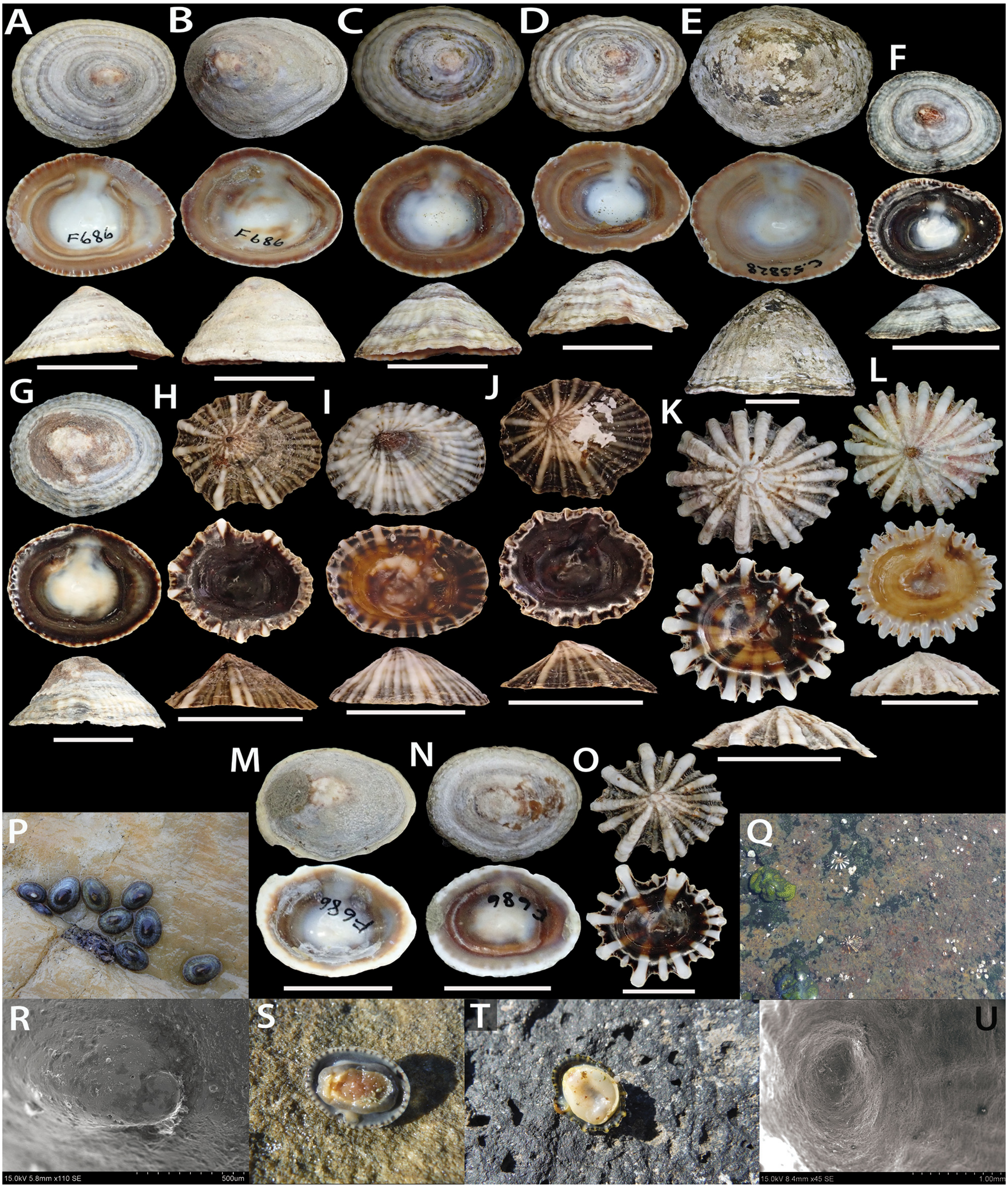

FIGURE 42. Shells of *S. tasmanica* and *S. incerta*. **A–G, M–N, P–R**, **S**. *S. tasmanica*, **A.** Neotype AM C.585259 [M114]. **B–C, M–N**. Syntypes of *S. zonata*, MV F.686. **D–E**. Largest syntypes of *S. nereis* AM C.108499. **F**. Largest syntype of *S. turrita* AM C.53828. **G**. Vic, Pt Lonsdale, AM C.585730 [M120]. **P.** Tas, Macquarie Harbour, *in situ*. **R**. Protoconch, AM C.585208 [SK019]. **S**. Tas, animal. **H–L, O, Q, T–U.** *S. incerta*, **H.** Neotype MNHN IM-2000-35954 [M263]. **I.** Réunion, Cap de la Houssaye, AM C.585204 [M260]. **J.** AM C.585205 [M261]. **K**. CI, Flying Fish Cove, AM C.584841 [M321]. **L.** CI, AM C.584843 [M309]. **O.** CI, TS, AM C.584840 [M320], **Q.** Réunion, *in situ*. **T.** Réunion, animal. **U.** Protoconch, AM C.585906 [M259]. Scale bars = 10 mm.

unraised brown ribs, a more scalloped edge, a wider ED, larger BC, and more thread-like SPM. *Siphonaria stowae* has smaller, lower, paler shell with an apex strongly offset to posterior, more prominent ribbing, a larger AO and BC, a smaller ED and a more thread-like SPM. Overall, the combination of shell geometry, size and colouration render *S. tasmanica* a rather distinctive species.

Tasmanian records of '*S. tristensis* Sowerby I, 1823' in Tate & May (1901) are incorrect and based on misidentified specimens of *S. tasmanica*. A record of '*S. tasmanica*' from Percy Island, Qld (Singleton, 1937: 396) is likely a misidentification of *S. normalis*. A specimen figured as *S. tasmanica* in Davey (1998: 118) is a specimen of *S. funiculata*.

Distribution and habitat. Endemic to cool temperate coasts of southern Australia, between Mallacoota, Vic, and Gibson Peninsula, SA, Tas (Fig. 37). Found in sheltered positions (e.g., rock hollows, crevices, cracks) on very exposed rocky shores, mid littoral level (Fig. 42P); frequently associated with black mussels; home scars prominent.

***Siphonaria acmaeoides* Pilsbry, 1894**

(Figs 43A–D, M–N, 44A–C)

Siphonaria acmaeoides Pilsbry 1894b: 6, pl. 6, figs 19–22 (type locality: Prov. Boshiu [Boso Peninsula], Japan).—Pilsbry 1895: 6, pl. 6, fig. 19–22; Hirase 1941: 94, pl. 121, fig. 15; Kuroda & Habe 1952: 86; Azuma 1960: 62; Baker 1964: 159; Galindo 1977: 416 (as '*acmeaodes*'); Christiaens 1980b: 466; Higo *et al.* 2001: 142, fig. G4976; White & Dayrat 2012: 60.

Siphonaria (*Patellopsis*) *acmaeoides*—Hubendick 1945: 70, fig. 19; 1946: 30, pl. 6, fig 12–15; Habe & Kikuchi 1960: 64; Kira 1962: 201, pl. 69, fig. 9a, b (misspelled as '*Patellops*').

Siphonaria zebra—Kuroda & Habe 1952: 86 (not *S. zebra* Reeve, 1856).

Planesiphon acmaeoides—Kuroda *et al.* 1971: 484, pl. 64, fig. 8; Habe *et al.* 1986: 23.

Siphonaria (*Mouretus*) *acmaeoides*—Christiaens 1980a: 79.

Siphonaria (*Mouretus*) *acmaeoides paulae* Christiaens 1980a: 79, pl. 4B, D (type locality: Ping [Peng] Chau, [Hong Kong, China].—Christiaens 1980b: 466.

Siphonaria (*Planesiphon*) *acmaeoides*—Inaba 1983: 149; Je 1989: 29; Noseworthy *et al.* 2007: 90.

Patellopsis acmaeoides—Trew 1983: 3.

Siphonaria zelandica—Dayrat *et al.* 2014: 261, 'unit 26' (in part), fig. 5A (not *S. zelandica* Quoy & Gaimard, 1833).

Material examined. *Type material.* Lectotype of *Siphonaria acmaeoides* Pilsbry, 1894 from Prov. Boshiu [Boso Peninsula], Japan; coll. Frederick Stearns (ANSP 70726a, Fig. 43A). Two paralectotypes same data as lectotype (ANSP 70726).

Holotype of *Siphonaria* (*Mouretus*) *acmaeoides paulae* Christiaens, 1980 from Ping [Peng] Chau, [Hong Kong, China] (NHMUK 1977171, Fig. 43D).

Other, non-type material. **Japan, Honshu:** Boso Peninsula,Po int S of Chitose Beach, 34°59.240'N, 139°58.304'E, JP02-2 (AM C.585393 10+p, AM C.584936 p [M496, SK315], C.584937 p [M500, SK319], C.585289 p [SK356], C.585513 p [SK334 protoconch H4], C.585918 p [SK335]).

Taxonomic remarks. The description of Pilsbry (1894b: 16) does not contain an original type designation. Subsequently, Pilsbry (1895: 2, pl. 6, fig. 19–22) republished the original description based on three specimens but giving the dimensions for only one specimen. Baker (1964: 159) designated the lectotype (ANSP 70726a), which matches the original dimensions given by Pilsbry (1894b: 16). Figures in Pilsbry (1895: pl. 6, figs 19–22) correspond reasonably well with the type specimens; fig. 19 (ventral) lectotype, figs 20 (ventral), 21 (dorsal) and fig, 22 (ventral) paralectotypes. The type specimen figured in Higo *et al.*(2001: fig. G4976, "ANSP 70726") differs from the specimens in Pilsbry (1894b: 16). The type specimens (ANSP 70726) of *S. acmaeoides* (Fig. 43A) are of the *plicata* group.

Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 43B, Table S1). Comparative morpho-anatomy and mitochondrial phylogenetics herein confirm that *S. acmaeoides* and *S. zelandica* are closely related, yet distinct species. Christiaens (1980a: 79) recorded *S. acmaeoides* from Hong Kong and described a new subspecies, *S. acmaeoides paulae* Christiaens (1980a: 79, pl. 4, figs B, D). The holotype of *S. a. paulae* (Fig. 43D) matches specimens of *S. acmaeoides* from Japan (Fig. 43B). The emphasised characters of this subspecies, a finer, thinner, more elliptical, lighter coloured shell without a 'marked' central area, are within the range of intraspecific variation. Therefore, we synonymize this taxon with the nominate form. Christiaens (1980a) record extends the distribution of *S. acmaeoides* from Honshu, Japan to Hong Kong (Fig. 35).

External morphology (Fig. 43N). Foot sole dark grey, paler to foot edge; foot wall, foot edge, mantle, cephalic folds and pneumostomal lobe all evenly pale grey/yellowish in colour; mantle thin, translucent, wider than foot wall, weakly lobed and unbanded edge; no black/dark pigmentation; pneumostome fold large, long between right ADMs and within mantle; vivid yellow or white subepithelial pustules on cephalic lobes and pneumostomal fold; two black 'Eye' spots prominent centrally on thickened cephalic lobes.

Shell (Figs 43A–C, M; Table S9). Medium sized (max sl mean = 14.5 mm, SD = 1.9 mm, n = 8), circular ovate; height low; apex offset slightly posterior and laterally central, apical sides even, weakly convex; exterior pale brown, with irregular darker/black flecks between primary ribs; rib count (mean = 57.4, SD = 10.3, n = 8), ~ 15 primary ribs, whitish, fairly straight, ridges rounded, broaden to shell edge; 3–4 finer secondary ribs between primary ribs, rib interstices dark grey; ribs align with shell edge; growth striae indistinct; siphonal ridge not prominent, formed by paired primary and secondary ribs, more protruding at shell edge; weak radial banding, darker to shell edge; protoconch direction central flat (n = 1; AM C.585513 [SK334]), shell whorl dextral. Interior shell lip finely corrugated; shell lip and margin white with dark flecks to dark chocolate brown rays aligning under primary rib interstices; spatula colour variable golden to dark chocolate brown; siphonal groove and ADM scar prominent, paler than margin and spatula; CMS convex to straight, indistinct; thickening and whitening of shell margin occurs.

Reproductive system (Figs 44A–B; n = 4). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned between BM and RAM; GA large, AO indistinct absent; ED very short, twisted, very broad; EG very large with folds, single long narrow looped flagellum F1 very short appears as an extension of ED at join with EG; GA and ED all muscular white tissue; BD and CD connect in parallel into GA close to ED joint, both ducts narrow, smooth, featureless, similar length pass together between outer RAM and inner foot wall (BD above CD), slightly bent before connecting into folds of MG; BD without distal loop or MA; BC small, translucent test, bulbous, embedded in MG; coiled brownish HD links white AG to finely granulated HG; MG and AG small folded soft white tissue; SV embedded within AG under BC; AG slightly smaller than HG, sides reflect curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 44C). Body bulbous, elongated (length = 1.03 mm, n = 1, AL = 11 mm), test thin; head tip bluntly rounded, section containing a white gelatinous core, tapers to a thin flagellum and tip; both sections smooth, featureless; head longer, thicker than flagellum (head length = 0.89 mm; 87% of SPM length; flagellum length = 0.14 mm; head width = 243 µm; flagellum width = 24 µm), 1 SPM in white gelatinous mass in BC of one topotypic specimen.

Radula. Dentition formula 26:1:26 (Hubendick 1946: 31).

Comparative remarks. *Siphonaria acmaeoides* (*atra* group, unit 91) is the closely related sister species of *S. zelandica* (Figs 1, 2). Both species differ by COI distances of ≥ 5.8% (Table S4). Both species have a disjunct distribution with one species found in the northern (*S. acmaeoides*) and one in the southern Pacific (*S. zelandica*), each. Throughout its range, *S. acmaeoides* has been found in sympatry with three congeners. For comparisons with *S. sirius* and S. *japonica* refer to comparative remarks under these species. *Siphonaria camura* **sp. nov.**, sympatric in Honshu and Hong Kong, has a smaller, taller shell with more raised ribbing, a darker brown interior, larger BC, and a larger, thread-like and barbed SPM. *Siphonaria acmaeoides* exhibits a shell morphology similar to other species of the *plicata* group; however, these are anatomically and genetically distinct: *S. zelandica* (temperate Australia), *S. plicata* (Tonga), *S. nuttallii* (Hawaii), *S. tongatapuensis* **sp. nov.** (Tonga), *S. namukaensis sp. nov.* (Fiji and NC) and *S. poindimiensis* **sp. nov.** (NC), *S. yagasaensis* **sp. nov.** (Fiji) and *S. monticulus* (NC, Lifou). *Siphonaria acmaeoides* resembles *S. zelandica* in shell sculpture, external morphology, and SPM. Both species occupy similar habitats (upper littoral, shallow rock pools, rarely on rock faces). However, closer examination of the type and topotypic specimens revealed that *S. acmaeoides* differs in shell geometry, wider rib ridges, external colouration, and secondary ribbing, larger size of GA and ED, smaller HD, longer and narrower BD and CD. Hubendick (1946: 31) correctly pointed out that '*S. acmaeoides*' and '*S. bifurcata*' (= *S. zelandica*) had 'very similar shells'. Dayrat *et al.* (2015: 268) considered both taxa as possibly conspecific based on similarities in shell morphology.

Distribution and habitat. Recorded from the type locality, Bose Peninsula, and Aichi Prefecture, Honshu, Japan (Fig. 45). In this study found to be common on exposed rocky shores in crevices and small rock pools, upper littoral level (Fig. 43M).

***Siphonaria sirius* Pilsbry, 1894**

(Figs 43E–F, O–P, 44D–E)

Siphonaria sirius Pilsbry 1894a: 9 (type locality: Sagami and Kashiurazaki, Boshiu, Japan).—Pilsbry 1895: 5, pl. 6, figs 23–28; Hirase 1907: 40; 1941: 94, pl. 121, fig. 16; Hubendick 1945: 29; Kuroda & Habe 1952: 86; Azuma 1960: 62; Kuroda 1960: 43; Baker 1964: 159; Shikama 1964: 6; Habe & Igarashi 1967: 28; Galindo 1977: 416 (as "*sinus*"); Christiaens 1980a: 79; Smith 1981: 9; Inaba 1983: 145; Trew 1983: 7; Je 1989: 29; Morton & Morton 1983: 298, pl. 1K; Higo *et al.* 2001: 142, fig. G4977; Hylleberg & Kilburn 2003: 133; Chim & Tan 2009: 270; White & Dayrat 2012: 67, Dayrat *et al.* 2014: 269, fig. 5H.

Siphonaria (*Siphonaria*) *sirius*—Hubendick 1946: 50, pl. 3, figs 24–27.

Siphonaria (*Mestosiphon*) *sirius*—Habe & Kikuchi 1960: 60; Kira 1962: 200–201, text-fig, pl. 69, figs 12a, b; Habe 1971: 15, pl. 4, fig. 12.

Anthosiphonaria sirius—Kuroda *et al.* 1971: 483, pl. 64, fig. 9; Christiaens 1980a: 79; Inaba 1983: 145; Habe *et al.* 1986: 23; Je 1989: 29; Fukuda *et al.* 1992: 76, pl. 23, fig. 361a, b.

Siphonaria laciniosa forma *sirius*—Christiaens 1980a: 79.

Siphonaria laciniosa—Springsteen & Leobrera 1986: 285, pl. 81, fig. 19 (not *S. laciniosa* (Linneaus, 1758)).

Siphonaria (*Anthosiphonaria*) *sirius*—Noseworthy *et al.* 2007: 90.

Material examined. *Type material.* Lectotype of *Siphonaria sirius* Pilsbry, 1894a from Sagami and Kashiurazaki, Boshiu, Japan; coll. Fredrick Stearns (ANSP 70720a, Fig. 43E). Six paralectotypes same data as lectotype (ANSP 70720). Seven paralectotypes of *Siphonaria sirius* Pilsbry, 1904 from Sagami Bay (AM C.117637).

Other, non-type material. **Japan, Honshu:** Point S of Chitose Beach, Boso Peninsula 34°59.240'N, 139°58.304'E, JP02-2 (AM C.585395 10p, C.584940 p [M501, SK320], C.584941p [M502, SK321], p [SK336]). **China, Hong Kong:** Cape D'Aguilar 22°12.28'N, 114°15.38'E (ZRC 2001-1768 21p, ZRC.MOL.24902 p [SK176]). **Philippines:** Mactan, Cebu 10°18.840'N, 124°01.707'E PHS04-1 (AM C.585339 p). **Singapore:** Lazarus Island 01°18.643'N, 103°57.077'E SI04-2 (AM C.585227 p [M339]); East Coast Park, seawall,

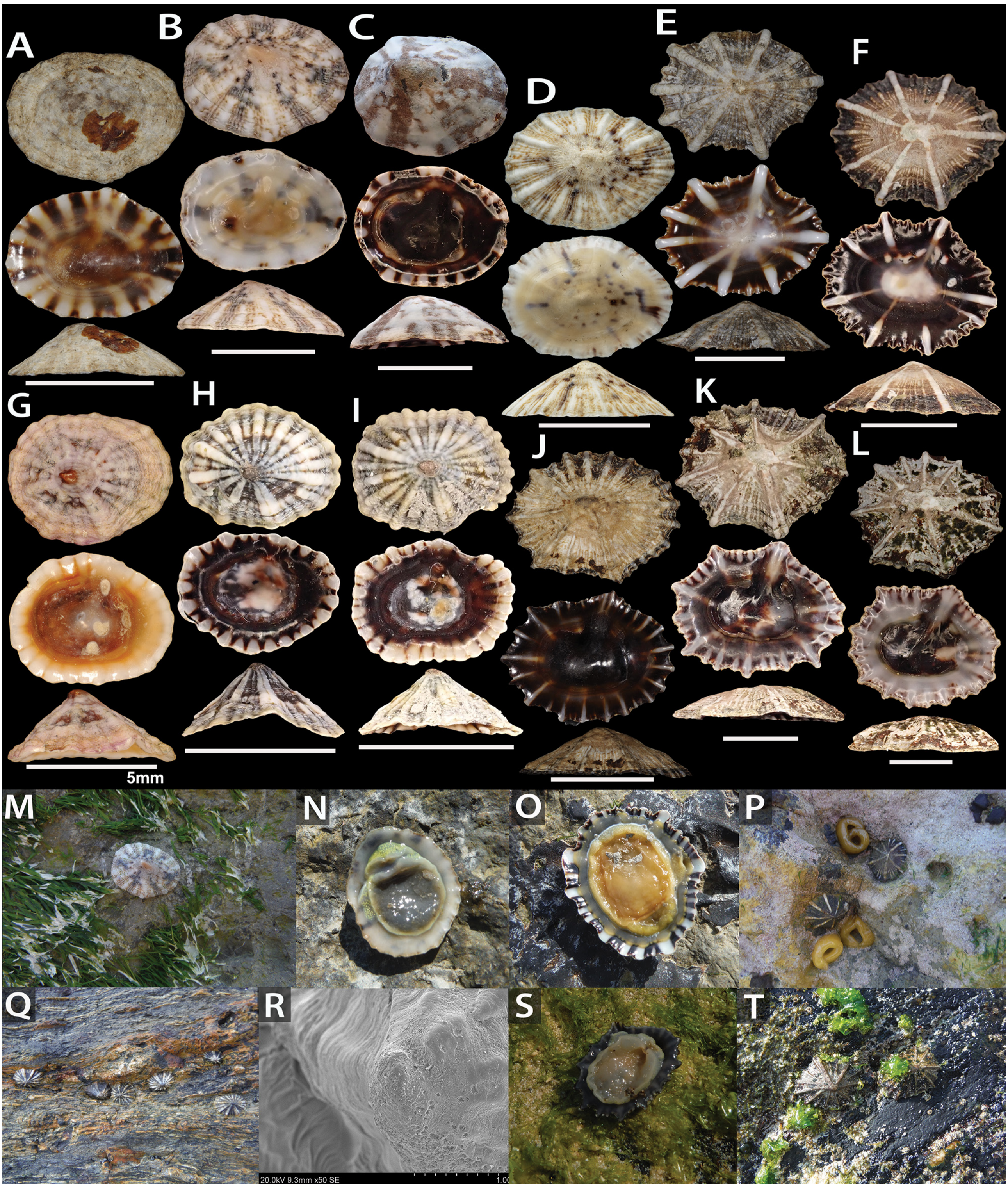

FIGURE 43. Shells of *S. acmaeoides*, *S. sirius*, *S. rucuana* and *S. subatra*. **A–D, M–N.** *S. acmaeoides*. **A.** Lectotype ANSP 70726a. **B–C.** Honshu, Boso Peninsula, TS. **B.** AM C.584936 [M496, SK315]. **C.** AM C.585918 [SK335]. **D.** Holotype of *S. acmaeoides paulae* NHMUK 1977171. **M.** Japan, *in situ*. **N.** Japan, animal. **E–F, O–P.** *S. sirius*. **E.** Lectotype ANSP 70720a. **F.** Japan, Boso Peninsula, AM C.584941 [M502]. **O.** Japan, animal. **P.** Japan, *in situ*. **G–I, Q–R.** *S. rucuana*. **G.** Lectotype ANSP 86131a. **H–I.** Okinawa, Tancha Bay, TS. **H.** AM C.584915 [M493, SK312]. **I.** AM C.584918 [M492, SK311]. **Q.** Okinawa, *in situ*. **R.** Protoconch, AM C.584912 [SK409]. **J–L, S–T.** *S. subatra*. **J.** Lectotype ANSP 86132a. **K.** AM C.584933 [M498]. **L.** AM C.584931 [M499]. **S.** Animal. **T.** *In situ*. Unlabelled scale bars = 10 mm.

01°18.643’N, 103°57.077’E SI01-2 (ZRC Moll. 9121, p). **Indonesia:** Pulau Panjang, Riau Islands 1°10.21’N, 104°18.905’E (ZRC EA-ZJ 09, 4p).

Taxonomic remarks. The description of Pilsbry (1894b: 9) does not contain an original type designation. Pilsbry (1895: 2, pl. 6, fig. 23–28) republished the original description with six figures and dimensions for a single specimen. Baker (1964: 159; ANSP 70720a) subsequently designated the lectotype, which matches the dimensions given in Pilsbry (1894a: 9) and the figures in Pilsbry (1895: 2, pl. 6, figs 23–24; Fig. 43E herein). A type was also figured in Higo *et al.* (2001: 142, fig. G4976). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 43F) and geographic series of additional specimens (Table S1).

The description of ‘*S. atra*’ in Reeve (1856: pl. 3, species 14) appears to be based on specimens of *S. sirius* and not *S. atra* (refer to taxonomic remarks under *S. atra*). Hubendick (1946: 50) listed ‘transitional’ forms between ‘*S. sirius* <> *S. subatra* <> *S. zanda*’, not explicitly linked to a specimen or locality. The figured specimen (Hubendick 1946: pl. 5, fig. 3, 4) is identified as a specimen of *S. sirius*. Je (1989: 29) incorrectly listed *S. subatra* as a synonym of *Anthosiphonaria sirius* (i.e., *S. sirius*). Christiaens (1980a: 79) considered *S. sirius* as one of three ‘forms’ of *S. laciniosa* in Hong Kong. He stated that the shell possesses ‘heavier ribbing than *atra*, with six or more solid white ribs’ and that the ‘siphon is formed by one rib’, which is consistent with features typical of *S. sirius* (Figs 43E, F).

External morphology (Fig. 43O). Foot wall, cephalic folds and pneumostomal lobe all evenly cream in colour, paler to foot edge, foot sole grey; mantle thin, translucent, wider than foot wall, weakly lobed with a thickened edge, white bands on mantle edge align with underside of ribs; irregular black blotches of pigmentation on foot wall and concentrated over cephalic lobes; two black ‘Eye’ spots prominent centrally on thickened cephalic lobes; pneumostome fold prominent with white subepithelial pustules.

Shell (Figs 43E–F; Table S9). Medium sized (max sl mean = 18.6 mm, SD = 8.97 mm, n = 9), elongate ovate; height medium; apex offset central sightly left, apical sides straight to weakly convex, protoconch direction homostrophic (n= 1), shell whorl dextral; growth striae prominent in bands, weak shades of radial banding may occur, shell thickness medium; rib count (mean = 41, SD = 3.9, n = 9), 9–10 primary ribs pale white, straight, broad, raised and protrude strongly (some > 1 mm) beyond shell lip to prominently scallop and corrugate the edge; 2–4 finer brown secondary ribs between primary ribs, interstices narrow, darker, single primary rib forms siphonal ridge. Interior shell margin dark brown to tan, white rays align on shell margin under primary/secondary ribs, siphonal groove distinct, same colour as shell edge, points to right anterior; spatula white, some specimens may be dark chocolate brown; ADM scar distinct, CMS straight, paler than shell lip; thickening of shell lip translucent, infills and reduces lip scalloping, spatula becomes whitened.

Reproductive system (Fig. 44D; n = 1). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned over back of BM and to side of RAM; AO prominent, broad bluntly pointed, joins to top of GA; ED relatively short, strongly twisted, very broad with MA on bend; EG small; single short broad looped flagellum F1 appears as an extension of ED at join with EG; AO, GA and ED all muscular white tissue; BD and CD with opposing connections (bulbous at CD) join into GA between ED, AO and GP; BD longer and narrower than CD with a prominent distal loop without an MA, and looped immediately before BC, both ducts smooth and pass together through RAM connecting into folds of MG (BD above CD); BC embedded in MG, translucent test, large and bulbous; HD brownish long coiled links AG to a small elongated narrow brownish coarsely granulated HG; MG and AG small folded soft white tissue; SV embedded within AG, AG larger than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 44E). Body cylindrical, thread-like (length = 15.21 mm, n = 1), test thin, smooth, featureless, translucent; head tip tapered bluntly rounded, containing a white gelatinous core, tapers to a thin flagellum and tip; head shorter thicker than flagellum (head length = 7.17 mm; 47% of SPM length; flagellum length = 8.41 mm; head width = 142 µm; flagellum width = 31 µm). 4 SPM tightly coiled in brown gelatinous mass in BC of one specimen.

Radula. Dentition formula 40:1:40 (Hubendick 1946: 51).

Comparative remarks. In our molecular tree (Figs 1, 2), *S. sirius* (*atra* group, unit 31) is the sister species of an unidentified species from Tonga (Dayrat *et al.* 2014, unit 30). Both differ from each other by COI distances of ≥ 12.5%. *Siphonaria sirius* differs from other species by COI distances of ≥ 22% (Table S9). Throughout its range, *S. sirius* has been found in sympatry with nine congeners. Two congeners are sympatric in Honshu: For comparison with *S. japonica* refer to comparative remarks under that species. *Siphonaria acmaeoides* has a paler, narrower ribbed shell with dual ribs forming the siphonal ridge, a weaker scalloped shell edge, a reduced AO, shorter wider ED and F1, smaller BC, longer unlooped BD, and a smaller, drop-shaped SPM. Three congeners are sympatric in Cebu, Philippines: For comparisons with *S. bifurcata* and *S. sipho* refer to comparative remarks under these species. *Siphonaria caubianensis* **sp. nov.** has a dual-ribbed siphonal ridge, a more posterior and left offset apex, stronger scalloped shell edge, a larger AO, a smaller BC, and no distal loop. Two congeners are sympatric in Singapore: For comparison with *S. viridis* refer to comparative remarks under that species. *Siphonaria alba* has a dual-ribbed siphonal ridge with a less flared end, a weaker scalloped shell edge, whiter interior colouration, a larger AO and a shorter F1. *Siphonaria radians*, sympatric on Riau Islands, S China Sea, has a weaker scalloped shell edge, a dual-ribbed siphonal ridge, a larger wider and more pointed AO, and a smaller BC. *Siphonaria camura*

sp. nov., sympatric in Hong Kong, differs by having a smaller, taller shell with a dual-ribbed siphonal ridge, a shorter, wider ED, a larger, bulbous BC, and barbed SPM.

Specimens from Japan figured in Hubendick (1946: pl. 3, figs 24–27), Kira (1962: 201, pl. 69, fig. 12a, b), Habe (1971: pl. 4, fig. 12), Kuroda *et al.* (1971: pl. 64, fig. 9), Fukuda *et al.* (1992: pl. 23, fig. 361a, b), and Dayrat *et al.* (2014: fig. 5H) are morphologically consistent with *S. sirius* as delineated herein. By contrast, a specimen from Korea figured as '*S. sirius*' in Yoo (1976: 89, pl. 19, fig. 5) is a misidentification. A figured specimen from Palawan identified as '*S. laciniosa*' in Springsteen & Leobrera (1986: pl. 81, fig. 19) is *S. sirius* (single rib forming siphonal ridge); the associated ventral figure appears to be a different specimen (i.e., not matching the scalloped edge; with a multi-rib siphonal ridge; possibly a specimen of *S. alba*); the stated synonymy of *S. atrata* (sic *atra*) with *S. laciniosa* is incorrect. The figured specimen of *S. sirius* in Dharma (1992: pl. 17, fig. 2) from Indonesia is a misidentification and likely a specimen of *S. alba* based on shell features and distribution.

Distribution and habitat. Known from Japan, China, Philippines, Vietnam, Singapore and Sumatra (Fig. 45). In this study found in sheltered positions on moderately exposed and exposed rocky shores, mid to upper littoral level, often associated with *Lithothamium* (Fig. 43P).

Siphonaria subatra **Pilsbry, 1904**

(Figs 43J–L, S–T, 44H–I)

Siphonaria subatra Pilsbry 1904: 36, pl. 6, figs 60, 60a, b (type locality: Chichijima, Ogasawara [Japan]).—Hirase 1907: 40; Abe 1940: 59; Hirase 1941: 94, pl. 121, fig. 13; Hubendick 1945: 29; Kuroda & Habe 1952: 86; Oyama *et al.* 1954: 19; Kuroda 1960: 43; Baker 1964: 159; Habe & Igarashi 1967: 28; Morrison 1972: 57; Galindo 1977: 416; Fukuda 1994: 50, 808, pl. 42; Higo *et al.* 2001: 142, fig. G4978; Hylleberg & Kilburn 2003: 133; Poppe 2010: 444; White & Dayrat 2012: 68.

Siphonaria (*Siphonaria*) *subatra*—Hubendick 1946: 51, pl. 3, figs 32–35.

Siphonaria atra—Lischke 1871: 105; Boettger 1892: 168; Pilsbry 1895: 5; Abe 1940: 59; Hirase 1941: 94, pl. 121, fig. 17; Kuroda 1941: 137; Kuroda & Habe 1952: 86; Oyama *et al.* 1954: 14; Habe 1964: 145, pl. 44, fig.17; Hirano & Inaba 1980; Fukuda 1994: 50, 804 (not *S. atra* Quoy & Gaimard, 1833).

Siphonaria (*Siphonaria*) *laciniosa* forma *subatra*—Christiaens 1980a: 79.

Mestosiphon atra—Habe & Kohno 1980: 23 (not *S. atra* Quoy & Gaimard, 1833)

Siphonaria (*Mestasiphon*) *subatra*—Kira 1962: 201, pl. 69, figs 10a, b; Habe & Kosuge 1966: 113, pl. 4, fig. 22; Okutani 1982: 32.

Siphonaria unit 38—Dayrat *et al.* 2014: 268, fig. 5 R.

Material examined. *Type material*. Lectotype of *Siphonaria subatra* Pilsbry, 1904 from Chichijima, Ogasawara [Japan] (ANSP 86132a, Fig. 43J). Two paralectotypes same data as lectotype (ANSP 86132).

Other, non-type material. **Japan, Okinawa:** Tancha Bay, 26°27.897'N, 127°49.131'E, JP01-5 (AM C.584932 1p, C.584932 p [SK332]), Tancha Bay, rocky point 26°27.941'N, 127°49.194'E, JP01-6 (AM C.585663 6p, C.584930 p [SK349], C.584931 p [M499, SK318], C.584933 p [M498, SK317]).

Taxonomic remarks. The original description is evidently based on a series of specimens (Pilsbry, 1904: 36, pl. 6, figs 61, 61a–b). Baker (1964: 159) subsequently designated the lectotype. Dimensions of the lectotype (Fig. 43J) match the original figure in Pilsbry (1904: 36) reasonably well. The lectotype has also been figured by Higo *et al.* (2001: 142, fig. G4978a). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 43K, L, Table S1). Hubendick (1946: 50) listed a 'transitional form'of '*S. subatra* <> *S. atra*' without mentioning the locality. However, the figured specimen (Hubendick 1946: 50, pl. 5, figs 5–6) is here identified as a specimen of *S. subatra*. Morrison (1972: 56–58) treated *S. subatra* as a synonym of *S. laciniosa* based on similarity in shell form and 'common reproductive development'. Christiaens (1980b: 79) treated *S. subatra* as a variety of *S. laciniosa* based on specimens from Ping Chau, Hong Kong. These samples indeed correspond to shell characteristics considered herein as typical of *S. subatra* (i.e., siphon ridge formed by 3–4 'coalescing' small ribs). Je (1989: 29) incorrectly listed *S. subatra* as a synonym of *Anthosiphonaria sirius* (= *S. sirius*).

External morphology (Fig. 43S). Foot wall, cephalic folds and pneumostomal lobe all evenly pale grey in colour with white subepithelial pustules; paler grey to foot edge, foot sole darker; mantle thin, translucent, wider than foot wall, weakly lobed without a thickened edge, pale band on mantle edge align with underside of ribs; no black pigmentation; two black 'Eye' spots prominent centrally on thickened cephalic lobes; pneumostome fold prominent.

Shell (Figs 43J–L; Table S9). Medium sized (max sl mean = 19.8 mm, SD = 3.3 mm, n = 7), ovate; height low; apex offset sightly posterior and central, apical sides convex, shell thickness thick; protoconch direction undetermined, shell whorl dextral; growth striae indistinct in bands; exterior uneven, dark brown to pale tan, weak radial colour banding, protoconch area pale, central band darker and shell edge dark brown; rib count (mean = 51.4, SD = 8.0, n = 7), primary rib ridges pale, narrow, ribs slightly bent, increasingly raised and strongly protrude beyond shell lip (often > 1mm) to unevenly scallop and corrugate the edge; 3–5 finer secondary ribs between primary ribs, rib interstices darker; siphonal ridge formed by closely paired primary ribs protrudes greatest. Interior shell margin dark chocolate brown to blue/grey, uneven blue/grey rays on shell margin aligned under primary ribs, siphonal groove prominent, often same colour as shell margin; spatula mottled dark chocolate to tan brown; ADM scar distinct, CMS convex, darker than shell lip;

thickening of shell lip common, overcoats brown markings on shell margin with blue/grey, infills and reduces lip scalloping.

Reproductive system (Fig. 44H; n = 3). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned between BM and RAM; AO prominent, large, reasonably long, broad bluntly pointed, joins at top of smallish GA; ED elongated, narrow, twisted; EG medium with folds, single bent thickish flagellum F1 appears as an extension of ED at join with EG; AO, GA and ED all muscular white tissue; BD and CD elongated, with opposing connections join into GA close to ED and AO; BD longer and narrower than CD with a prominent distal coiling with an MA on bend attaching to inner foot wall, CD broadens to MG end, BD smooth, both ducts pass together through outer side of RAM (BD above CD) and bent before connecting into folds of MG; BC small, prominent with internal purple gel, embedded in MG, translucent test, medium and bulbous; coiled HD with brown markings links AG at lower end of a block-like elongated yellowish finely granulated HG; MG and AG soft white folded tissue; SV embedded within AG, AG larger than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 44I). Body cylindrical, thread-like, test thin, translucent, smooth, featureless (length = 9.17 mm, head length = 7.85 mm, n = 1, 86% of SMP length, AL = 16 mm; head tip tapered bluntly rounded, section containing a white core, tapers to a thin short flagellum; two SPM tightly folded in brown gelatinous mass in BC of one specimen.

Radula. Dentition formula 34:1:34 (Hubendick 1946: 51).

Comparative remarks. In our phylogeny (Figs 1, 2), *S. subatra* (*atra* group, unit 38) is the sister species of *S. tenebrae* **sp. nov.** (unit 92) from CI. Both species combined from the sister lineage of *S. vudaensis* **sp. nov.** (unit 37) from Fiji. *Siphonaria subatra* differs from *S. tenebrae* by COI distances of ≥ 15.1% and from *S. vudaensis* by distances of ≥ 13.3% (Table S3). *Siphonaria subatra* has been found in sympatry with three congeners in Okinawa. *Siphonaria rucuana* has a smaller, taller, shell with stronger ribbing and weaker edge scalloping, a larger, bulbous, blunt AO, and a longer BC. *Siphonaria camura* **sp. nov.** has a smaller, taller, more fragile shell with a less scalloped edge, larger, bulbous BC, BD without a distal loop, and a barbed SPM. *Siphonaria tanchaensis* **sp. nov.** has a larger, taller, paler shell with greater edge scalloping, patterned exterior, and a smaller AO and BC. For comparison with *S. sipho* refer to comparative remarks under that species. *Siphonaria subatra* exhibits a similar shell morphology to other species in the *atra* group. However, the extended projection of the multi rib formed siphonal ridge beyond shell edge is a major difference. A shell figured as '*S. atra*' from Japan in Hirase (1941: pl. 121, fig. 17) corresponds well with characteristics typical of *S. subatra*. It is well outside the known distribution of this species. Specimens depicted as '*S. subatra*' in Hubendick (1946: pl. 3, figs 32–35) are of two different species; figs 32, 35 from 'Japan' are specimens of *S. subatra* and figs 33, 34 from Mindanao and Java Sea are likely specimens of *S. alba*. Figured specimens in Kira (1962: pl. 69, figs 10a, b) from Amami Islands as well as from Okinawa (*atra* group, unit 38) in Dayrat *et al.* (2014: fig. 5R, UF351784) exhibit features typical of *S. subatra.*

Distribution and habitat. Recorded from Okinawa, Japan (Fig. 45). In this study, found on exposed rocky shores at sheltered positions across the mid-littoral level (43T).

Siphonaria rucuana Pilsbry, 1904

(Figs 43G–I, Q–R, 44F–G)

Siphonaria rucuana Pilsbry 1904: 36, pl. 6, figs 61, 61a, b (type locality: Riukiu Island [Ryukyu Islands, Japan]).—Hirase 1907: 40; 1941: 94, pl. 121, fig. 14; Hubendick 1946: 62; Kuroda & Habe 1952: 86; Oyama *et al.* 1954: 14; Habe 1962: 96, pl. 44, fig. 16; Baker 1964: 159; Christiaens 1980a: 81; Fukuda 1994: 50, 806; Higo *et al.* 2001: 142, fig. G4973; White & Dayrat 2012: 67.

Siphonaria zebra—Kuroda 1941: 137, pl. 3, figs 49–50 (not *S. zebra* Reeve, 1856).

Siphonaria laciniosa rucuana—Habe 1964: 144, pl. 44, fig. 16.

Siphonaria radians—Habe & Kosuge 1966: 113, pl. 42, fig. 24, 25 (not *S. radians* H. Adams & A. Adams, 1855).

Siphonaria (*Siphonaria*) *rucuana*—Higo 1973: 287; Noseworthy *et al.* 2007: 90.

Material examined. *Type material.* Lectotype of *Siphonaria rucuana* Pilsbry, 1904 from 'Riukiu Island' [Japan] (ANSP 86131a, Fig. 43G). Three paralectotypes, same data as lectotype (ANSP 86131).

Other, non-type material. **Japan, Okinawa:** Tancha Bay, 26°27.897'N, 127°49.131'E, JP01-5 (AM C.585662 4p,C.584912 p [SK409, protoconch H9], C.584915 p [M493, SK312]; C.584916 p [SK355]; C.584917 p [SK377], C.584919 p [SK345], C.585082 p [SK406], C.585914 p [SK354], C.585915 p [SK383], rocky point, 26°27.941'N, 127°49.194'E, JP01-6 (AM C.585627 6p, C.585917 p [M397], C.584918 p [M492, SK311]).

Taxonomic remarks. The original description of Pilsbry (1904: 36, pl. 6, figs 60a–b) is based on a series of specimens. Baker (1964: 159) subsequently designated the lectotype. The dimensions of the lectotype (Fig. 43G) match the original dimensions in Pilsbry (1904: 36) reasonably well. The lectotype has also been figured by Higo *et al.* (2001: 142, fig. G4973). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 43H–I, Table S1). '*Siphonaria zebra* (?)' figured in Kuroda (1941: 137, pl. 3, figs 40, 50) is a specimen of *S. rucuana*. The 'uncertain' records of '*S. rucuana'* in Hubendick (1955: 7) are likely misidentified specimens of *S. denticulata* (from Etty Bay, Qld, MV F15040) and S. *viridis* (from Cape Edgecumbe [sic], Bowen, Qld, MV F15041). Habe (1962: 96, pl. 44, fig. 16) treated *S. rucuana* as an accepted species;

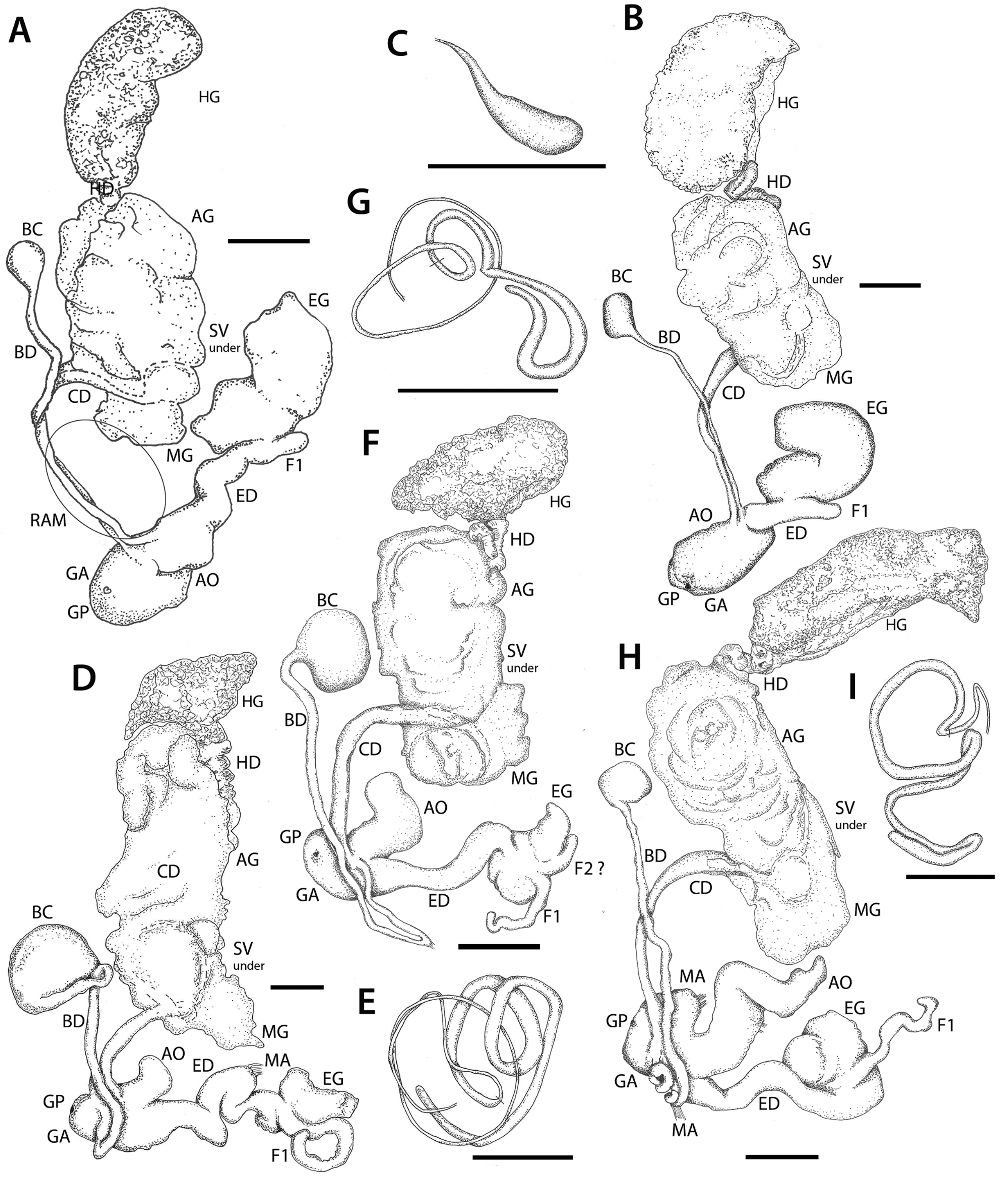

FIGURE 44. Reproductive morphology of *S. acmaeoides*, *S. sirius*, *S. rucuana* and *S. subatra*. **A–C.** Honshu, Boso Peninsula, TS. **A.** AM C.584936 [M496, SK315]. **B–C.** AM C.585918 [SK335]. **D–E.** *S. sirius,* Hong Kong, ZRC.MOL.24902 [SK176]. **F–G.** *S. rucuana,* Okinawa, Tancha Bay, TS. **F.** AM C.584918 [M492, SK311]. **G.** AM C.584917 [SK377]. **H–I.** *S. subatra.* **H.** AM C.584933 [M498, SK317]. **I.** AM C.584931 [M499, SK318]. Scale bars = 1 mm.

however, Habe (1964: 144, pl. 44, fig. 16) treated it as a subspecies of *S. laciniosa*. This later treatment is not accepted.

External morphology. Foot sole pale brown, paler to foot edge; foot wall, mantle, cephalic folds and pneumostomal lobe all evenly dark yellowish; mantle thin, translucent, weakly lobed with a thickened dark yellowish banded edge; faint irregular black blotches of pigmentation on foot wall and cephalic lobes; pneumostome fold long between right ADMs and within mantle; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two centrally touching unpigmented cephalic folds.

Shell (Figs 43G–I, R; Table S9). Small sized (max sl me = 9.2 mm SD = 0.7 mm, n = 10); ovate to elongate, height medium; apex offset central to weakly posterior; protoconch direction weakly heterostrophic (n = 2; Fig. 43R), shell whorl dextral; apical sides convex, posterior weakly concave to straight; radial colour banding, protoconch area dark brown, centre pale grey, darker to uneven shell edge; growth lines distinct; rib count (mean = 28, SD = 3.1, n = 10) primary ribs whitish grey, straight, rib interstices dark brown/black; rib ridges rounded, broader to and weakly extend beyond shell lip, paired primary ribs form siphonal ridge, 0–1 finer grey secondary ribs between primary ribs, number greater either side of siphonal ridge. Interior shell lip weakly corrugated, with white rays aligning under primary ribs, and narrower dark brown/black markings under rib interstices; ADM scar prominent, CMS straight to weakly convex; shell margin and siphonal groove evenly dark chocolate brown, spatula white/grey; thickening or whitening of inner shell lip and spatula not observed.

Reproductive system (Fig. 44F; n = 2). Positioned within coelom under the respiratory cavity, occupies the entire right side of coelom, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned over back of BM; GA prominent with singular GP through foot wall; AO medium, broad, blunt, joined to upper GA alongside ED; ED elongated, broad, slightly bent (no MA), joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG soft whitish tissue, slightly folded, joins ED; single broad flagellum (F1) with possible 2nd shorter flagellum; appears as a continuous extension of ED to EG, laid over BM; BD and CD connect together in opposing directions into GA between ED/AO joint and GP, both ducts short, straight, smooth, thickened, whitish, featureless, pass closely together through outer side of RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex medium; BD narrower than CD, straight looped, end of loop attached to inner foot wall; BC medium, spherical, thin translucent test, embedded in outer folds of AG/MG; HD short, thickened, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobbed; AG larger than HG, outer sides of both matches curvature of inner foot wall.

Spermatophore (Fig. 44G). Thread-like (length = 6.88 mm, n =1), translucent, test thin; head section bluntly rounded, cylindrical, containing a core white gelatinous mass, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless. Head section shorter wider than flagellum (head length = 2.74 mm, ~ 40% of SPM length; head width = 90 µm, flagellum width = 17 µm); 1 SPM in one BC (AM C.584917).

Comparative remarks. *Siphonaria rucuana* (*normalis* group, unit 83) differs from other species by COI distances of ≥ 24% (Table S6, Figs 1, 4). The species has been found in sympatry with four congeners on Okinawa. *Siphonaria camura* **sp. nov.** has a smaller, taller, paler, fragile shell with a more offset apex and prominent ribbing, a smaller BC and AO, and a barbed SPM. *Siphonaria tanchaensis* **sp. nov.** has a larger, paler shell, with a patterned exterior and greater edge scalloping, and a smaller BC and AO. For comparison with *S. sipho* and *S. subatra* refer to comparative remarks under these species. Specimens figured as '*Siphonaria radians'* in Habe & Kosuge (1966: pl. 42, figs 24, 25) are attributed herein to *S. rucuana*. *Siphonaria radians* has less raised, finer ribbing, and a less prominent siphonal ridge.

Distribution and habitat. Known only from Okinawa, Japan (Fig. 45). In this study, found on exposed rocky shores in sheltered positions (i.e., rock crevices and hollows; Fig. 43Q), mid to upper littoral level (amongst green algae).

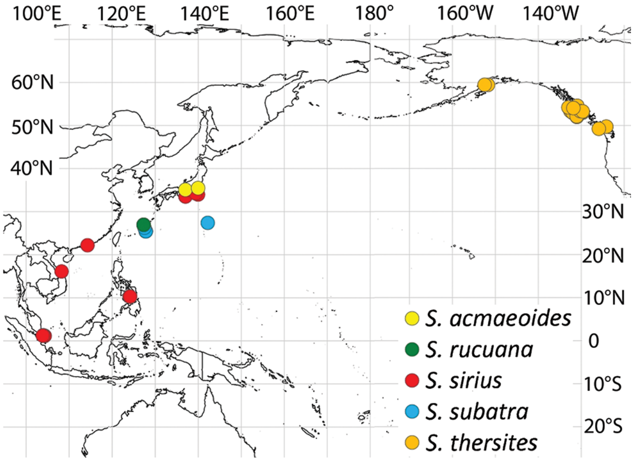

FIGURE 45. Known occurrence records of *S. thersites*, *S. acmaeoides*, *S. sirius*, *S. subatra* and *S. rucuana*

Siphonaria stowae **Verco, 1906**

(Figs 46A–C, M–O, 47A–B)

Siphonaria stowae Verco 1906: 223–224, pl. 8, figs 3–8 (type locality: Pandolowie [incorrect spelling of Pondalowie] Bay, Spencers Gulf; SA).—Gatliff 1907: 35; Verco 1907: 105; 1912: 205; Hedley 1915: 752; Hubendick 1945: 70; Cotton 1959: 411; Galindo 1977: 416; White & Dayrat 2012: 68.

Kerguelenia stowae—Hedley,1916b: 215; 1917b: M96; May 1921: 89; Gatliff & Gabriel 1922: 156; May 1922: 156; 1923: 87, pl. 41, fig. 5.

Pugillaria stowae—Iredale 1924: 276; Cotton & Godfrey 1932: 155, pl. 3, fig. 5; Macpherson & Chapple 1951: 142; Cotton 1959: 411; Macpherson & Gabriel 1962: 264; Macpherson 1966: 256; Grove *et al.* 2006: 60; Jenkins 2018: 276, figs 2A–V, 3A, B, 4A–D.

Pugillaria stowae comita Iredale 1924: 183 (type locality: Twofold Bay, NSW).—Iredale & McMichael 1962: 82; White & Dayrat 2012: 61; Jenkins 2018: 276, figs 2J–O.

Siphonaria (*Pugillaria*) *stowae*—Thiele 1931: 472; Morrison 1963: 7.

Siphonaria (*Kerguelenia*) *stowae*—Hubendick 1945: 59, 63, 70.

Siphonaria (*Liriola*) *stowae*—Hubendick 1946: 26, 28, 29.

Kerguelenella stewartiana—Hubendick 1946: 28 (not *K. stewartiana* Powell, 1946).

Kerguelenella stowae—Burn & Bell 1976: 234.

Siphonaria (*Kerguelenella*) *stowae*—Christiaens 1980a: 80.
Pugillaria comita—Grove *et al*. 2006: 60.

Material examined. *Type material.* Lectotype of *Siphonaria stowae* (SAM D.33484; figured in Verco 1906: figs 3–5; Jenkins, 2018: fig. 2A–C). Eight paralectotypes of *Siphonaria stowae* from Pandolowie [sic Pondalowie] Bay, Spencers Gulf], SA (SAM D.13590, lot labelled as 'holotype', largest figured in Jenkins 2018: fig. 2D–F).

Three syntypes of *Pugillaria stowae comita* from Twofold Bay, NSW, [Australia] coll. R. Bell [undated], T. Iredale coll. (AM C.265927, two figured in Jenkins 2018: fig. 2J–O).

Other, non-type material. **Australia, NSW:** Woody Head, near Iluka, 29°22.0′S, 153°22.50′E (AM C.116737 6d); Clarence River, 29°25.50′S, 153°21.00′E (AM C.398326 2d), 29°25′S, 153°21′E (AM C.265949 2d); Woolgoolga, 30°06.70′S, 153°12.300′E (AM C.398328 d); Port Stephens, between beacons, 32°42.397′S, 152°11.502′E (AM C.265967 d); North Fingal Bay, 32°44.750′S, 152°10.500′E (AM C.398325 6d); Fingal Bay, 32°45.0′S, 152°10.500′E (AM C.398324 d); Patonga, Broken Bay, 33°33.111′S, 151°16.570′E (AM C.265961 4d); Collaroy Beach, N of Sydney, 33°44.0′S, 151°18.0′E (AM C.398336 d), 33°43.700′S, 151°18.0′E (AM C.398335 d); Manly Beach, 33°47.817′S, 151°17.368′E (AM C.265964 d); Ocean Beach, Manly, 33°47.853′S, 151°17.398′E (AM C.265970 3d); Middle Harbour, between Grotto and Dobroyd Points, 33°48.897′S, 151°16.085′E (AM C.265966 d); Balmoral Beach, 33°49.700′S, 151°15.030′E (AM C.030179 2d); Off Chinamans Beach, 33°48.870′S, 151°14.965′E (AM C.265976 2d); Sydney Harbour, Quarantine Bay, 33°50.863′S, 151°14.438′E (AM C.265973 d); Bradleys Head, 33°51.300′S, 151°14.700′E (AM C.398327 2d); Sydney, Little Coogee Bay, 33°55.300′S, 151°15.600′E (AM C.398322 d); Botany Bay, Kurnell, 34°0.580′S, 151°12.380′E (AM C.398332 2d); Port Hacking, S of Sydney, Cronulla, Gunnamatta Bay, 34°3.950′S, 151°8.550′E (AM C.398330 d); SW end Gunnamatta Bay, 34°4.300′S, 151°8.700′E (AM C.398334 d); Sussex Haven and Wreck Bay, 35°10.203′S, 150°41.293′E (AM C.22532 d; AM C.265932 d); Off Montague Island, Narooma, 36°14.347′S, 150°13.015′E (AM C.265974 4d); Twofold Bay, Murrumbulga Point, 37°04.702′S, 149°53.103′E (AM C.150582 p). **Vic:** 1.6 km N of Gabo Island, 37°34.0′S, 149°56.0′E (AM C.398323, 1 d); Mallacoota, 37°34.0′S, 149°46.600′E (AM C.50394 2d); Bear Gully, Waratah Bay, 38°20′S, 146°00′E (MV F169206 1p); Inverloch, 38°38′S, 145°43′E (MV F161257 2p); San Remo, Western Port, 38°32.0′S, 145°23.0′E, V07-1 (AM C.030683 2d, C.585616 p [SK393]), 38°31.489'S, 145°21.858'E (AM C.585583 3p); Flinders, Western Port Bay, 38°29.0′S, 145°1.0′E (AM C.398366 d, AM C.265936 d); 'Clondrisse' E of Cape Schanck, 38°29.583′S, 144°53.654′E (MV F193073 p); Port Phillip Bay, 38°09′S, 144°46′E (MV F185072 2p); Cheviot Beach, Point Nepean, 38°18′S, 144°40′E (F.87801 p); Andersons Point, Portland, 38°19.967′S, 141°36.604′E (MV F126944 p). **Tas:** King Island: Gulchway, S of Surprise Bay, 40°08.023′S, 143°54.205′E (MV F193075 p); Fraser Beach, Sea Elephant Bay, 39°54.410′S, 144°06.584′E (AM C.265930 d); West Head, Greens Beach, Tamar River mouth, 41°5.0′S, 146°45.0′E (AM C.398367, 1 d); Park Beach Dodges Ferry 42°51.716'S, 147°36.665'E (AM C.585469 11p, C.584835 p [M109, SK018], C.584914 p [SK216], C.585264 p [SK007], C.585265 p [M110]). **SA:** Guichen Bay, near Cape Dombey, 37°7.233′S, 139°45.967′E (SAM D.33486 3d); Stokes Bay, N coast of Kangaroo Island, 35°37′S, 137°12′E (AM C.265968 2d); Normanville, S of Adelaide, 35°26.800′S, 138°18.500′E (AM C.398369 d); Adelaide, Glenelg Beach, S of Adelaide, 34°58.0′S, 138°32.0′E (AM C.265963 d, AM C.398370 d); Henley, 34°55.430′S, 138°29.595′E (AM C.265962 2d); Grange, 34°58.215′S, 138°30.471′E (SAM D.33490 4d); Spencer Gulf, Eyre Peninsula, Tumby Bay, 34°22.0′S, 136°8.0′E (AM C.398372,1 d); Arno Bay, 33°56.0′S, 136°35.0′E (AM C.398368 10+d); Pondalowie Bay, 35°13.989'S, 136°49.892'E (AM C.585492 p); Near Salmon Point, Elliston Bay, 33°39.0′S, 134°53.0′E (AM C.265905 1d); Sceale (sic Sceales) Bay, Cape Blanche, 33°00.237′S, 134°11.502′E (SAM D.33485 11d); Franklin Islands, Investigator Group, 32°26.450′S, 133°39.735′E (SAM D.33489 3d); Point Sinclair, 32°6.0′S, 132°59.0′E (AM C.398371 d). **WA:** Gnarabup Beach, S of Margaret River, 34°1.0′S, 114°59.0′E (AM C.398365 d); Kilcarnup, N side Margaret River, 33°57.0′S, 114°59.0′E (AM C.398360 3d); Ellensbrook (S Cowaramup), near Margaret River mouth, 33°53.0′S, 114°59.0′E (AM C.398361 d, AM C.265965 9d, AM C.398363 d, AM C.398364 9d); N side Cape Naturaliste Lighthouse, 33°32.752′S, 115°0.418′E (AM C.265975 d); Bunbury, 33°18.750′S, 115°39.061′E (SAM D.33488 2d); Point Peron, 48 km S of Perth, 32°16.0′S, 115°41.0′E (AM C.398358 d, AM C.398357 3d); Garden Island, S of Perth, 32°14.0′S, 115°41.0′E (AM C.398359 11d); Cockburn Sound, Jervoise Groyne, 1.6 km S of Woodmans Point, 32°9.0′S, 115°46.0′E (AM C.398362 d); Rottnest Island, 32°00.683′S, 115°30.993′E (SAM D.33492 7d); Geraldton, 28°46.143′S, 114°36.283′E (SAM D.33491 d).

Taxonomic remarks. The lectotype has been designated by Jenkins (2018: 3). Examinations of freshy collected topotypic specimens herein (Fig 46A–C) validate the identity of *S. stowae* and confirm that *S. stowae comita* is its junior synonym. Hedley (1916a: 220) transferred *S. stowae* to the genus *Kerguelenia*. Refer to Jenkins (2018: 276) for comments on type specimens, including labels. The present description is based on the re-description of this species in Jenkins (2018: 276) and is expanded upon for completeness and taxonomic consistency.

External morphology (Fig. 46O). Foot wall, mantle, pneumostomal lobe and cephalic folds pale grey to cream, foot sole darker grey paling to foot edge; mantle narrow, thin, translucent with thickened unlobed fringe, even pigmented shading only at foot wall mantle join; pneumostomal lobe on right side within mantle, covering inconspicuous anus in foot wall; two black 'Eye' spots prominent centrally on touching cephalic folds; genital pore inconspicuous, positioned in foot wall posterior to right cephalic fold.

Shell (Figs 46A–C, M; Table S9). Small sized (max sl

< 10 mm), ovate, cap-like, arched dorsally, height medium to tall; apex lower than shell height, dorsally aligned close to or over posterior edge (Jenkins 2018: fig. 2), laterally offset 10–15° to left of transverse centre line (cl); exterior white to cream with irregular red-brown apical striations and blotches, coloration and patterning variable; Shell whorl dextral, protoconch direction homostrophic (n=1; Jenkins 2018: fig. 2V); posterior margin weakly concave, other margins convex (Jenkins 2018: fig. 2); in larger specimens (sl > 8 mm), lip thickened, opaque, ribs prominent, irregularly spaced, flattened, weakly corrugated, often distorted by prominent growth striae (Jenkins 2018: fig. 2F, M); rib interstices are irregular and red-brownish denoted by coloured apically aligned bands or streaks (Jenkins 2018: fig. 2A–C); growth striae prominent and uneven; in small specimens, shell translucent, exterior smooth and polished, ribs indistinct, lip thin, unscalloped and translucent to edge, red-brown exterior of irregular rib interstices shows through to interior between ADM scar and lip (Jenkins 2018: fig. 2H, Q); interior smooth, cream coloured, spatula smooth and white; ADM scar indistinct, weakly indented, posterior of scar shaded red-brown (Jenkins 2018: fig. 2), cephalic ADM scar (cam) indistinct, straight to slightly convex; siphonal groove weakly indented.

Reproductive system (Fig. 47A; n=3). Predominantly located in posterior of coelom; HG granulated, HD and folds of AG situated to posterior under digestive gland and pallial cavity; a small rounded brownish BC and BD located behind pneumostomal opening and beside posterior RAM; BD narrow elongate; HG connected by several short thin translucent ducts; MG and AG with translucent folds; SV positioned to side of these folds; EG, ED and small bulbous GA are situated to right side of BM just behind RAM; two short thick flagellum present at join of ED and EG; outer layer of GA translucent whitish with white opaque central layer; BD passes through the RAM; a thickened coiled CD decreasing in diameter opens into GA; a single (monoaulic) small GP opens from GA through foot wall posterior to right cephalic fold and in front of right anterior RAM; BD and CD open separately into GA close to GP.

Spermatophore (Fig. 47B). Thread-like (length = 3.63 ± 1.06mm, n = 2), translucent, test thin; head section, tip bluntly rounded, evenly cylindrical, elongate, containing a white gelatinous mass; taper region into the filamentous transparent flagellum is short; both sections smooth, featureless. Head shorter and thicker than flagellum (head length = 1.46 ± 0.11 mm, ~ 41% of SMP length, head width = 120 ± 20 µm; flagellum width = 13 ± 15 µm). We found 7 SPM tightly coiled each in two bursas.

Radula (Jenkins 2018: fig. 4A–D). each transverse row has a single narrow central rachidian tooth flanked squarely by mirrored half rows of block-like lateral teeth (fig. 4A); tooth size in a single row decreases rapidly from the more solid (around 4× larger) innermost laterals to smaller outermost mid laterals, the gap between rows notably increases (fig. 4B, D); each half row has on average eight mid and eight outer lateral teeth; inner teeth interlock via forks and notches, centrals anterior dual-pronged fork, blunt posterior notch; laterals possess a single outward pointing basal prong and notch (fig. 4B); central tooth significantly lower and smaller than adjacent lateral teeth with single weakly-pointed mesocone, basal plate of similar length, narrower than adjacent laterals (fig. 4A); inner laterals (i.e., without ecto/endocones) uncommon, irregular (fig. 4A); mid lateral mesocones around half length of base, edge shallow 'U' shaped, bluntly bi-cuspidate (some weakly tricuspidate), tips of inner lateral mesocones often erode back of tooth in front; single ectocone increasing from almost no ectocone to very prominent ectocone almost width and half height of mesocone (figure 4B); outer lateral (fig. 4B) mesocone single cusped, ecto/endocones variably-shaped bluntly-pointed tooth bases progressively widen to outer ribbon edge; outside outer laterals (from tooth 13) possess additional endocone, ecto/endocones appear as separate cones, some almost as large as mesocones size, without an angle of separation from mesocone. Radula dentition agrees with original description (Verco 1906: 224) apart from having four fewer laterals per half row than Verco's formulae ('around 22'); and for the lack of evidence that the central tooth 'tends to be bilobed' (i.e., bi-cuspidate). Dentition formula 16:1:16 +/− 2 (n = 3; row count not assessed), 22:1:22 (Hubendick 1946: 29).

Comparative remarks. *Siphonaria stowae* (*atra* group, unit 52) is member of a subclade of Clade H containing the species *S. zelandica* (unit 26), *S. acmaeoides* (unit 91), and *S. restis* (unit 54) (Figs 1, 2). It differs from these species by COI distances of ≥ 17.5% (Table S4). Throughout the range of *S. stowae* we found ten congeners with partly sympatric distributions. Four species are sympatric in south-eastern Australia. *Siphonaria emergens* has a smaller, mottled orange/brown shell with less edge scalloping, *S. pravitas* **sp. nov.** has a larger, lower shell with stronger ribbing and edge scalloping, a more prominent siphonal ridge, a larger AO and BC, and a longer ED. *Siphonaria scabra* has a larger, taller shell with greater edge scalloping, a larger AO, longer ED, and a longer SPM. For comparison with *S. denticulata* refer to comparative remarks under that species. Five species have been found in sympatry in southern Australia: For comparisons with *S. diemenensis*, *S. funiculata*, *S. jeanae*, *S. tasmanica*, and *S. zelandica* refer to comparative remarks under these species. One species occurs in sympatry in south-western Australia: *Siphonaria restis* **sp. nov.** has a larger, lower shell with stronger raised ribbing and greater edge scalloping, a larger, bulbous, blunt AO, and a longer BC. The combined shell geometry, size and colouration of *S. stowae* is very distinctive and unlike any other siphonariid.

Distribution and habitat. Southern coasts of Australia, from Iluka, northern NSW, through Vic, Tas, SA to Geraldton, WA (Fig. 48). Found in sheltered rocky intertidal platforms and rocky areas, often on rocks in tidal pools and associated with white *Lithothamnion* algae, at mid littoral level (Fig. 46N).

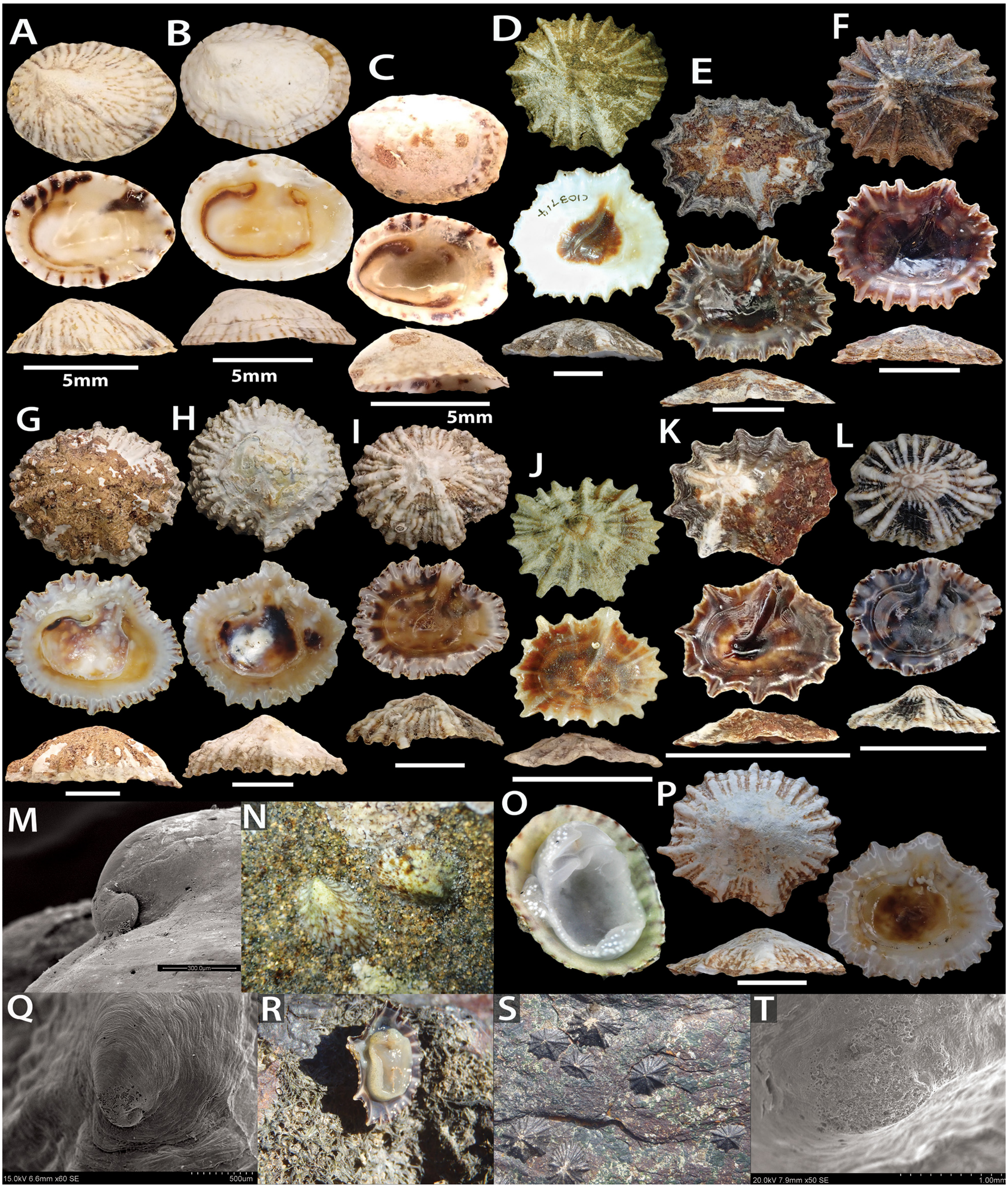

FIGURE 46. Shells of *S. stowae*, *S. opposita*, *S. madagascariensis* and *S. lentula*. **A–C, M–O.** *S. stowae*. **A–B.** Tas, Dodges Ferry. **A.** AM C.585265 [M110]. **B.** AM C.584835 [M109]. **C.** Vic, San Remo, AM C.585616 [SK393]. **M.** WA, Gnarabup Beach, AM C.398365, protoconch. **N.** Vic, *in situ*. **O.** Vic, animal. **D–F, R–T.** *S. opposita*. **D.** Lectotype of *Mallorisiphon oppositus* AM C.103714. **E.** Qld, Yeppoon, TS, AM C.585135 [M424]. **F.** Qld, Gladstone, AM C.585866 [M213]. **P.** Qld, Scarborough, AM C.585819 [M458, SK181]. **R.** Qld, animal. **S.** Qld, *in situ*. **T.** Protoconch, AM C.585126 [SK136]. **G–I.** *S. madagascariensis*, Madagascar, Itampolo. **G.** AM C.584818 [M267]. **H.** AM C.584959 [M272]. **I.** AM C.584957 [M270]. **J–L, Q.** *S. lentula*. **J.** Lectotype of *Mestosiphon lentulus* AM C.103712. **K.** LHI, TS, AM C.608189 [SK051]. **L, Q.** Protoconch, LHI, TS, AM C.546718 [SK053]. Unlabelled scale bars = 10 mm.

Siphonaria madagascariensis Odhner, 1919

(Figs 46G–I, 47H–I)

Siphonaria madagascariensis Odhner 1919: 20, pl. 1, figs 10–12 (type locality: Majunga [Mahajunga, Madagascar]).—Dautzenberg 1923: 24; Hubendick 1945: 29, fig. 50; 1946: 55, pl. 4, figs 20–24; White & Dayrat 2012: 65.

Material examined. *Type material.* Lectotype of *Siphonaria madagascariensis* Odhner, 1919, present designation, from Majunga [Mahajunga, Madagascar]; coll. M.W. Kaudern, 1912 (UUZM UUMS 2000). Two paralectotypes, same data as lectotype (UUMS; not seen).

Other, non-type material. **Madagascar:** Ambatobe, Bavarama, 25°27.9’S, 44°57.6’E, BM06, (MNHN IM-2009-14095 p [M582]); Plage de Lavanono, 25°25.2’S, 44°56.3’E, BM01 (MNHN IM-2009-13779 p [M577]); SW coast, Itampolo, Fringing reef, 24°50.885’S, 43°59.693’E MA09-1a (AM C.585971 10p, AM C.584818 d [M267, SK372]; C.584819 p [M268, SK370], C.584820 p [M269, SK371]); Inner lagoon shore, 24°50.885’S, 43°59.693’E MA09-1b (AM C.608184 7p, C.584957 p [M270], C.584958 [M271], C.584959 p [M272]).

Taxonomic remarks. The largest syntype is herein designated as the lectotype of *S. madagascariensis* for the stabilisation of the name (Art. 74.1 of the Code). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 46G–I) and geographic series of additional specimens (Table S1). Morrison (1972: 56–58) treated *S. madagascariensis* as a junior synonym of *S. laciniosa* based on similarity in shell form and ‘common reproductive development’. This synonymy is not supported by examination of type specimens and comparative morpho-anatomy.

External morphology. Foot wall, mantle, cephalic folds and pneumostomal lobe all evenly pale cream in colour paler to foot edge, darker to foot sole; faint irregular dark brown pigmentation markings over foot wall and centre of cephalic folds; mantle narrower than foot wall, lobed with a thickened cream edge band; mantle lobes align with undulations of primary shell ribs, foot wall and pneumostome pustulose, pneumostome wide between right ADMs and within mantle.

Shell (Figs 46G–I; Table S9). medium sized (max sl mean = 19.3 mm, SD = 2.1 mm, n = 6), ovate, flattened, shell height low, apex offset strongly to left and posterior of centre, apical sides convex, growth lines prominent, surface uneven; protoconch direction heterostrophic (n = 1), shell whorl dextral; growth striae distinct; ribs raised, whitish, wavy rib count (mean = 42.7, SD = 1.6, n = 6), ridges rounded, width increases strongly to shell lip, rib interstices narrow, dark brown; 11–14 prominent primary ribs, extend up to 1mm beyond shell edge; siphonal ridge prominent, formed by dual primary ribs, 1–2 interspersed secondary ribs; shell lip uneven, weakly scalloped and unevenly corrugated aligning with protruding ribs. Interior colouration matches white primary ribs and dark brown rib interstices, from shell lip, over shell margin to the dark chocolate brown coloured spatula; ADM scar impression distinct, same as shell margin colouring, siphonal groove prominent, indented; CMS straight to convex; thickening / faint whitening of shell interior occurs; white layering thickens and covers shell margin, spatula coated white (e.g., Fig. 46G).

Reproductive system (Fig. 47H; n = 2). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior over back of BM. Join of AO and ED to top of GA distinct, AO larger than GA, elongated, broad, bluntly pointed, slightly bent, much thicker than ED; ED longer and narrower than AO; AO, GA and ED all muscular white tissue; EG large, bluntly pointed with a single long broad bent flagellum F1; BD and CD connect in opposing directions into GA, CD at inner side and BD in front of ED entry; BD with bulbous entry and weak distal loop, in front of GA/ED join, BD and CD similar in thickness, BD longer, both ducts smooth and pass together through RAM connecting into MG (BD over CD), BC large, bulbous, embedded in MG/AG and against digestive tract; HD long broad coiled, links under digestive tract against foot sole, a small broad AG to a separated broad yellowish granulated HG, MG small, AG and MG folded, soft white tissue, AG slightly smaller than curved HG reflecting the close positioning to curvature of inner foot wall at right posterior quarter of coelom; SV embedded on left side of AG close to BC.

Spermatophore (Fig. 47I). Thread-like, test thin, translucent (length = 10.96 ± 4.5 mm, n = 4, mean AL = 9.4 mm); head section cylindrical, bulbous, centrally bent, rounded tip; test thin, smooth, featureless, translucent, contains a white core, tapers into short flagellum; head slightly shorter, wider than translucent flagellum (head length = 8.5 ± 1.7 mm, ~ 82% of SPM length, head width = 155 ± 20 µm, flagellum width = 47 ± 10 µm, n = 4); 8 SPMs tightly coiled in BC of one specimen.

Radula. Dentition formula 30:1:30 (Hubendick 1946: 56).

Comparative remarks. *Siphonaria madagascariensis* (*atra* group, unit 44) differs from its sister species *S. belcheri* (Figs 1, 2) by COI distances of ≥ 21.4% (Table S5). *Siphonaria madagascariensis* occurs in sympatry with two other congeners in Madagascar: *Siphonaria striata* **sp. nov.** has a smaller, taller, paler shell with a more posteriorly offset apex, less raised ribbing and darker interior, distal and bursal BD loops, a smaller BC and a wider ED. *Siphonaria itampoloensis* **sp. nov.** has a smaller, taller, paler shell with less raised ribbing, a smaller AO and BC, and a shorter ED. Based on comparatively ‘greater number of [shell] ribs’ and ‘stouter genital retractor’, Hubendick (1946: 56) doubted that *S. madagascariensis* should be ‘specifically distinguished’ from *S. kurracheensis*. However, apart from being genetically clearly different, *S. madagascariensis* has consistently broader and larger RS epiphallic parts (including genital retractor) than *S. kurracheensis*.

Distribution and habitat. Endemic to Madagascar (Fig. 48). Found in sheltered positions on moderately exposed fringing reef and inner lagoon shores, mid littoral level.

Siphonaria lentula (Iredale, 1940)

(Figs 46J–L, Q, 47J–K)

Mestosiphon lentulus Iredale 1940: 439, fig 14, 15 (type locality: Lord Howe Island [Australia]).—Jenkins 1983: 29; White & Dayrat 2012: 64.

Siphonaria australis—Hubendick 1946: 49 (in part; not *Siphonaria australis* Quoy & Gaimard, 1833).

Siphonaria (*Mestosiphon*) *laciniosa*—Morrison 1972: 57 (not *Siphonaria laciniosa* (Linnaeus, 1758)).

Material examined

Type material. Lectotype of *Mestosiphon lentulus* Iredale, 1940, present designation, from LHI; coll. R. Bell, 1912–14 (AM C.103712, Fig. 46J). Forty-one paralectotypes, same data as lectotype (AM C.103713).

Other, non-type material. **Australia, LHI:** Off NE side ; 31°30.43'S, 159°04.22'E (AM C.356975 d); 31°32.5'S, 159°03.75'E (AM C.103712 d; AM C.103713 41d); near runway 31°32.176'S, 159°04.258'E, LHI2017Apr04-102 (AM C.482039 p); lagoon near wharf 31°31.5'S, 159°03.45'E (AM C.356974 d); Signal Point, 31°31.5'S, 159°03.88'E (AM C.356977 d); 31°31.501'S, 159°03.580'E, LHI2017Apr04-104 (AM C.585957 3p); 31°31.501'S, 159°03.578'E, LHI2017Apr04-099 (AM C.546717 5p; C.546718 14p, C.585955 p [SK053], C.585956 p [SK054], C.585958 p [SK234], C.595975 p [M040]); between Old Settlement Beach and Dawson Point, 31°31.18'S, 159°03.45'E (AM C.356978 6p, C.608189 p [SK051]).

Taxonomic remarks. The description contains no original type designation (Iredale, 1940: 439). There are two registered type lots in AM reference collection, one labelled 'holotype' (AM C.103712) and another with same data as the 'holotype' (AM C.103713, 41 d, paralectotypes). We consider all these specimens as syntypes. The specimen AM C.103712 is herein designated as the lectotype of *M. lentulus* for the stabilisation of the name (Art. 74.1 of the Code). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Figs 46K–L; Table S1). The lectotype is the specimen figured in Iredale (1940: 441, pl. 34, fig. 14–15) matching the shell dimensions given in the original description. Hubendick (1946: 49) incorrectly treated *S. lentula* as a synonym of '*S. australis'* without examining types or topotypes. However, *S. australis* is a distinct species (Jenkins 1983: 1, fig. 3a). Morrison (1972: 56–58) treated '*M. lentulus'* as a synonym of *S. laciniosa* based on similarity in shell form and 'common reproductive development'. This synonymy is not supported by examination of type specimens and comparative morpho-anatomy.

External morphology. Foot sole, foot wall, cephalic folds, mantle evenly dark grey/brown; foot edge; mantle narrow, mantle edge unlobed thickened paler band, bands dark pigmentation aligning with rib interstice furrows; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two thick centrally touching dark grey cephalic folds; thin, pale grey, large pneumostomal lobe part of the mantle, between the right ADMs, closes the pneumostome and anus at the mantle edge.

Shell (Figs 46J–L, Q; Table S9). Small sized (max sl mean = 9.9 mm, SD = 1.0 mm, n = 13); ovate often elongate; height medium; flattened, apex offset central slightly to posterior; apical sides anteriorly concave posteriorly convex; protoconch direction homostrophic (n = 3; Fig. 46Q), shell whorl dextral; growth striae prominent growth lines often distorted, undulating; rib count (mean = 22, SD = 2.5, n = 13), whitish primary ribs raised, bent and crooked, broaden to, extend beyond and scallop the often growth deformed shell lip; 2–3 interspersed darker secondary ribs, black to brown rib interstices; fairly distinctive primary rib pattern, abutting paired raised primary ribs on siphonal ridge, flare out shell lip; segment area immediately behind siphonal ribs clear of any ribbing, 4–5 primary ribs span posterior end, 4 primary ribs span anterior end. Interior shell margin brown, shell lip coloured cream/white rays and black/brown infilling under primary/secondary ribs and rib interstices respectively; spatula dark brown, siphonal groove dark brown or white, ADM scar indistinct, coloured same as shell margin, cephalic muscle car concave; Thickening of shell lip and spatula occurs across larger shell sizes, translucent, infills and reduces lip scalloping, spatula becomes whitened;

Reproductive system (Fig. 47J; n = 2). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned between BM and to side of RAM; AO large, elongated bulbous, bluntly pointed (embeds into MG), centrally bent, merges with top of indistinct GA; ED long narrow, slightly twisted; EG relatively large, folded, elongated and pointed; flagellum F1 absent; AO, GA and ED all muscular white tissue; BD and CD jointly connect into GA between ED, AO and GP; BD longer and much narrower than CD with a prominent loop close to BC, both ducts smooth curved and pass together (BD above CD) through RAM connecting into folds of MG; BC small translucent test bulbous, embedded in soft white folds of AG/MG complex; HD short coiled, links AG to a small brownish finely granulated HG; dark SV embedded within AG, AG larger than HG.

Spermatophore (Fig. 47K). Test thin, translucent (length = 1.47 mm, n = 1, possibly longer as flagellum appears incomplete); head bulbous, tip bluntly rounded, containing a white gelatinous mass; very short taper region into the filamentous transparent flagellum; both sections smooth, featureless; head shorter and much thicker than flagellum (head length = 0.69 mm, ~46% of SPM length; flagellum length = 0.78 mm; head width = 120 µm; flagellum width = 24 µm, n = 1); single SPM coiled in one bursa (AM C.356978).

Comparative remarks. *Siphonaria lentula* (*atra* group, unit 73) is the sister group of an unidentified species from Molokai ('*S. atra* group, unit 36' by Dayrat *et al.* 2014). Both sequences together form a well-differentiated subclade (Figs 1, 2). *Siphonaria lentula* differs from its sister lineage by COI distances of ≥ 16.6% (Table S3). *Siphonaria lentula* occurs in sympatry

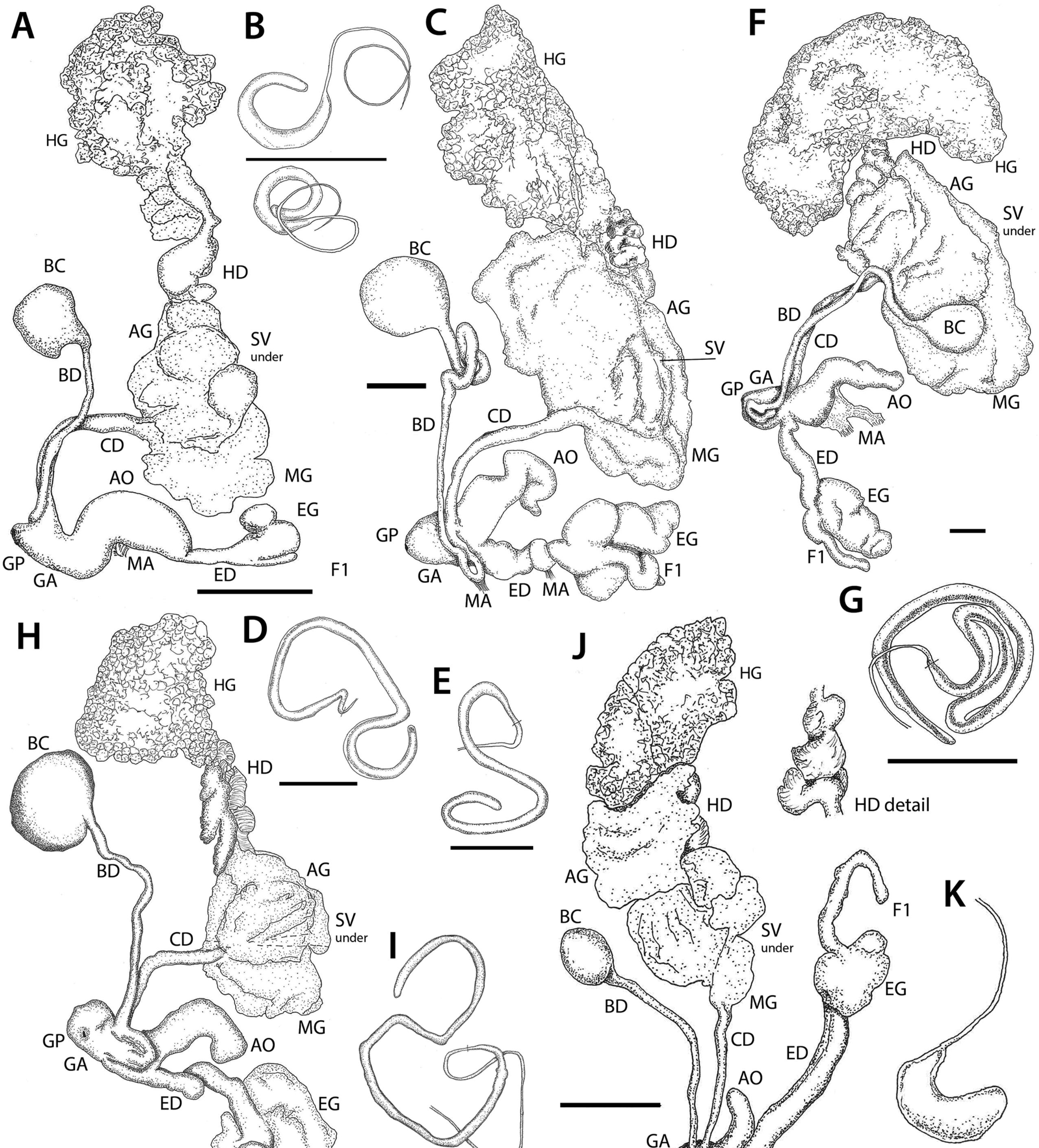

FIGURE 47. Reproductive morphology of *S. stowae*, *S. opposita*, *S. madagascariensis* and *S. lentula*. **A–B.** *S. stowae,* Tas, Dodges Ferry. **A.** AM C.584914 [SK216]. **B.** AM C.585264 [SK007]. **C–G.** *S. opposita.* **C–D.** Qld, Scarborough, AM C.585819 [M458, SK181]. **E.** Qld, Yeppoon, TS. AM C.585135 [M424, SK237]. **F–G.** Qld, Scarborough, AM C.585863 [M431, SK135]. **H–I.** *S. madagascariensis,* Madagascar, Itampolo, AM C.584818 [M267]. **J–K.** *S. lentula,* LHI, TS, AM C.608189 [SK051]. Scale bars = 1 mm.

with two congeners on LHI: For comparison with *S. exulum* refer to comparative remarks under that species. *Siphonaria pravitas* **sp. nov.** has more raised ribbing and edge scalloping, a shorter ED and BD, with no distal loop, a larger BC, and a more threadlike SPM. The SPM of *S. lentula* is not typical of the *atra* group. It is very short, bulbous (Fig. 47K).

Distribution and habitat. Endemic to LHI (Fig. 48). In this study, found in sheltered to exposed places on rocky shores, at upper to mid-littoral level.

Siphonaria opposita (Iredale 1940)

(Figs 46D–F, R–T, 47C–G)

Siphonaria siquijorensis—Hedley 1909: 369 (not *S. siquijorensis* Reeve, 1856).

Mallorisiphon oppositus Iredale 1940: 440 (type locality: Keppel Bay, [Qld, Australia]).—Short & Potter 1987: 122; White & Dayrat 2012: 66, 70.

Siphonaria (*Siphonaria*) *atra* var. *oppositus*—Hubendick 1946: 52.

Siphonaria (*Siphonaria*) *savignyi*—Hubendick 1955: 2 (not *S. savignyi* Krauss, 1848).

Siphonaria oppositus—Cernohorsky 1972: 210.

Siphonaria '*atra* group, unit 34'—Dayrat *et al.* 2014: 264, fig. 5L.

Material examined. *Type material.* Lectotype of *Mallorisiphon oppositus* Iredale, 1940, present designation, from Keppel Bay, [Qld, Australia]; coll. H. Bernhard [1940] (AM C.103714, Fig. 46D). Four probable paralectoypes from North Keppel Is, [Qld]; coll. H. Bernhard, [1 Jan 1934] (AM C.108527).

Probable paralectotype of *Mallorisiphon oppositus* Iredale, 1940 from Emu Park, Keppel Bay, Qld. Pres. T. Iredale, 22 May 1953 'Paratype' (MV F13839)

Other, non-type material. **PNG:** Kranket Is, N end, Madang, 5°11'S, 145°51'E (AM C.595915 p [SK545], C.595916 p [SK544]); Biliau I., 05°11.8'S, 145°48.2'E, PM38 (MNHN IM-2013-15195 p [M560]). **Australia, Qld:** W side Kissing Pt, Townsville, 19°14.332'S, 146°48.040'E, Q26-2 (AM C.585150 p [M189]); Mackay breakwater wall, 21°06.415'S, 149°14.033'E, Q14-2 (AM C.584998 d [R21282]); Yeppoon**,** Wreck Pt, 23°08.736'S, 150°45.865'E, Q08-4 (AM C.585598 4p, C.585135 p [M424,SK237],C.585136p[M425],C.585137p[SK237]), Double Head, 23°09.908'S, 150°47.638'E, Q08-3 (AM C.585701 8p); Buff Pt, 23°11.123'S, 150°47.830'E, Q08-2 (AM C.585597 4p, C.585860 p [SK113], C.585867 p [M210], C.585868 p [M211]); Zilzie, 23°16.778'S, 150°49.553'E, Q08-1 (AM C.585343 p). Canoe Pt Gladstone 23°56.155'S, 151°21.964'E, Q07-2 (AM C.585671 6p, C.585865 p [M212], C.585866 p [M213]); Bagara, Hervey Bay, 24°49.180'S, 152°28.011'E, Q06-1 (AM C.585700 8p, C.585129 p [SK180]); Urangan, Hervey Bay 25°17.504'S, 152°54.664'E, Q05-1 (AM C.585341 1p, C.585864 p [M209]); Scarborough, Nth Reef, 27°11.432'S, 153°06.755'E, Q03-5 (AM C.585126 p [SK136]); 27°11.451'S, 153°06.722'E, Q03-4 (AM C.585596 4p); 27°11.589'S, 153°06.892'E, Q03-6 (AM C.585637 5p, C.585819 p [M458, SK181], C.585863 p [M431, SK135]), Drury Pt, Q03-7 (AM C.585409 10+p), Scarborough Pt, 27°12.168'S, 153°06.980'E, Q03-8 (AM C.585670 6p).

Taxonomic remarks. Iredale (1940: 440) stated in the original description that *M. oppositus* was collected 'from many places in Qld'. The description was evidently based on more than one specimen and did not contain a type designation. Therefore, all types are syntypes. The largest syntype labelled 'holotype' (Fig. 46L) is herein designated as the lectotype of *M. oppositus* for the stabilisation of the name (Art. 74.1 of the Code). Through this designation, the type locality is herein restricted to Keppel Bay, Qld.

Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 46E–F) and geographic series of additional specimens (Table S1). Hubendick (1946: 52) and Cernohorsky (1972: 210) incorrectly treated *S. opposita* as a synonym of *S. atra.* However, the figured specimen of '*S. atra*' in Cernohorsky (1972: 210, pl. 60, fig. 1) is a specimen of *S. vudaensis* **sp. nov.** Morrison (1972: 56–58) treated '*Mallorisiphon oppositus*', as a synonym of *S. laciniosa* based on similarity in shell form and 'common reproductive development'. This synonomy is not supported by examination of type specimens and comparative morpho-anatomy.

External morphology (Fig. 46R). Foot sole, foot wall, foot edge, cephalic folds and pneumostomal lobe evenly cream; mantle thick translucent in larger specimens, thin in smaller specimens, edge thickened, whitish, lobed, with very light black pigmentation at mantle edge aligning with large primary rib interstices; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two centrally touching, centrally black pigmented cephalic folds; pneumostomal lobe long, under the mantle, unpigmented, behind right cephalic fold.

Shell (Figs 46D–F, R, T; Table S9). Medium sized (max sl mean = 20.8 mm, SD = 1.9 mm, n = 11), ovate; height very low; apex offset central and strongly to left, apical sides convex to straight, protoconch direction homostrophic (n = 1; Fig. 46T), shell whorl dextral; growth striae prominent, without radial banding, exterior often evenly light brown, whitened if eroded; shell thickness thin to thickened; rib count (mean = 50, SD = 3.7, n = 11), 17–21 primary ribs pale, fairly evenly spread radially, narrow, raised and protrude strongly (often > 1mm) beyond shell lip to unevenly scallop and corrugate the edge; 1–2 distinctly smaller, finer secondary ribs between primary ribs; rib interstices slightly darker; dual slightly spaced primary ribs over siphonal ridge, slightly more prominent, protruding more than other primary ribs, interstice gap wider either side of siphonal ridge. Interior; shell margin dark brown to white, narrow white rays align on grooves over shell margin under primary ribs, weakly furrowed, extend from lip to spatula; siphonal groove distinct, bent, same colour as shell edge; spatula evenly dark chocolate brown to mottled tan, ADM scar distinct, CMS convex, similar colour shell margin; thickening of shell lip commonly occurs, infills interior rib furrows and margin reducing lip scalloping, spatula not whitened.

Reproductive system (Fig. 47C, F; n = 4). HG/AG/MG complex positioned within right side of coelom, against foot wall over foot muscle, under the respiratory cavity; epiphallic parts relatively large, positioned between BM and RAM; GA small indistinct, with singular GP through foot wall; AO large broad elongated pointed, joined to upper GA; ED short, broad, coiled, twisted, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG large, longer than ED, soft whitish tissue, folded, joins ED; single short broad flagellum (F1), shorter and narrower than ED, appears as an extension of ED; BD and CD connect from opposite directions into GA between ED join and GP, distal loop in BD, both ducts long straight smooth thickened whitish featureless, pass closely together through RAM (BD over slightly wider CD) into soft white folded tissues of MG; MG/AG complex relatively large; BC embedded in folds of AG/MG complex close to embedded blackish SV; BD with short distal twisted loop, twisted coiling immediately prior to BC, slightly thinner but much longer than CD; BC relatively small, bulbous, thin whitish translucent test; HD short wide coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; AG usually larger than HG.

Spermatophore (Figs 47D, E, G). Relatively short and wide (length = 6.37 ± 0.93 mm, n = 6), head section cylindrical, tip bluntly rounded, central white core; flagellum very thin, transparent, tapering to a thread-like end; both sections smooth, featureless; test thin, translucent (head length = 4.9 ± 0.76 mm, ~80% of SPM length, head width = 114 ± 20 µm; flagellum width = 14 ± 2 µm, n = 6); prominent twist before short taper region into filamentous transparent flagellum; three SPMs coiled, embedded in brown gelatinous mass in BC of two specimens.

Comparative remarks. *Siphonaria opposita* (*atra* group, unit 34) is the sister species of *S. plana* (unit 35); both species together are the sister group of *S. denticulata* (unit 33) (Figs 1, 2). *Siphonaria opposita* differs from *S. plana* by COI distances of ≥ 8.1% and from *S. denticulata* by distances of ≥ 15.8% (Table S3). Throughout its range, *S. opposita* has been found in sympatry with eight congeners: For comparisons with *S. zelandica*, *S. denticulata*, *S. normalis*, *S. scabra*, *S. atra*, *S. viridis*, and *S. javanica* refer to comparative remarks under these species. The specimen figured as '*atra* group, unit 34' in Dayrat *et al.* (2014: fig. 5L) exhibits features consistent with *S. opposita.* The shell of. *S. opposita* has frequently been mistaken for *S. eumelas* (= *S. atra*).

Distribution and habitat. Endemic to Qld, between Townsville and MacKay (Fig. 48). In this study, found on sheltered rocky shores, at upper to mid littoral level.

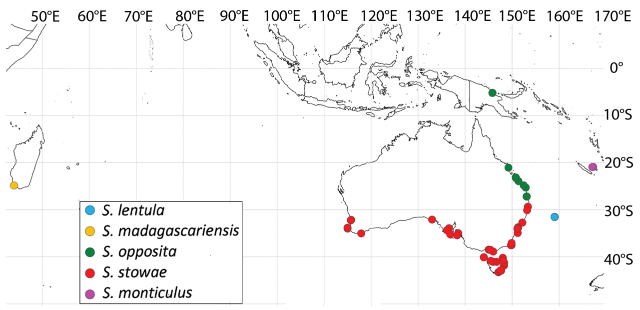

FIGURE 48. Known occurrence records of *S. stowae*, *S. madagascariensis*, *S. lentula*, *S. opposita* and *S. monticulus*

Siphonaria monticulus (Iredale, 1940)

(Figs 49A–C, O–P, T, 50A–D)

Hebesiphon monticulus Iredale 1940: 441, pl. 34, figs 11–13 (type locality: Lifu [sic Lifou], Loyalty Islands, NC).—Hubendick 1945: 29; White & Dayrat 2012: 65.

Siphonaria (*Siphonaria*) *monticulus*—Hubendick 1946: 45, pl.3, figs 7–9.

Material examined. *Type material.* Lectotype of *Hebesiphon monticulus* Iredale, 1940, present designation, from 'Lifu' [Lifou], Loyalty Islands, NC; coll. 1905 (AM C.103720 'holotype', Fig. 49A). Paralectotype, same data as lectotype (AM C.410720).

Other, non-type material. **NC, Lifou:** Drueulu, 20°55.570'S, 167°05.067'E LFU02-1 (AM C.585397 10+p, C.585875 p [SK058], C.584948 p [M384], C.584949 p [M385], C.584950 p [M386], C.584951 p [M387]); We Baie de Chateaubriand East coast, 20°54.779'S, 167°15.636'E LFU01-1 (AM C.584944 p [SK057], C.584945 p [SK056]).

Taxonomic remarks. The original description does not contain a type designation. Hence all types are considered as syntypes. The specimen labelled as 'holotype' (Fig. 49A) is herein designated as lectotype of *H. monticulus* for the stabilisation of the name (Art. 74.1 of the Code). This specimen is probably the shell figured in Iredale (1940: 441, pl. 34, fig. 11–13) and matches the shell dimensions given in the original description. The lectotype is a small specimen displaying a particularly tall shell profile. Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 49C) and geographic series of additional specimens (Table S1). While the description of *S. monticulus* in Hubendick (1946: 45) agrees with our concept of this species, the specimen figured from 'Wijnkoopsbai, south coast of Java' (Hubendick 1946: pl. 3, figs 7–9) is not of *H. monticulus*. Moreover, Hubendick (1946) did not examine any specimens from Lifou, Fiji or Tonga. Hence, he has probably misidentified specimens of *S. javanica*.

External morphology (Fig. 49T). Foot sole grey; foot wall, pneumostome, cephalic folds and mantle evenly cream; two small black epithelial eye spots centralised on two thick centrally touching cephalic folds; genital pore inconspicuous, located on foot wall posterior to right cephalic fold; mantle thin translucent extends to shell edge, edge weakly lobed with white band and light black bands aligning to rib interstices; pneumostomal lobe thin and within mantle between the right ADMs, closes the pneumostomal and anal openings at the mantle edge; light black pigmentation over centre of cephalic folds.

Shell (Figs 49A–C, O; Table S9). Small sized (max sl mean = 12.56 mm, SD = 1.2 mm, n = 5), ovate; height medium to tall; apex offset central to sightly posterior, apical sides convex, protoconch direction central to weakly heterostrophic (n = 1; Fig. 49O), shell whorl dextral; growth striae distinct, exterior uneven, shell thickness thick; rib count (mean = 42.8, SD = 4.6, n = 5), no clear distinction between primary and secondary ribs, ribs pale white, fairly straight, rib interstices paler, mottled radial colouration band appears to be algal growth in hollows; increasingly raised and protrude slightly beyond shell lip, edge uneven weakly scalloped, strongly corrugated; 3–4 fused ribs form an indistinct siphonal ridge. Interior shell lip and margin white, dark to pale brown rays aligning under primary/secondary ribs, span shell margin to golden/whitish spatula, siphonal groove distinct raised above shell lip, same colour as shell edge/margin, ADM scar distinct, CMS straight, paler than shell lip; thickening of shell lip translucent, infills and reduces lip scalloping, spatula becomes whitened.

Reproductive system (Figs 50A, C; n = 3). Positioned within and right side of coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior over BM against digestive organs; GA prominent with singular GP through foot wall; AO large, bluntly pointed, joined to upper GA alongside ED; ED elongated, broad, twisted and coiled (without prominent MA), joins to side of GA above BD; GA, AO, ED all white muscular fibrous tissue; EG large, soft whitish tissue, slightly folded, joins ED; single long thick flagellum (F1), similar length to ED, appears as a continuous extension of ED to EG, laid over BM; BD and CD connect close in opposing directions into GA between AO join and GP, BD with distal loop and prominent MA; both ducts long, straight, smooth, similar thickness of narrow, whitish, featureless, pass closely together through centre of RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex relatively large; BC embedded in folds of AG/MG close to embedded SV; BC large, flat rounded, thin translucent test; HD long, thickened, coiled, brown markings, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobbed; AG/MG much larger than HG.

Spermatophore (Figs 50B, D). Thread-like, test thin, translucent (length = 13.09 mm, n = 1); head section cylindrical, tip bulbous bluntly rounded, containing a white gelatinous core, tapers into the filamentous transparent flagellum; both sections smooth, featureless; head longer and much thicker than flagellum (head length = 7.71 mm, n = 1; head ~58.8 % of SPM length; head width = 80 µm; flagellum width = 13 µm). Single SPM embedded in red-brown gelatinous mass in one BC (AM C.584951).

Radula. Dentition formula 39:1:39 (Hubendick 1946: 46).

Comparative remarks. *Siphonaria monticulus* (*plicata* group, unit **57**) represents a well-differentiated lineage. It is the sister species of a subclade containing *S. lirata*, *S. tanguissonensis* **sp. nov.**, *S. mauiensis* **sp. nov.** and *S. undans* **sp. nov.** (Figs 1, 3). *S. tanguissonensis* **sp. nov.** and *S. lirata* differ by COI distances of ≥ 15.4 % and ≥ 17%, respectively (Table S7). *Siphonaria monticulus* has been found in sympatry with three congeners on Lifou, Loyalty Islands: For comparison with *S. normalis* refer to comparative remarks under that species. *Siphonaria hienghenensis* **sp. nov.** has a larger, darker shell with a more prominent and flared siphonal ridge, stronger edge scalloping, a shorter ED, narrower BD, smaller BC, and a less thread-like SPM. *Siphonaria bourailensis* **sp. nov.** has a lower, darker shell with more prominent and fewer primary ribs, and a shorter ED and F1. *Siphonaria monticulus* exhibits a shell morphology similar to that other species of the *plicata* group, such as *S. nuttallii* (Hawaii), *S. tongatapuensis* **sp. nov.** (Tonga), *S. lirata* (Guam), *S. plicata* (Lifou), *S. namukaensis* **sp. nov.** (Fiji), and *S. yagasaensis* **sp. nov.** (Fiji). A specimen from Java figured as '*S. monticulus'* in Hubendick (1946: 91, pl. 3, fig. 7–9) is a misidentification of *S. javanica*.

Distribution and habitat. Endemic to Lifou, Loyalty Islands, NC (Fig. 48). In this study found in sheltered positions (e.g., hollows of rocky platforms, cliff bases) on exposed rocky shores, mid and lower littoral levels (Fig. 49P).

Siphonaria alba Hubendick, 1943

(Figs 49D–G, U–V, 50E–F)

Siphonaria ferruginea—Smith 1909: 369; 1911: 315; Tomlin 1934: 82; Tan & Low 2014: 367 (not *S. ferruginea* Reeve, 1856).

Siphonaria alba Hubendick 1943: 2, figs 3a, b, 7, 10, 11, 13 (type locality: Nordwatcher Javasee [near Singapore, Java Sea]). Morrison 1972: 57; Christiaens 1980a: 78; White & Dayrat 2012: 60.

Triellsiphon acervus—Hubendick 1945: 29 (not *Triellsiphon acervus* Iredale, 1940).

Siphonaria (*Siphonaria*) *alba*—Hubendick 1945: 72.

Siphonaria (*Siphonaria*) *acervus*—Hubendick 1946: 46, pl. 3, figs 10–12 (not *S. acervus* (Iredale, 1940)).

Siphonaria (*Siphonaria*) *atra*—Hubendick 1946: 52, pl. 4, figs 5–7 (not *S. atra* Quoy & Gaimard, 1833).

Siphonaria (*Siphonaria*) *alba*—Hubendick 1946: 56, pl. 4, figs 30–31.

Siphonaria sirius—Springsteen & Leobrera 1986: 285, pl. 81, fig. 20; Dharma 1992: 78, pl. 17, fig. 2 (not *S. sirius* Pilsbry, 1894).

Siphonaria atra—Berry 1977: 186, 190, fig. 3; Morton & Morton 1983: 298; Tan & Chou 2000: 117, fig. 117; Tan & Woo 2010: Tan & Low 2014: 367 (not *S. atra* Quoy & Gaimard, 1833).

Siphonaria (*Anthosiphonaria*) *laciniosa*—Dharma 2005: pl.79, figs 20a, b (not *S. laciniosa* (Linnaeus, 1758)).

Siphonaria '*atra* group, unit 39' Dayrat *et al.* 2014: 264, fig. 5S.

Material examined. *Type material.* Lectotype of *Siphonaria alba* Hubendick, 1943; 2. fig. 3, 7, present designation, from Nordwatcher, Javasee [near Singapore, Java Sea]; coll. C. Aurivillius, 1891. (UUZM 1574-3957, colour image unavailable). Paralectotype, same data as lectotype (UUZM 1574-3957).

Other, non-type material. **Singapore:** Lazarus Island causeway, St Johns Island, 01°13.288'N, 103°51.195'E SI04-3 (AM C.585229 p [M332], C.585230 p [M334], C.585231 p [M335], C.585232 p [M337], C.585237 p [SK175]); Lazarus Island, 01°13.355'N, 103°51.148'E SI04-2 (AM C.585352 p); Fort Road, drain seawall 01°17.605'N, 103°53.809'E SI01-3 (AM C.585602 5p); East Coast Park, seawall, 01°18.643'N, 103°57.077'E SI01-2 (ZRC Moll. 9121 7p, ZRC.MOL.24914 p [M474, SK281], ZRC.MOL.24915 p [SK294]). **PNG:** Rempi Area, S Dumduman Is., 05°00,2'S, 145°47,6'E PM12 (MNHN IM-2013-12000 p [M557]). **Timor-Leste:** N of Dili, Christi Rea Beach, 8°32.072'S, 125°36.868'E

TL01-2 (AM C.585905 4p, C.585274 p [M440]. **Australia, WA:** Kimberley, between the Maret Islands, 14°24'S, 124°58'E (WAM S72337 p); Caffarelli Is., 16°01.991'S, 123°18.625'E, WA19-1 (AM C.584678 p [M323]); Conilurus Is, Kimberley, 16°08.875'S, 123°35.234'E, WA18-1 (AM C.585653 3p, WAM S74082 2p); Catamaran Bay, Cape Levique, Kimberley, 16°27.622'S, 123°00.242'E, WA22-1 (AM C.585655 4p, C.585296 p [SK424], C.585299 p [M070]); Gantheaume Point, Broome, 17°58.384'S, 122°10.677'E, WA26-2 (AM C.584735 15p, WAM S74083 5p), **CI:** Ethel Beach, 10°27.827'S, 105°42.497'E CI02-1 (AM C.584845 p [M304]).

Taxonomic remarks. The largest syntype (UUZM UUMS 3957/1574) is herein designated as the lectotype of *S. alba* for the stabilisation of the name (Art. 74.1 of the Code).

Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 49D, E–F) and geographic series of additional specimens (Table S1). We attribute the record of '*S. ferruginea*' from Christmas Is in Smith (1909: 369) to *S. alba* based on the similar shell and because *S. alba* occurs on CI while there is no confirmed record of *S. ferruginea* (= *S. plana*). Throughout the taxonomic literature, *Siphonaria alba* has frequently been misidentified as *S. atra*. Records in Berry (1977), Morton & Morton (1983) from Hong Kong, Tan & Chou (2000) from Singapore, Tan & Kastoro (2004) from South China Sea, Tan & Woo (2010) from Singapore, and Tan & Low (2014) from CKI are attributed here to *S. alba* because these records are within the range of *S. alba* but outside of the range of other species in the *atra* group that exhibit similar shells, such as *S. bifurcata* (Philippines), *S. sirius*, *S. atra* and *S. subatra* (Japan).

Morrison (1972: 56–58) treated *S. alba* as a synonym of *S. laciniosa* based on similarity in shell form and 'common reproductive development'. This synonymy is not supported by examination of type specimens and comparative morpho-anatomy.

External morphology (Fig. 49V). Foot sole, foot wall, foot edge, mantle, pneumostomal lobe and cephalic folds evenly cream; faint irregular black blotches of pigmentation over centre of cephalic lobes and parts of foot wall; mantle narrow with edge thickened, heavily lobed and white band; genital pore indistinct, located on foot wall to right anterior of right cephalic fold; small black epithelial eye spots centralised on each centrally touching cephalic folds; pneumostomal lobe under the mantle, between the right ADMs.

Shell (Figs 49D–G; Table S9): medium sized (max sl mean = 21.9 mm, SD = 3.1 mm, n = 9); height low; circular ovate; apex offset central (commonly eroded); apical sides convex, protoconch direction homostrophic (n = 1,), shell whorl dextral; growth striae indistinct, shell margin thick; rib count (mean = 40.8, SD = 4.6, n = 9), primary ribs narrow to broad, solidly raised, pale white protrude beyond shell lip to unevenly scallop and corrugate the edge, some primary ribs protrude 1–2 mm beyond shell lip, protrusion at shell lip greater at siphonal ridge and the forming primary ribs larger, interspersed with 1–3 pale white finer secondary ribs size; radial colour banding occurs, protoconch area brown, central band paler and shell edge dark brown; rib interstices darker. Interior; spatula, shell margin, ADM scar and siphonal groove evenly white (Fig. 49D) or dark chocolate brown (Fig. 49F), white rays from shell lip to margin, align under ribs and match rib width; siphonal groove distinct, same colour as shell edge, slightly curved to right anterior; CMS convex thin; thickening and whitening of shell lip occurs (e.g. Fig. 49D).

Reproductive system (Fig. 50E; n = 2). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole; GP small, singular, positioned through foot wall behind right cephalic fold, GA small, prominent; AO medium sized, elongated, bluntly pointed, slightly bent centrally, joins to top of GA; ED long, narrow, slightly twisted, thickened, joins to back side of GA alongside AO; EG very small, white, folded; single short broad flagellum (F1), appears as extension of ED; AO, GA and ED all muscular white tissue; BD and CD connect closely but in opposing directions into GA between ED and AO joins, both ducts long narrow smooth featureless, pass together through RAM connecting into MG (BD above CD), BD with distal loop and short MA attached to inner foot wall, additional loop immediately in front of BC; BC large spherical, embedded in folds of MG, test translucent; SV embedded on left side of AG; HD short, thick coils, links small AG to similar sized yellowish granulated HG; MG and AG folded, soft white tissue; sides match curvature of inner foot wall on right posterior of coelom.

Spermatophore (Fig. 50F). Relatively long thread-like (length = 13.87 ± 3.24 mm, n = 2, possibly longer as flagellum on one appears incomplete); test thin, translucent, containing a white gelatinous core mass; over half-length comprises a translucent bulbous cylindrical head section (head length = 8.86 mm, SD = 0.65 mm, n = 2; mean ~ 65% of SPM length); tip bluntly rounded; head section much thicker than flagellum (head width = 116 ± 16 μm, flagellum width = 12 ± 0 μm, n = 2); both sections smooth, featureless; 7–8 SPM tightly coiled in one BC (AM C.585237).

Radula. Dentition formula 44:1:44 (Hubendick 1946: 56).

Comparative remarks. *Siphonaria alba* (*atra* group, unit 39) is the sister species of a subclade formed by *S. atra* and *S. hienghenensis* **sp. nov.** (Figs 1, 2). It differs from these two species by COI distances of ≥ 13% (*S. atra*) and ≥ 8.3% (*S. hienghenensis* **sp. nov.**) (Table S3). Throughout its range, *S. alba* has been found in sympatry with fifteen congeners. Four congeners are sympatric in Singapore: *Siphonaria costellata* **sp. nov.** has a taller shell with slightly more raised and even ribbing, a shorter ED and BD, smaller AO and BC, and a shorter SPM. *Siphonaria caubianensis* **sp. nov.** has a darker shell exterior and interior, broader and more raised primary ribs, a more posterior and left offset apex, a stronger scalloped shell edge, a smaller AO and BC, no BD distal loop. For comparisons with *S. normalis* and *S. sirius* refer

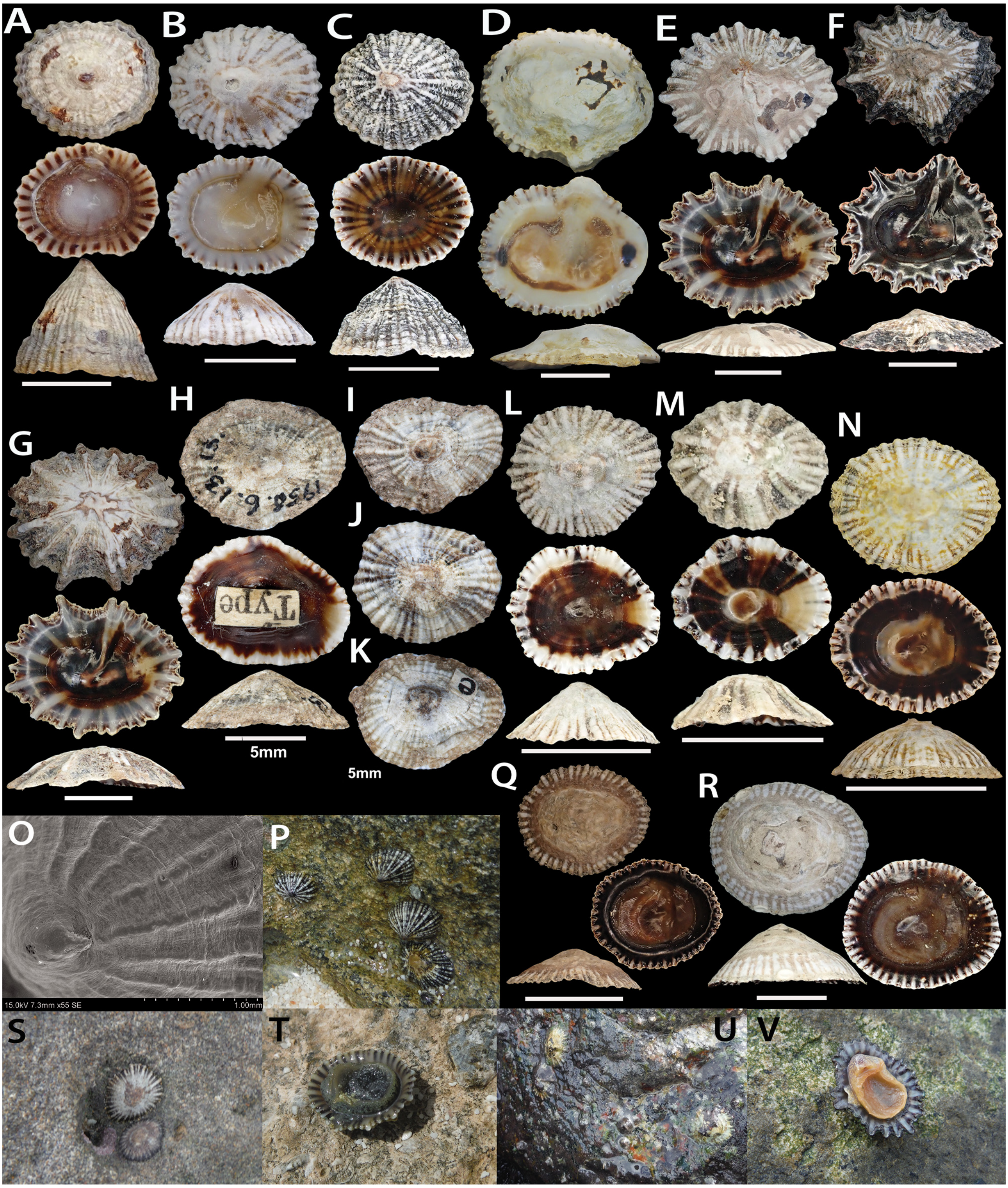

FIGURE 49. Shells of *S. monticulus*, *S. alba* and *S. asghar*. **A–C, O–P, T.** *S. monticulus.* **A.** Lectotype of *Hebesiphon monticulus* AM C.103720**. B–C.** NC, Lifou, TS. **B**. AM C.584951 [M387]. **C.** AM C.584950 [M386]. **O.** Protoconch, AM C.584945 [SK056]. **P, T.** Lifou, *in situ* and animal. **D–G, U–V.** *S. alba*. **D.** Singapore, ZRC.MOL.24915 [SK294]. **E.** Singapore, AM C.585230 [M334] **F.** WA, AM C.585299 [M070]. **G.** Singapore, AM C.585237 [SK175]. **U–V.** Singapore, *in situ* and animal. **H–N, Q–S.** *S. asghar.* **H.** Holotype NHMUK 1958.6.13.13. **I–K.** Paratypes NHMUK 1958.6.13.14. **L–R.** Pakistan, Karachi, TS. **L.** AM C.585845 [M245]. **M.** AM C.585844 [M244]. **N.** AM C.585846 [M256, SK190]. **Q.** AM C.586001 [SK532]. **R.** AM C.585855 [M236]. **S.** *In situ***.** Unlabelled scale bars = 10 mm.

to comparative remarks under these species. Two species are sympatric in Cebu, Philippines: For comparisons with *S. bifurcata* and *S. sipho* refer to comparative remarks under these species. *Siphonaria umbra* **sp. nov.** is sympatric in CI. It has a smaller, darker shell with more even ribbing, smaller AO, shorter, wider ED, and larger BC. Six species are sympatric in Timor-Leste: For comparisons with *S. atra*, *S. viridis*, and *S. javanica* refer to comparative remarks under these species. *Siphonaria campestra* **sp. nov.** has a smaller, darker shell with less prominent siphonal ridge and weaker edge scalloping, a smaller AO and BC, shorter ED and BD, and a shorter SPM. *Siphonaria forticosta* **sp. nov.** has a larger shell with a slightly more posteriorly offset apex, weaker edge scalloping and darker interior, a smaller AO, shorter ED, and a larger F1. *Siphonaria planucosta* **sp. nov.** has a smaller, darker shell with less raised ribbing and weaker edge scalloping, a smaller AO, shorter ED, and shorter SPM. Three species are sympatric in WA (along with *S. atra*, and *S. viridis*): *Siphonaria gemina* **sp. nov.** has smaller, taller, paler shell with stronger edge scalloping, a smaller AO, shorter ED and BD, and a less thread-like SPM. *Siphonaria restis* **sp. nov.** has a paler shell with more uneven ribbing and stronger edge scalloping, a smaller AO, shorter wider ED, and larger BC. For comparison with *S. zelandica* refer to comparative remarks under that species.

The RS (Fig. 50E) and SPM (Fig. 50F) of *S. alba* shown herein correspond well the RS and SPM figured in Hubendick (1943: 3, fig. 10–11; 1945: 3 figs 10–11) although no serration on SPM flagellum was observed. A specimen from Mindanao figured as '*S. acervus*' in Hubendick (1946: pl. 3, figs 10–12) is probably a specimen of *S. alba* for exhibiting typical shell characteristics. It is within the known distribution of *S. alba*. A specimen from Palawan figured as '*Siphonaria sirius*' in Springsteen & Leobrera (1986: 285, pl. 81, fig. 20) is a misidentification and likely a specimen of *S. alba* for the siphonal ridge exhibiting multiple and not just a single rib. A specimen from Seribu Islands, Java Sea figured as '*S. laciniosa*' in Dharma (2005: pl.79, figs 20a, b) is a misidentification and likely a specimen of *S. alba* as it matches the shell morphology of this species (Fig. 49D–G; paired siphonal ribs) and is from within the known range of this species. A specimen from Long Dong, Taiwan figured as '*atra* group, unit 39' in Dayrat *et al.* (2014: 263, fig. 5S) is morphologically consistent with *S. alba.*

Distribution and habitat. Widely distributed through tropical northwestern Pacific, including Taiwan, Sulawesi, Singapore, Thailand, Philippines, CI, northern Australia (Kimberey, WA) and Timor-Leste, Dili (Fig. 45). In this study found at sheltered positions on moderately exposed rocky shores, at upper and lower littoral levels (Fig. 49U).

Siphonaria asghar Biggs, 1958

(Figs 49H–N, Q–S, 50G–H)

Siphonaria asghar Biggs 1958: 249 (type locality: Hormuz Island, Persian Gulf).—Biggs 1973: 375; Galindo 1977: 416; Christiaens 1980: 81; Vakani *et al.* 2021: 134, fig. 2b.

Siphonaria tenuicostulata—Smythe 1982: 80, pl. 4g (not *S. tenuicostulata* Smith, 1903)

Siphonaria ashgar—Bosch *et al.* 1995: 184, fig. 858; Ali *et al.* 2011: 1086, fig. 1B; White & Dayrat 2012: 61, 70; Dayrat *et al.* 2014: 266, 'unit 3', fig. 3C; Gonzàlez-Wevar *et al.* 2018: 5, fig. 2 (incorrect subsequent spellings of *asghar*).

Material examined. *Type material.* Holotype of *S. asghar* Biggs, 1958 from Hormuz Island, Persian Gulf; coll. 12 May 1933 (NHMUK 1958.6.13.13, Fig. 49H). Six paratypes of *S. asghar* Biggs, 1958 same data as holotype (NHMUK 1958.6.13.14–19, Figs 49I–K).

Other, non-type material. **Pakistan:** Karachi, Clifton Beach, 24°45.500’N, 67°05.968’E, PA02-1 (AM C.585895 p); French Beach, 24°50.345’N, 66°49.244’E, PA01-2 (AM C.585899 5p); 24°50.367’N, 66°49.387’E, PA01-1 (AM C.585818 13p, C.585843 p [M243], C.585844 p [M244], C.585845 p [M245], C.585846 p [M456, SK190]); Karapir Beach, 24°50.590’N, 66°53.927’E, PA01-3 (AM C.585901 7p, C.585847 p [SK144], C.585854 p [M235], C.585855 p [M236], C.586001 p [SK532]); Bubiji Beach, 24°53’N, 67°01’E 24°53’N, 67°01’E (WAM S72336 9p, S74084 p [SK408], S74085 p [SK407], S74086 p [SK303], S74087 p [SK359], S74088 p [SK421]), S113648 [SK530], S113649 [SK531]).

Taxonomic remarks. The holotype of *S. asghar* (Fig. 49H) is a worn or malformed specimen, unlike the paratypes (Fig. 49I–K). Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 49L, M; Table S1). Smythe (1979: 69) incorrectly considered *S. asghar* as a synonym of *S. rosea* (= *S. crenata*). However, both species differ conchologically and anatomically. The RS structure of *S. tenuicostulata* (= *S. carbo*) figured in Hubendick 1947a: fig. 1) differs from that of *S. asghar*. A specimen figured as '*S. asghar*' in Dayrat *et al.* 2014: fig. 3C) corresponds well with the paratypes; Figs 49I–K). Compared to freshly preserved specimens from Karachi (Figs 49L–M), the types (Figs 49H–K) are rather small, around half the size of the topotypes.

External morphology. Foot sole, foot wall, foot edge cephalic folds and pneumostomal lobe evenly cream coloured; black pigmentation absent except for central patch on cephalic folds; mantle cream coloured, narrower than foot wall, edge lobed thickened; pneumostome under mantle between right ADMs.

Shell (Figs 49H–N, Q, R; Table S9). Small sized (max sl mean = 15.1 mm, SD = 2.2 mm, n = 8), ovate, height medium; apex offset weakly to posterior and left, apex usually eroded (often upper 2/3rds eroded), apical sides strongly convex, protoconch direction undetermined, shell whorl dextral; growth striae inconspicuous, shell thickness medium; rib count (mean = 45, SD = 4.9, n = 8), ribs flat/unraised, narrow, sometimes wavy, very even in width, pale grey/brown; non-protruding at shell lip; shell edge weakly corrugated, not scalloped; few secondary ribs, rib interstices darker; siphonal ridge indistinct.

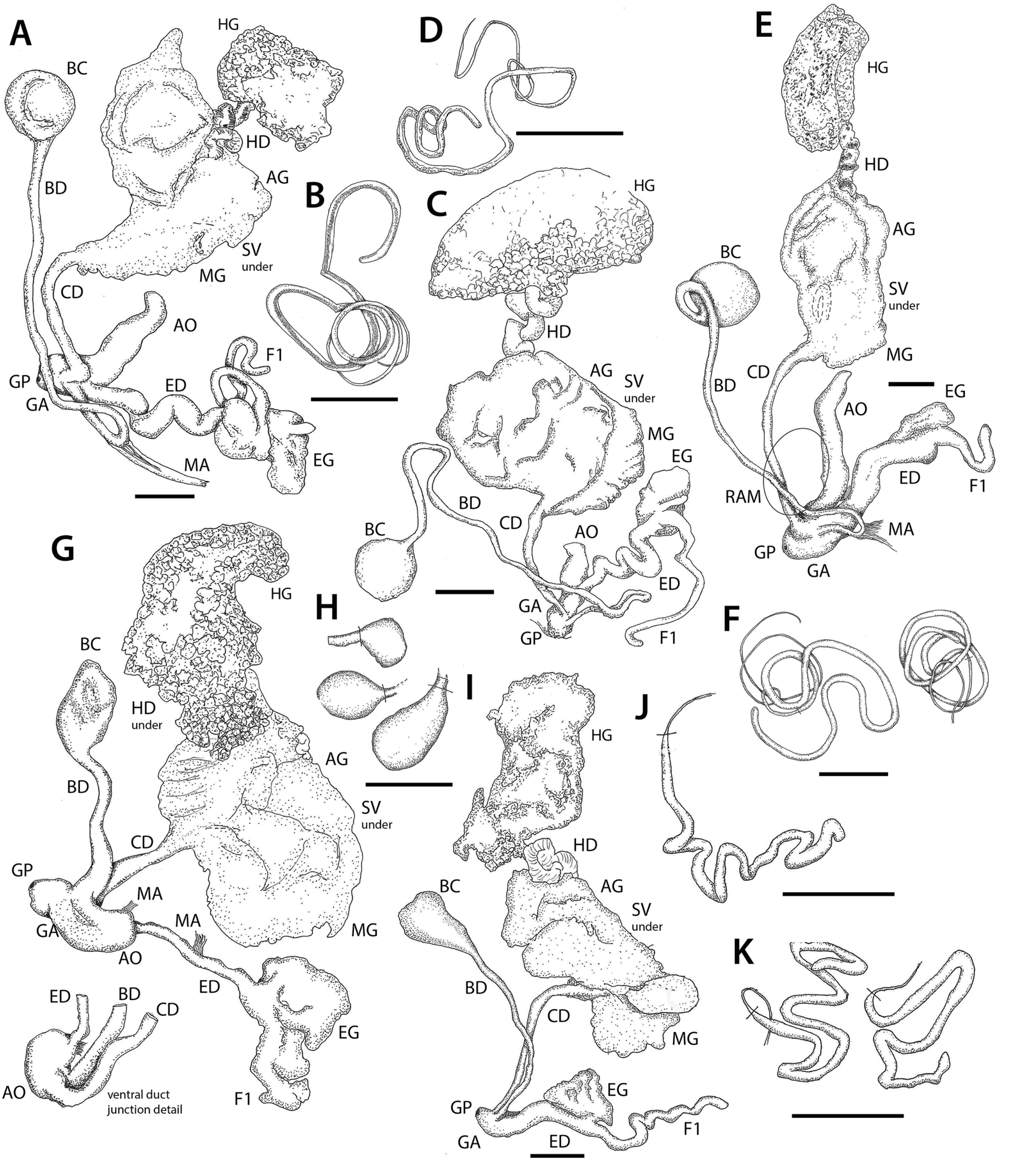

FIGURE 50. Reproductive morphology of *S. monticulus*, *S. alba*, *S. asghar* and *S. propria*. **A–D.** *S. monticulus*, TS, Lifou. **A–B.** AM C.584951 [M387]. **C–D.** AM C.584944 [SK057]. **E–F.** *S. alba*, Singapore, Lazarus Is, AM C.585237 [SK175]. **G–H.** *S. asghar*. **G.** Pakistan, Karachi, AM C.585846 [M458, SK190]. **H.** Karachi, AM C.586001 [SK532]. **I–K.** *S. propria* NZ, N Island, NMNZ M.331452 [M509]. Scale bars = 1 mm.

Interior shell margin brown and white; brown rays even in width and depth, widen from lip to margin, align under rib interstices, siphonal groove indistinct; spatula and ADM scar chocolate brown paler in parts; ADM scar distinct, CMS weakly convex.

Smaller shells tend to display greater white rays on shell margin, a paler brown / white spatula. Juvenile specimens show paired primary ribs over siphonal ridge.

Reproductive system (Fig. 50G; n = 4). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and on foot muscle, epiphallic parts positioned between RAM and BM, EG in front of BM, F1 lies on foot muscle to left side/under BM; AO small, broad, rounded, MA on side, bluntly pointed, joins at top of larger GA; ED relatively short (often embedded in soft tissue), narrow, straight; EG medium with folds, broad flagellum F1 appears as an extension of ED at join with EG; AO, GA and ED all muscular white tissue; BD and CD closely connecting, join into GA close to ED and AO (very distinct); BD longer and narrower than CD without distal loop or MA, CD and BD smooth, narrow, both pass together through RAM (BD above CD) and bent before connecting into folds of MG; BC embedded in MG, size medium, bulbous test soft translucent; HD long, brown flecked, sac-like, edge lobed, links AG to small elongated narrow brownish granulated HG; MG and AG small folded soft white tissue; SV embedded within AG, AG larger than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 50H). Elongated drop-shaped, test thin, translucent (length = 1.28 ± 0.3 mm, n = 3), head bulbous, broad, tip bluntly rounded, containing a white gelatinous mass; taper region to flagellum reduced; both sections; head much larger than flagellum (head length = 0.85 ± 0.03 mm, n = 3, ~ 66% of SPM length); tip bluntly rounded; head section much thicker than flagellum (head width = 580 ± 51 µm, flagellum width = 120 ± 35 µm, n = 3), both sections smooth, featureless; 3 SPM tightly coiled in one BC (AM C.586001).

Comparative remarks. *Siphonaria asghar* (*pectinata* group, unit 3) is the sister species of the species pair *S. carbo* and *S. itampoloensis* **sp. nov.** (Figs 1, 4). It differs from these species by COI distances of ≥ 10.9% (*S. itampoloensis*) and ≥ 11.1% (*S. carbo*) (Table S8). *Siphonaria asghar* has been found in sympatry with four congeners at Karachi, Pakistan: For comparisons with *S. crenata*, *S. belcheri*, and *S. kurracheensis* refer to comparative remarks under these species. *Siphonaria perexigua* **sp. nov.** has a taller, internally paler shell with less raised and wider ribs, shorter, bulbous AO, longer and narrower BD, wider ED and a longer F1. Conchologically similar are *S. capensis* (SE Africa) and *S. striata* **sp. nov.** (Madagascar), but *S. asghar* exhibits finer, more numerous, and flatter ribs.

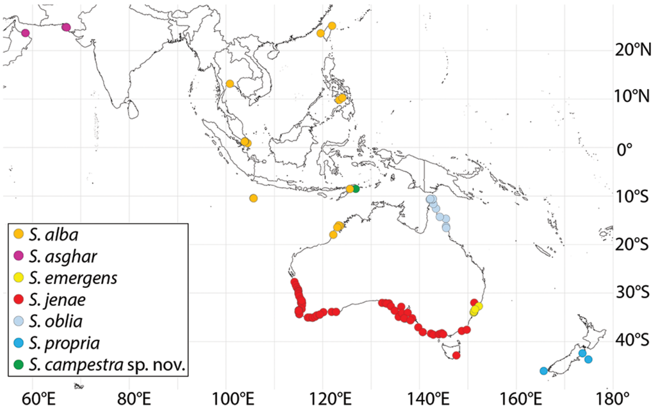

FIGURE 51. Known occurrence records of *S. alba*, *S. asghar*, *S. propria*, *S. jeanae*, *S. emergens*, *S. oblia* and *S. campestra* **sp. nov.**

Distribution and habitat. Coasts of the Arabian Sea, recorded at Q'rum, Muscat (Oman), Karapir, Karachi (Pakistan) and western coast of India (Fig. 51). In this study found in sheltered positions on exposed rocky shores, upper and mid littoral levels (Fig. 49S).

Siphonaria propria Jenkins, 1983

(Figs 50I–K, 52A–D, M–N)

Siphonaria propria Jenkins 1983: 23, fig. 5a–e, pl. 5a–f, 6g–j (type locality: Lower littoral, S side Kaikoura Peninsula, E coast, South Island, NZ).—Paul 1984: 28; Raven & Bracegirdle 2010: 46; White & Dayrat 2012: 67.

Siphonaria cookiana—Suter 1909b, 258; 1913: 599; 1915: pl. 24, figs 7a, b; Iredale 1915: 478; Odhner 1924: 55; Powell 1933: 186; 1937: 86; 1939 : 217; 1946 : 91; 1957a: 114; Dell 1960: 148; Morton & Miller 1968: 302, pl. 19, fig. 9, 9a; Berry 1977: 197; Powell 1979: 292, pl. 54, figs 8, 9; White & Dayrat 2012: 62 (not *S. cookiana* Suter, 1909).

Siphonaria cookeana—Galindo 1977: 416 (incorrect subsequent spelling of *S. cookiana*).

Siphonaria (*Simplisiphonaria*) *cookiana*—Hubendick 1945: 70, fig. 21, 24, 26; 1946: 36, pl. 6, figs 20–22 (not *S. cookiana* Suter, 1909).

Siphonaria (*Simplisiphonaria*) *cheesemani*—Hubendick 1946: 36, pl. 6, fig. 50 (not of *S. cheesemani* Oliver, 1915).

Simplisiphonaria cookiana—Trew 1983: 8.

Material examined. *Type material.* Holotype of *S. propria*, from Lower littoral, S side Kaikoura Peninsula, E coast, South Island, NZ (NMNZ M.77363, Fig. 52A). Twenty-six paratypes same data as holotype (NMNZ M.77364, 10 p; AM C.130361, 5 d, 11 p).

Lectotype of *Siphonaria cookiana* Suter, 1909b: 258, designation by Boreham (1959: 71), GNS TM1197 (figured in Jenkins, 1983: 21, pl. 3e). Six paralectotypes same data as lectotype (GNS TM1198-1202, 5, figured in Jenkins, 1983: 21, pl. 3f–g; AM C.29118, 1).

Other, non-type material. **NZ, North Island:** Fiordland, Centre Island, Beetles, Preservation Inlet, 46°8'S, 165°40'E (MA.100954 4p); N end Seaview Marina, Lower Hutt, South Island, NZ, 41°14.85'S, 174°54'E, Stn 2011011 (NMNZ M.331452 6p, [M509, SK429], [M510, SK430], [M511, SK431], [SK428 protoconch H12]).

Taxonomic remarks. The original description of *S. cookiana* (Suter, 1909b: 258) was based on a series of syntypes that represented two distinct species. Boreham (1959: 71) subsequently designated the lectotype without realising that the syntypes were a mixed series. The lectotype was subsequently identified as a juvenile of *S. australis* (Jenkins 1983: 29, pl. 3e) rendering the name *S. cookiana* a junior synonym of the latter. However, the paralectotypes of *S. cookiana* represented an unnamed species for which Jenkins (1983) described *S. propria*. The statement in Hutton (1873: 55) that '*S. denticulata* is also found in Tasmania and Australia' is erroneous and probably refers to specimens of *S. propria* rather than *S. australis*. *Siphonaria denticulata* as delineated herein does not occur in New Zealand. Raven & Bracegirdle (2010: 46) erroneously listed *S. cookiana* as a synonym of *S. propria*.

External morphology. Foot sole broad, smooth and cream to pale yellow. Foot wall smooth to weakly pustulose, superficially unevenly mottled with grey to black markings, concentrated over two cephalic folds; mantle wide and thin, greyish with irregular black bands corresponding under rib interstices, mantle edge banded white to cream; small black eye spot centralised on each cephalic fold; pneumostomal lobe long, whitish, weakly shaded with mottled black markings.

Shell (Figs 52A–D, M–N; Table S9). Ovate, small sized (max sl mean = 12.5 mm, SD = 1.4 mm, n = 5), posteriorly wide, height medium; apex weakly offset to posterior and left (Jenkins 1983: pl. 5, fig. a–f), and to left of shell centre line; protoconch notched, direction homostrophic (n = 2; Fig. 52M), shell whorl dextral; exterior pale brown, apical sides weakly convex, growth striae irregular prominent; rib count (mean = 34.6, SD = 1.7, n = 5), ribs slightly raised, irregularly spaced; curve, broaden from apex to protrude weakly beyond shell lip; 1–2 secondary ribs between primary, dual juxtapose primary ribs form distinct siphonal ridge. Interior dark brown, spatula tan to cream, siphonal groove clear, purple-brown to dark brown, curving from shell edge to spatula; white rays weakly corrugate shell edge, extend to shell margin, aligned under external ribs; CMS narrow, shallow, concave. Shell lip may be thickened, whitish or purple-brown.

Reproductive system (Fig. 50I; n = 2). Positioned within entire right side of coelom, against foot wall on foot muscle; epiphallic parts positioned between BM and RAM. GA small, with singular GP through foot wall behind right cephalic fold; AO indistinct, ED short, broader than BD and CD, unbent, joins to top of GA; GA, AO, ED all white muscular fibrous tissue; EG small, folds of soft whitish tissue, joins ED; single flagellum (F1), with minor bends, appears as a slightly longer and narrower extension of ED; BD and CD connect side-by-side into GA between ED join and GP, both ducts long, narrow, slightly bent, minor unevenness, whitish, pass closely together just inside outer RAM (BD over CD) into soft white folded tissues of MG; CD connects to ducts in MG/AG complex; BC embedded in MG folds close to large embedded whitish SV; BC spherical to sack-like, thin whitish translucent test; HD short, wide, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobbed; AG larger than HG, outer sides match curvature of inner foot wall.

Spermatophore (Figs 50J–K): Thread-like (length = 4.63 ± 0.26 mm, n = 3), translucent, test thin; head section bluntly rounded, cylindrical, containing a core white gelatinous mass, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless. Head section shorter wider than flagellum (head length = 4.01 ± 0.16 mm, ~ 87% of SPM length, head width = 112 ± 13 µm; flagellum width = 17 ± 0 µm, n = 3), 3 SPM tightly folded in one BC (NZNM M.331452).

Radula. (Jenkins 1983: 27, pl. 6 g–j). Mean dentition formula is 21:1:21 (SD = 3.9, n = 6) with 108 weakly curved (anteriorly convex) transverse rows (SD = 10.9, n = 6), single central tooth with pointed mesocone, flanked by 21 half row laterals, 9 (SD = 2.6) mid and 12 (SD = 1.4) outer lateral teeth means (n = 6), inner lateral teeth are absent; mid lateral mesocone bicuspidate separated by a shallow “U” to “V” shaped cleft, with the inner cusp longer than the outer, with strongly branching pointed ectocone; aberrant laterals are common appearing as extremely broad teeth; outer laterals have a square basal plate supporting a broad, flat ‘chisel’ like unicuspidate mesocone flanked by pointed single ecto- and endocones, widths and angles of separation of endo and ectocones are variable.

Comparative remarks. In our mitochondrial phylogeny, *S. propria* (*lateralis* group, unit 90) is the sister species of *S. australis* (Figs 1, 4). Both species form a well-differentiated subclade and differ from each other by COI distances of ≥ 10.4 % (Table S8). In NZ this species has been found in sympatry with two congeners: For comparisons with *S. australis* and *S. obliquata* refer to comparative remarks under these species. The RS and SPM of ‘*S. cookiana*’ figured in Hubendick (1945: figs 21, 24, 26; reproduced in Berry 1977, fig. 19) are consistent with RS and SPM of *S. propria* (Figs 50I–K) shown here except for details of the RS (CD/BD/GP/GA junction, which Hubendick portrayed as wider and with ducts more separated). The radula was briefly described by Hutton (1883: 143) as ‘*S. zelandica*’, which was repeated by Suter (1913: 601). The cusps and type of lateral teeth as seen here agree with Hutton (1883: 143, pl. 17, fig. D). However, the number of teeth and rows recorded by Hutton (33-40:1:40-33 with 130–140 rows) are well above those reported here.

Distribution and habitat. Endemic to New Zealand (southern end of North Island, South Island, Stewart and Chatham Islands; Fig. 51). In this study found in sheltered positions on moderately exposed to exposed rocky shores, mid to lower littoral levels (Fig. 52N).

Siphonaria jeanae Jenkins, 1984

(Figs 52G–I, Q–S, 53A–B)

Siphonaria (*S.*) *jeanae* Jenkins 1984: 114, pls. 1a–j, 2a–i, figs 1, 2 (type locality: Near boat wharf, Ceduna, SA [Australia]).—Johnson & Black 1984b: 1371; Grant & Utter 1988: 283; Campton *et al.* 1992: 255; Vadopalas *et al.* 2004; 693, 703; White & Dayrat 2012: 64.

Siphonaria sp.—Johnson & Black 1984a: 295.

Material examined. *Type material*. Holotype of *S. jeanae* from near boat wharf, Ceduna, SA; coll. B.B. Collette and J.R. Paxton, 4 Feb 1970 (AM C.123712, Fig. 52G); 23 paratypes; same data as holotype (AM C.123713 3p, 4d; SAM D.16383 6p); Neptune Bay, SA (MV F15260 5p); Radar Reef, Rottnest Island, WA coll. R. Black, 4 Aug 1979 (WAM 1798–83 5d).

Other, non-type material. **Australia, Vic:** Bastion Head Mallacoota, 37°34.429’S, 149°45.927’E, V09-

1 (AM C.585360 p); Cape Conran, 37°48.798'S, 148°43.608'E, V08-2 (AM C.585727 9p); Cape Schanck, 38°29.951'S, 144°53.369'E, V06-4 (AM C.585609 4p); Point Lonsdale (nr Queenscliff), 38°17.276'S, 144°36.977'E, V05-1 (AM C.585440 10+p, C.585288 p [M102]); Loutit Bay Lorne, 38°31.190'S, 143°59.429'E, V03-2 (AM C.585434 10+p, C.585285 p [M103]); Crofts Bay, 38°35.363'S, 142°50.633'E, V01-3 (AM C.585649 5p); Armstrong Bay, 38°21.012'S, 142°21.633'E, V01-2 (AM C.585571 3p). **Tas:** Park Beach Dodges Ferry, 42°51.716'S, 147°36.665'E, T03-4 (AM C.585263 p [M108]); Haleys Beach Gibson Peninsula, 32°45.084'S, 134°05.490'E, SA03-4 (AM C.585207 p [M101]). **SA:** Cape Northumberland, 38°03.503'S, 140°40.378'E, SA15-1 (AM C.585547 20+p, C.585219 p [M203], C.585220 p [M204]), Port MacDonnell, 38°03.308'S, 140°39.398'E, SA15-2 (AM C.585546 20+p, C.585221 p [SK017], C.585222 p [M202]); Cape Thomas, 37°04.461'S, 139°44.659'E, SA14-1 (AM C.585545 20+p, C.585217 p [M201]); Fisheries Bay, Lands End, 35°37.999'S, 138°06.921'E, SA13-2 (AM C.585567 3p); Groper Bay nr West Cape, 35°14.108'S, 136°49.883'E, SA10-1 (AM C.585484 19p, C.585214 p [SK011]); Pondalowie Bay, 35°13.989'S, 136°49.892'E, SA10-2 (AM C.585425 10+p); Fishery Bay, Cape Wiles, 34°55.107'S, 135°41.086'E, SA05-1 (AM C.585709 8p); Port Neill, 34°07.102'S, 136°21.271'E, SA06-1 (AM C.585424 10+p, C.585213 p [SK012]); Port Moonta, 34°03.273'S, 137°33.592'E, SA09-1 (AM C.585711 8p); Salmon Point, 33°38.547'S, 134°51.916'E, SA04-2 (AM C.585537 20+p); ESE of Pt Lincoln, Dangerous Reef, 32°49.05′ S, 136°13.05'E AM C.595961 4p) Wellesley Point, 33°38.483'S, 134°51.963'E, SA04-1 (AM C.585544, 20+p, C.585212 p [M123]); Haleys Beach Gibson Peninsula, 32°45.084'S, 134°05.490'E, SA03-4 (AM C.585441, 10+p, C.585207 d , C.585211 p [M122]); Rocky Point, 32°12.250'S, 133°14.861'E, SA02-4 (AM C.585472, 16p); Ceduna near boat wharf, 32°8'S, 133°41'E (AM C.123712 d, AM C.123713 4 d, 13p); Port Le Hunte Point Sinclair, 32°05.681'S, 132°59.299'E, SA02-1 (AM C.585419 10+p), 32°05.554'S, 132°59.476'E, SA02-2 (AM C.585420 10+p); Cactus Beach, Point Sinclair, 32°05.135'S, 132°58.943'E, SA02-3 (AM C.585439 10+p, C.585209 p [M121]); Wandrilla Beach, nr Cape Nuyts, 32°01.894'S, 132°16.052'E, SA01-1 (AM C.585418 10+p). **WA:** Alexander Bay 2 33°53.467'S, 122°44.995'E, WA64-4 (AM C.584775 5p, WAM S74133 5p); Alexander Bay, 33°53.374'S, 122°44.922'E, WA64-3 (AM C.584715 5p, WAM S74132 5p); Salmon Beach Esperance, 33°53.254'S, 121°50.381'E, WA64-2 (AM C.584685, 2p, WAM S74131 2p); Bremer Bay Boat Harbour 34°25.613'S, 119°23.818'E, WA63-2 (AM C.584772, 5p, WAM S74130 5p); Point Henry 34°28.177'S, 119°21.708'E, WA63-1 (AM C.584771, 5p, C.585313 p [M027], WAM S74129 5p); Cape Riche 34°36.213'S, 118°45.401'E, WA62-5 (AM C.584713, 5p, WAM S74128 5p); Lookout Point Point Gardner 34°53.449'S, 118°25.397'E, WA62-4 (AM C.584770, 5p, WAM S74127 5p); Cave Point 35°06.965'S, 117°54.080'E, WA62-1 (AM C.584767, 5p, WAM S74125 5p); Whaling Cove 35°03.372'S, 117°55.598'E, WA62-3 (AM C.584769, 5p, WAM S74126 5p); Peaceful Bay; 35°02.989'S, 116°55.769'E, WA60-8 (AM C.584746, 15p, WAM S74122 5p), 35°02.865'S, 116°55.722'E, WA60-7 (AM C.584745, 15p, WAM S74121 5p); Wilson Head Ocean Beach 35°02.250'S, 117°19.894'E, WA61-1 (AM C.584766, 5p, WAM S74124 5p); Augusta 34°20.451'S, 115°10.069'E, WA60-5 (AM C.584778, 5p, WAM S74120 5p); Sarge Bay Cape Leeuwin 34°22.091'S, 115°08.820'E, WA60-4 (AM C.584728, 5p, WAM S74119 5p); Point Dalling Dunsborough 33°35.955'S, 115°06.315'E, WA59-4 (AM C.584777, 5p, C.585312 p [M130], WAM S74116 3p); Point Casuarina Bunbury 33°18.544'S, 115°38.201'E, WA59-3 (AM C.584686, 2p, WAM S74115 3p); groyne nr Robert Point Mandurah 32°31.270'S, 115°42.409'E, WA59-1 (AM C.585577, 3p); Fremantle Hbr breakwater 32°03.342'S, 115°43.987'E, WA58-5 (AM C.584765, 5p, WAM S74114 5p); Quinns Rock 31°39.822'S, 115°41.345'E, WA58-4 (AM C.584671, 3p, WAM S74113 2p); **Rottnest Is:** Longreach Bay point, 31°59.333'S, 115°32.063'E RI01(AM C.585757, 3p, C.585820 p [SK215]); Radar Reef, 32°S, 115°18.72'E (AM C.595962, 10+p); W end Thomson Bay, 32°S, 115°32'E (AM C.320123 8p); Strickland Bay, 32°S, 115°30'E (AM C.595963 10+p). Cape Leschenault, 31°17.508'S, 115°27.089'E, WA58-3 (AM C.584726 6p, WAM S74112 6p); Grey, 30°39.968'S, 115°08.072'E, WA58-2 (AM C.584670 1p, WAM S74111 2p); Jurien Bay, 30°17.244'S, 115°02.482'E, WA58-1 (AM C.584695 3p, WAM S74110 2p); Bunker Bay, 33°32.300'S, 115°01.951'E, WA60-2 (AM C.584747 15p, WAM S74118 5p); Yallingup, 33°38.358'S, 115°01.481'E, WA60-9 (AM C.584779 7p, WAM S74123 5p); Sugarloaf Rock Cape Naturaliste, 33°33.536'S, 115°00.467'E, WA60-1 (AM C.584700 3p, WAM S74117 4p); Cowaramup Point, 33°51.934'S, 114°58.904'E, WA60-3 (AM C.585520 2p); Freshwater Point, 29°36.256'S, 114°58.464'E, WA57-3 (AM C.584762 5p, WAM S74107 5p); Cambawarra Head Green Head, 30°04.136'S, 114°57.830'E, WA57-6 (AM C.584764 5p, WAM S74109 5p); Illawong, 29°42.254'S, 114°57.542'E, WA57-5 (AM C.584763 5p, WAM S74108 5p); S end Leander Point Port Denison, 29°16.725'S, 114°54.918'E, WA57-2 (AM C.584761 5p, WAM S74106 5p); Leander Point Port Denison, 29°16.568'S, 114°54.858'E, WA57-1 (AM C.584759 5p, WAM S74105 5p); Cape Burney Geraldton, 28°52.084'S, 114°38.056'E, WA54-1 (AM C.584757 5p, WAM S74104 5p); Horrocks, 28°21.469'S, 114°24.751'E, WA53-1 (AM C.584780 6p, WAM S74103 6p); Chinamans Rock Kalbarri, 27°42.776'S, 114°09.361'E, WA52-1 (AM C.584742 12p, WAM S74102 8p).

Taxonomic remarks. Our delineation of this species is informed by comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Fig. 52H–I; Table S1).

External morphology (Fig. 52S). Foot sole evenly dark grey; foot wall darker than sole with evenly dispersed subepithelial pustules, paler to foot edge; fringing mantle narrow translucent at foot wall gradually becoming opaque with a thickened paler band at the unlobed mantle edge;

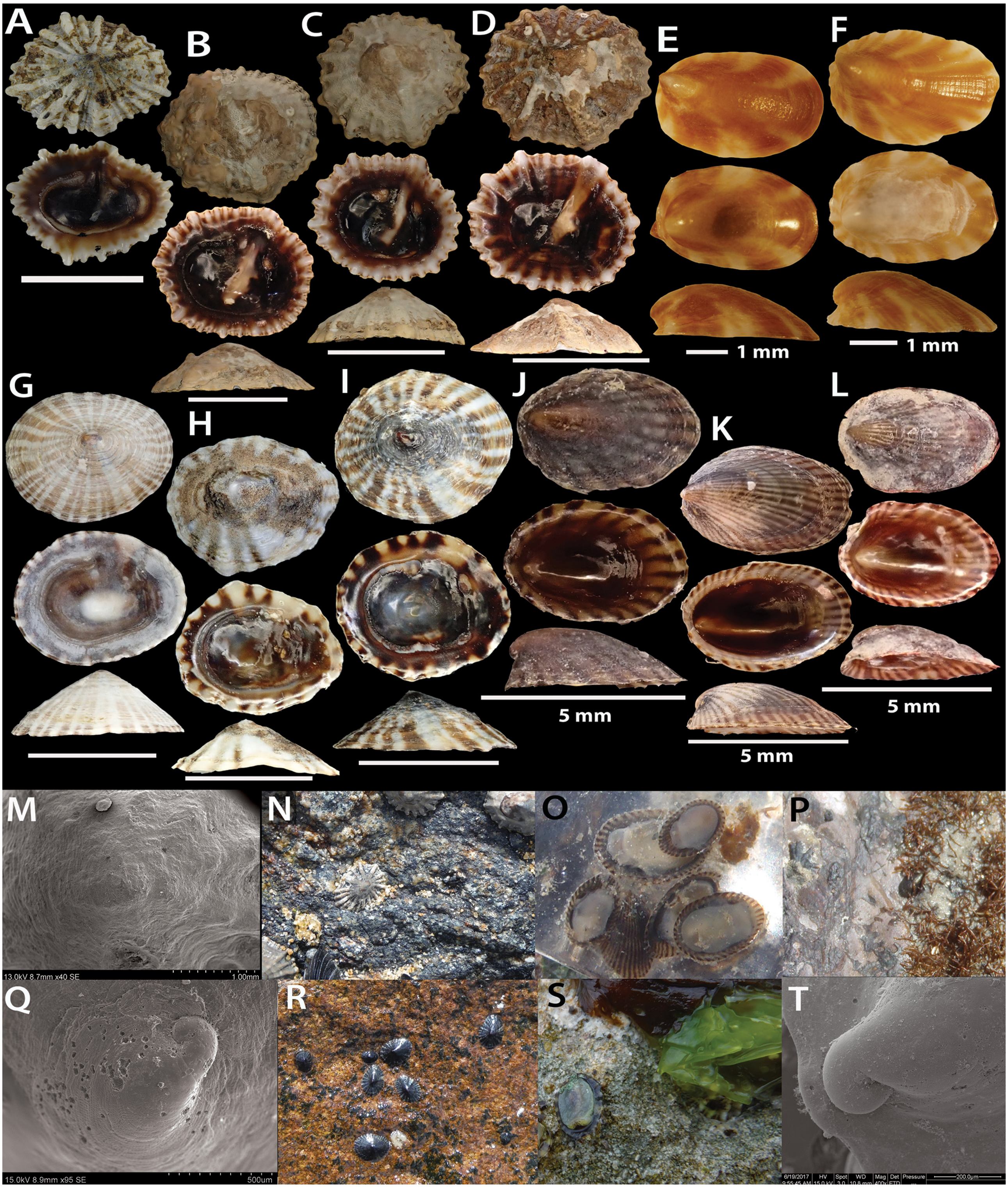

FIGURE 52. Shells of *S. propria*, *S. jeanae*, *S. emergens* and *S. oblia*. **A–D, M–N.** *S. propria*. **A.** Holotype NMNZ M.77363. **B–N.** NZ, N Island, NMNZ M.331452. **B.** [M509]. **C.** [M510]. **D.** [M511]. **M.** Protoconch [M514]. **N.** *In situ*. **E–F, T.** *S. emergens*. **E.** Holotype AM C.532860. **F.** Paratype AM C.265919. **T.** Protoconch, AM C.265919. **G–I, Q–S.** *S. jeanae*. **G.** Holotype AM C.123712. **H.** Vic, Point Lonsdale, AM C.585288 [M102]. **I.** WA, Point Dalling, AM C.585312 [M130]. **Q.** Protoconch, AM C.585213 [SK012]. **R.** WA, Point Dalling, *in situ*. **S.** WA, Point Dalling, animal. **J–L, O–P.** *S. oblia,* **J.** Qld, AM C.585755 [M105]. **K.** Qld, Cape York, AM C.584902 [M042]. **L.** Qld, Cape Kimberley, AM C.585505 [SK392]. **O–P.** Qld, Cape Kimberley, animals, *in situ*. Unlabelled scale bars = 10 mm.

genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two thick centrally touching dark grey cephalic folds; thin pale grey pneumostomal lobe part of the mantle, between the right ADMs, closes the pneumostome and anus at the mantle edge.

Shell (Figs 52G–I, Q–S; Table S9). Small sized (max sl mean 8.7 mm, SD = 1.7 mm, n = 10), ovate; height medium, slightly broader posteriorly; thickness thin; apex offset posterior and left; apical sides convex; protoconch direction heterostrophic (n = 3; Fig. 52Q), shell whorl dextral; siphonal ridge is indicated externally by two broad juxtaposed radial ribs on the right side of the shell. These siphonal ribs don't project beyond the shell lip. Growth striae may be regular and indistinct (Jenkins, 1984: pl.1a, d, g) or more commonly irregular and coarse (Jenkins, 1984: pl. 2a, c, e). This variation in growth striae, only apparent in specimens from Ceduna SA, may be due to differences in habitat exposure, compared to most locations where *S. jeanae* occurs, Ceduna is sheltered. The radial ribbing is flat and unraised with irregular, pale blue-grey ribs and narrower brown interstices, both of which narrow and curve ad-apically, rib count (mean = 27, SD = 3.8, n = 10), variable as is rib width (Jenkins, 1984: pl. 1a–i). The shell interior is smooth and glossy with a white to pale blue spatula. Between the thin, purplish grey ADM scar and the spatula, the interior is purplish brown. The siphonal groove is shallow and straight. The brown to grey outer lip is thickened and unsculptured with white radial bands corresponding with exterior radial ribs. Most specimens from south-western Australia have eroded exteriors, irregular growth striae and thickened shell lips (Jenkins, 1984: pl.2a, c, e).

Reproductive system (Fig. 53A; n = 2). HG (ovotestis), AG/MG complex located in posterior region of coelom, against inner foot wall and under the respiratory system; HG large, yellow, granular, joined to anterior of the soft white translucent semicircular folds of smaller AG by a short pink lobed HD; HD passes through folds of AG/MG complex. SV small ovate pinkish, embedded in anterior of AG/MG complex, connected via a short thin duct to the junction of the HD and emerging CD. BC small and embedded in folds of MG/AG close to SV. BD and CD long, thin, white, smooth, non-looped, featureless, pass together through the ADM and both enter adjacently into the GA. BC small, brown, appears spherical when holding SPM but deflated when empty. ED long, thick, white and may be centrally looped (Jenkins, 1984: fig 1b), enters the GA almost opposite the BD and CD juxtapose points of entry. No accessory organ present; EG, cream, soft, lobed, longer than ED, situated to the right posterior of the BM; Single flagellum, F1 short, white, branching from the junction of the EG and ED. GP small, opens from the GA through the foot wall, under the mantle and posterior to the right cephalic fold.

Spermatophore (Fig. 53B) (original description in Jenkins, 1983: 115). Short, bulbous (length = 5.5 mm ± 0.14 mm, n = 2); body cylindrical, weakly bulbous; test thin, white opaque core, short tapering section merging head with filamentous flagellum; head bluntly rounded, shorter thinner than translucent flagellum (head length = 2.15 ± 0.07 mm; ~ 39% of SPM length; head width = 200 ± 40 µm, flagellum width = 50 ±10 µm, n = 2); 4 SPMs tightly coiled in BC of one specimen (AM C.585820).

Radula and jaw (original description in Jenkins, 1984: pl. 2 g, h, i). The radula has a typically siphonariid morphology; a central tooth with an individually variable number of mid and outer lateral teeth arranged in longitudinal rows. The mean dentition formula is 25:1:25 (n = 3, SD = 2.6) with about 95 transverse rows (SD = 5.3). These rows are parallel and weakly curved (anteriorly convex). One central tooth is present and of the 25 half row laterals, 10.5 (SD = 1.2) are mid and 14.5 (SD = 2.1) outer lateral teeth means respectively. All teeth are weakly concave posteriorly. The central tooth is narrow with a short, pointed mesocone (Jenkins 1984: pl. 2g, h) with a lower profile than the flanking laterals. Inner laterals characterised by having no side denticles, are absent. The central tooth's base is narrow in the mid-section with an anterior cleft and a posterior notched point providing interlocking articulation with adjacent central teeth. Bases of the mid lateral teeth interlock posteriorly and anteriorly. The mesocones of the inner 5–7 mid laterals frequently wear a hole in the back of the tooth in front (Jenkins, 1984: pl. 2i). Outer laterals do not interlock between transverse rows. The spaces between rows increases to the ribbon edges coupled with a gradual decrease in tooth size. The mid lateral teeth are broad based and elongated without flanking ectocones (outer side denticles). The outer lateral teeth have both ecto and endo cones and a squared flat mesocone. The mid lateral's mesocone can be either pointed or bicuspidate. Of the 3 radulae examined, 2–4 of the inner (mean = 2.66, SD = 1.2) and invariably 2 of the outer mid laterals were bicuspidate, while the central 3–7 mid laterals (mean = 5.66, SD = 2.3) were pointed (Jenkins, 1984: pl. 2h, i).

Comparative remarks. In our molecular phylogeny, *S. jeanae* (*lateralis* group, unit 75) represents a well-differentiated lineage (Figs 1, 4). It is the sister species of a clade formed by *S. australis*, *S. propria* and *S. diemenensis*. *Siphonaria jeanae* differs from other species by COI distances of ≥ 16.6% (Table S8). Throughout its range, *S. jeanae* has been found in sympatry with seven congeners. Two congeners are sympatric in SE to SW Australia: For comparisons with *S. stowae* and *S. tasmanica* refer to comparative remarks under these species. Three species are sympatric in SE Australia: For comparisons with *S. funiculata*, *S. diemenensis*, and *S. zelandica* refer to comparative remarks under these species. One species is sympatric in western WA: *Siphonaria restis* **sp. nov.** has a lower, paler off-white coloured shell with greater uneven ribbing and scalloped edge, a paler, golden-brown spatula, a larger AO and BC, and longer ED and F1. RS (Fig. 53A) and SPM (Fig. 53B) depicted here correspond well with the original description of Jenkins (1984).

Distribution and habitat. Endemic to southern coasts of Australia, from Cape Conran Vic, near Hobart, Tas, SA and to Kalbarri, WA (Fig. 51). In this study, commonly found in exposed and sheltered positions (in crevices, holes) on moderately exposed to exposed intertidal marine rocky shores, upper and mid littoral levels (Fig. 52R).

Siphonaria emergens (Jenkins, 2018)

(Figs 52E–F, T)

Pugillaria emergens Jenkins 2018: 279, fig. 5A–M (type locality: North Fingal Bay, Port Stephens, NSW [Australia]).

Material examined. *Type material.* Holotype of *P. emergens* from North Fingal Bay, Port Stephens, NSW, 32˚44.750’S, 152˚10.500’E, on beach in shell sand; coll. J. Voorwinde, 1950-60 (AM C.532859), two paratypes, same data as holotype (AM C.532860 2d).

Other, non-type material. Australia, NSW: Off Port Stephens, 32°42′S, 152°15′E (AM C.265971 2d); North Fingal Bay, Port Stephens, 32°44.750′S, 152°10.500′E (AM C.265919 20+d); Shelly Beach, Bateau Bay, S of The Entrance, 33°22′S, 151°29′E (AM C.265912 d); Blue Lagoon Beach, S of Tuggerah Lakes, 33°21′S, 15,1°30′E (AM C.265924 d); Long Reef near Collaroy, 33°44.498′S, 151°19.117′E (AM C.265920 d); Collaroy Beach, 33°43.700′S, 151°18.0′E (AM C.532861 d); Manly Beach, 33°47.817′S, 151°17.368′E (AM C.265913 d); Middle Harbour, 33°49.088′S, 151°15.427′E (AM C.265921 2d); off Chinamans Beach, 33°48.870′S, 151°14.965′E (AM C.265928 d); Bronte, 33°54.355′S, 151°16.252′E (AM C.265925 9d); Little Coogee Bay, 33°55.300′S, 151°15.600′E (AM C.265923 d, C.265914 2d, C.265915 d, C.265922 4d, C.265926 d); 2 km E of Mistral Point, 33°56.700′S, 151°16.700′E (AM C.265916 d); Cronulla, 34°2′S, 151°10′E (AM C.265931 4d, C.265929 d).

Shell (Figs 52E–F, T; Table S9). Small sized (max sl < 5 mm); height medium; weakly elongate; apex well offset to posterior, aligning with or beyond shell edge (Jenkins 2018: figs 5A, G, J), to left of shell centre line; protoconch direction homostrophic (n = 1; Fig. 52T) below apex and shell height (Jenkins 2018: figs 5C, F, I, L); anterior and lateral apical sides convex, posterior concave almost notch-like; shell thin glassy translucent; dorsally arched with prominent curvature in shell-growth, growth striae irregular prominent; ribs radiate from apex to lip, indistinct, flat unraised; siphonal ribs not prominent on exterior, exterior coloration tan /red-brown with up to ten irregular white apical rib interstice bands extending and widening over lower half of sides to shell edge; lip fragile, undulated; spatula small, glossy, tan/red-brown, interior coloration reflects exterior coloration through translucent shell (Jenkins 2018: figs 5B, E, K), ADM scar horseshoe-shaped, weakly indented and shallow; cephalic ADM scar straight to weakly convex (Jenkins 2018: fig. 5E, H) between rounded left and right ADM scars, siphonal groove indistinct, very weakly indented.

Comparative remarks. *Siphonaria emergens* (*atra* group) has been found in sympatry with six congeners in Sydney Harbour, NSW: For comparisons with *S. stowae*, *S. denticulata*, *S. diemenensis*, *S. funiculata*, *S. scabra*, and *S. zelandica* refer to comparative remarks under these species. This species in known only from shells and its anatomy remains undocumented. Consequently, no DNA sequences have been available for genetic study.

Distribution and habitat. Incompletely known, yet to be live collected. Endemic to the, warm temperate central coast of NSW between Port Stephens and Cronulla Sydney, Australia (Fig. 51).

Siphonaria oblia (Jenkins, 2018)

(Figs 52J–L, O–P)

Pugillaria oblia Jenkins 2018: 281, figs 3C–E, 4E–H, 6A–J (type locality: Hospital Point, Thursday Island, Torres Strait, Qld [Australia]).

Material examined. *Type material.* Holotype of *S. oblia* from Hospital Point, Thursday Island, Torres Strait, Qld, 10°35.318’S 142°12.573’E; coll. Ponder and Loch, 29 Jun. 1976, on moderately exposed rocky reef (AM C.125603, figured in Jenkins 2018: fig. 6), 15 paratypes, same data as holotype (AM C.125604 11p, 4d).

Other, non-type material. **Australia, Qld:** Torres Strait: N end Prince of Wales Island, beach opposite Hospital Point, Thursday Island, 10°35.748′S, 142°12.280′E (AM C.265974 8d); S side of Thursday Island, 10°35.133′S, 142°13.257′E (AM C.532862 8p); Wednesday Island, 10°31.0′S, 142°17.0′E (AM C.265909 20+d); Bampfield Point, W side of Prince of Wales Island, 10°43.043′S, 142°6.833′E (AM C.532863 9p; AM C.532864 10+p); Cape York Peninsula: Albany Passage, 10°44.278′S, 142°35.758′E (AM C.265907 d); Mutee Head, 10°54.682’S, 142°15.204’E, Q50-2 (AM C.585755 p [M105]); Somerset, S side of Fly Point, 10°45.195′S, 142°36.292′E, Q47-1 (AM C.265910 8p, 6d; C.584902 p [M042]); Captain Billy Landing, 11°38.019′S, 142°51.472′E, Q46-1 (AM C.559470 2p); Portland Road, 12°35.588′S, 143°24.660′E, Q45-1 (AM C.559471 p); Point S of Bathurst Head, 14°17.583′S, 144°11.845′E, Q41-1 (AM C.559473 10p); Lizard Island, Casuarina Beach, 14°40.447′S, 145°26.703′E, Q40-1 (AM C.266052 d), 14°40.908′S, 145°27.007′E (AM C.559473 3p); Point Archer, 15°35.558′S, 145°19.788′E (AM C.49513 5d); Cape Kimberley, 16°16.535’S, 145°28.737’E, Q35-1 (AM C.585478 17p, C.585172 p [M076], C.585505 p [SK392]); Port Douglas, 4 Mile Beach, 16°30.470′S, 145°28.168′E (AM C.265953 d), 16°29.468′S, 145°28.425′E (AM C.265908 2d); Pebbly Beach, Yule Reef ,Trinity Bay, 16°35.031’S, 145°30.823’E, Q32-2 (AM C.608188 2p); Red Cliff Pt N of Cairns 16°41.294’S, 145°35.080’E, Q33-3 N of Cairns, Buchan Point, 16°44.172′S, 145°39.973′E (AM C.265951 7d).

Taxonomic remarks. Our delineation of this species is based on comparative analyses of the morpho-anatomy and mitochondrial genetics of freshly collected topotypes (Figs 52J–L) and a geographic series of additional specimens (Table S1).

External morphology (Fig. 52O). Animal tissue translucent; foot sole and foot wall evenly pale grey to cream; mantle thin, translucent with large whitish subepithelial pustules in thickened fringe, positioned along top edge of foot wall, forming a broad flat band, radial markings on mantle aligned with shell colour bands; foot wall narrow; faint brown/red splotches present on lower foot wall around body but not extending under mantle; pneumostomal lobe on right side narrow translucent with pointed lobe, covering inconspicuous anus in foot wall; brown markings on posterior lobe of pneumostomal lobe; two black 'Eye' spots prominent centrally on thickened cephalic lobes, centrally touching and marked with brown/reddish splotches; genital pore inconspicuous, positioned in foot wall posterior to right cephalic fold.

Shell (Figs 52J–L; Table S9). Small sized (max sl < 5 mm), ovate, height medium; centrally broad, thickness thin, maybe glassy translucent; apex well offset to posterior edge and left of centre line, apex below shell height, dorsally dark tan/brown in colour; offset growth reflected in apical ridge; protoconch direction weakly heterostrophic (n = 1; Jenkins 2018: 282, fig. 6J), shell whorl dextral; anterior and lateral apical sides convex, posterior weakly concave; apex ribs radiate from apex to shell lip, flat unraised, appear as bands, tan in colour, rib count (mean = 35, SD = 3.7, n = 32); siphonal ribs not prominent on exterior, apical cream banding of rib interstices prominent, colour bands widen slightly over lower half of sides to lip; number of apical bands varies within individuals, lip fragile, unscalloped, even; growth striae irregular, prominent; light periostracum covers lower parts of exterior sides, often freely extending; spatula glossy, brown, interior colouration reflects exterior colouration through translucent shell; ADM scar horseshoe-shaped, weakly indented shallow; cephalic ADM scar straight to weakly convex, between left and right rounded ADM scars; siphonal groove very weakly indented.

Reproductive system (Jenkins 2018: 278, fig. 3C–D). Located in posterior region of coelom and partly covered by pallial cavity and digestive gland; HG granulated; MG and AG folded; a thickened weakly coiled brown-coated HD emerges from HG; small rounded SV enveloped within AG folds; CD emerges from base of AG folds, progressively decreasing in diameter anteriorly and narrowing to open in rear of GA, AO indistinct; bulbous EG and narrow elongate ED are located between BM and RAM; ED slightly coiled prior to entering GA close to single GP; what appear to be two prominent flagellum both close to join of ED and EG, one broad and blunt, other narrow and elongate (Jenkins 2018: fig. 3B–C); BC pale brown bulbous with a thin translucent test, located beside posterior RAM; BC may appear deflated when without SPM (Jenkins 2018: fig. 3B); elongate thickened BD leads from BC and, coupled with anterior section of CD, passes through RAM; both ducts enter separately into GA and opposite to entry of ED.

Spermatophore (Jenkins 2018: fig. 4E). Over half length comprises a translucent cylindrical head section, tip bluntly rounded; flagellum very thin, transparent, tapering to a thread-like end; both sections smooth, featureless (length = 0.49 mm; head length = 0.19 mm, ~ 38 % of SPM length, head width = 17 µm, flagellum width = 4 µm, n = 1). Two SPMs coiled, embedded in a white gelatinous mass in BC of one paratype (AM C.125604).

Radula (Jenkins 2018: 284, fig. 3E–G, 4E, F). Each half row has around six mid and nine outer lateral teeth; central tooth with single pointed mesocone, about one-third base length; inner laterals (i.e., without ecto/endocones) absent; first mid lateral has prominent bicuspidate pointed mesocone, other mid laterals possess single cusped elongate mesocone, single cusped ectocones offset from side of mesocone; central tooth basal plate as long as adjacent mid-lateral teeth; mid-lateral teeth possess a single outward pointing forked prong and notch, rows interlock via these basal forks and notches; outer lateral teeth distinctly different in shape to mid laterals, teeth block-like with single cusped chisel-like mesocone, all possess a pointed endocone; starting around laterals 8–9 the number of ectocones is doubled on outer teeth, endocones and ectocones appear as separate cones, are variably-shaped, bluntly pointed, some almost as large as the mesocone. Dentition formula 15:1:15 +/−1 (n = 3; row count was not assessed).

Jaw (Jenkins 2018: 283, fig. 4H). Located inside front of buccal cavity, orange-brown, arch shaped with unevenly 'shingle'-arranged cone-like rods, ~ 80 rods wide (~ 0.8 mm) by ~ 9–10 rods deep (length = 27 µm, width = 8 µm, n = 12); tip bluntly rounded.

Comparative remarks. Genetically S. *oblia* (*normalis* group, unit 77) is a well-differentiated lineage (Figs 1, 4). It differs from other species by COI distances of ≥ 15.6% (Table S8). In N Qld, this species has been found in sympatry with five congeners: For comparisons with *S. viridisS. atra*, and *S. normalis* refer to comparative remarks under these species. *Siphonaria jiigurruensis* **sp. nov.** has a larger, taller, paler shell with greater edge scalloping, a larger AO, longer ED, and a smaller BC. The combined shell geometry, size, and colouration of S. *oblia* is highly distinctive.

Distribution and habitat. Endemic to tropical NE coast of Australia, Qld, from Torres Strait to just N of Cairns (Fig. 51). In this study, found on moderately exposed rocky intertidal marine shores in sheltered positions (e.g., on under-surface of rocks, amongst oysters, amongst fringes of coralline algae and in crevices), upper and mid littoral levels (Fig. 52P).

***Siphonaria campestra* sp. nov.**

(Figs 53C–D, 54A–C, M–N)

Material examined. *Type material.* Holotype, from Dolokoan Beach 8°31.424'S, 125°37.091'E, N of Dili, Timor-Leste; coll. B.W. Jenkins, TL01-1, 14 July 2019 (AM C.584823 [M447, SK230 (RS)], Fig. 54A). Three paratypes, same data as holotype (AM C.585353 p [SK265], AM C.585354 p [SK266], Fig. 54B; AM C.585355 p [SK267], Fig. 54C).

External morphology (Fig. 54N). Foot sole evenly grey; foot edge and cephalic folds cream, slightly lobed; foot wall, mantle and pneumostomal lobe evenly shaded dark grey, lighter to foot edge; mantle narrower than foot wall, translucent, elongated at anterior, edge thickened, lobed with grey/black banding (over mantle width) aligning with rib interstices and interstice width; pneumostome elongated.

Shell (Figs 54A–C; Table S9). Small sized (max sl mean = 8.1 mm, SD = 0.6 mm, n = 4), ovate; height low to medium; apex offset to posterior and slightly left; apical sides convex, concave and elongated to posterior; protoconch direction homostrophic (n = 1), shell whorl dextral; growth striae prominent uneven, shell thickness thin; shell edge uneven; rib count (mean = 28.3, SD = 2.3, n = 4), exterior with dual shaded bands, paler apical (white ribs and pale brown interstices) and darker shell edge (white ribs and black/dark brown interstices); primary ribs white, crooked, broaden to shell lip, weakly protrude beyond shell lip to unevenly scallop and corrugate the edge, 0–1 interspersed pale white finer secondary ribs; loosely paired primary ribs form siphonal ridge, no more prominent than other primary ribs; interior shell margin very dark brown to black, white rays on shell margin to lip align under primary/secondary ribs, siphonal groove indistinct, spatula very dark chocolate to black with some underlying white; ADM scar distinct, CMS straight; thickening of shell lip not apparent.

Reproductive system (Fig. 53C; n = 2). Positioned within entire right side of coelom, against foot wall on foot muscle, under the respiratory cavity occupying large proportion of animal body volume; epiphallic parts positioned over BM. GA small, with singular GP through foot wall; AO very small, narrow, bluntly pointed, joined to lower ED and upper GA; ED very short, very broad, centrally bent, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG very large, soft whitish tissue, slightly folded, joins ED; extension joins in parallel to single very broad flagellum (F1), similar width to ED, appears as an extension of ED; BD and CD connect side-by-side into GA between ED join and GP, both ducts short, slightly bent, smooth, thickened, whitish, featureless, pass closely together inside outer RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex medium; CD connecting to ducts, BC embedded in folds close to embedded purplish SV; BD without distal loop and MA, with loop immediately prior to BC; BC relatively large, spherical, thin whitish translucent test; HD short, narrow, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobbed; AG larger than HG, outer sides match curvature of inner foot wall.

Spermatophore (Fig. 53D). Broad head with short flagellum (length = 2.38 mm, n = 1); head section cylindrical, bulbous, centrally twisted, rounded tip; test thin, smooth, featureless, translucent encasing a white opaque central core; short tapering section merges head to filamentous flagellum; head shorter, wider than translucent flagellum (head length = 0.95 mm, ~ 40% of SPM length, head width = 103 µm; flagellum width = 17 µm, n = 1); 1 SPM found coiled in two BCs (Fig. 53D).

Comparative remarks. *Siphonaria campestra* **sp. nov.** (*normalis* group, unit **82**) is most closely related to *S. normalis*, *S. madangensis*, *S. fuliginata*, and *S. costellata*, with which it forms a sub-clade in the *normalis* group (Figs 1, 4). However, it is well-differentiated from other species by COI distances of ≥ 18% (Table S2). This species has been found in sympatry with five congeners in TL: For comparisons with *S. alba*, *S. javanica*, and *S. viridis* refer to comparative remarks under these species. *Siphonaria forticosta* **sp. nov.** has a larger, darker shell with a more distinct siphonal ridge, a larger BC and narrower ED. *Siphonaria planucosta* **sp. nov.** has a larger shell with more raised ribbing, a less prominent siphonal ridge, a narrower AO, BD with distal loop, and a larger BC.

Distribution and habitat. Recorded from Dolokoan Beach, Timor-Leste (Fig. 51). In this study, found in sheltered positions (mainly crevices) on moderately exposed rocky shores, upper and lower littoral levels (Fig. 54M).

Etymology. From ‘campestris' (Latin = level, even), referring to the level or even primary ribs on the shell.

Siphonaria camura sp. nov.

(Figs 53E–F, 54D–E, O–P)

Material examined. *Type material.* Holotype, from Tancha Bay, 26°27.897'N, 127°49.131'E, Okinawa, Japan; coll. B.W. Jenkins, JP01-5, 20 March 2020 (AM C.585614 [M491, SK310]). Paratype, same data as holotype (AM C.585195 p [SK331]); paratype from Tancha Bay point, 26°27.941'N, 127°49.194'E, Okinawa, Japan; coll. B.W. Jenkins, JP01-6, 20 March 2020 (AM C.584920 p [M490, SK309]); 5 paratypes from Moon Bay, Onna, Okinawa; coll. B.W. Jenkins, JP01-4, 18 March, 2020 (AM C.585621 5p).

Other, non-type material. **Japan, Okinawa:** Sun Marina Beach, seawall, 26°27.842'N, 127°48.755'E, JP01-1 (AM C.585617 8p); Tancha Bay 1, 26°27.897'N, 127°49.131'E, JP01-5 (AM C.585951 5p, C.585195 p [SK331]); Tancha Bay 2, 26°27.941'N, 127°49.194'E, JP01-6 (AM C.585950, 4p, C.585613 p [SK510]). **China, Hong Kong:** Repulse Bay 22°14.1'N, 114°11.71'E (ZRC. MOL.24899 p).

External morphology (Fig. 54P). Foot sole dark yellowish/grey, paler to foot edge; foot wall, mantle, cephalic folds and pneumostomal lobe all evenly dark yellowish/green in colour; mantle thin, translucent, narrower than foot wall, weakly lobed with a thickened yellow banded edge; faint irregular black blotches of pigmentation on foot wall and cephalic lobes; pneumostome fold long between right ADMs and within mantle.

Shell (Figs 54D–E; Table S9). Small sized (max sl mean = 11.6 mm, SD = 0.9 mm, n = 8), ovate, height tall; shell thin, apex offset strongly posterior and central; apical sides convex, strongly concave at posterior; protoconch direction homostrophic (n=2; Fig. 54P), peaked, hooked to posterior, shell whorl dextral; growth striae uneven; rib count (mean = 35, SD = 0.7, n = 8), exterior unevenly brown, weak radial banding, protoconch area dark brown, paler to shell edge; ribs uneven, increasingly broader and align to uneven fragile and corrugated shell edge, periostracum freely extending; rib interstices darker; siphonal ridge prominent formed by paired primary ribs. Interior shell margin and spatula evenly dark chocolate brown, white rays on shell lip align under rib ends, fade

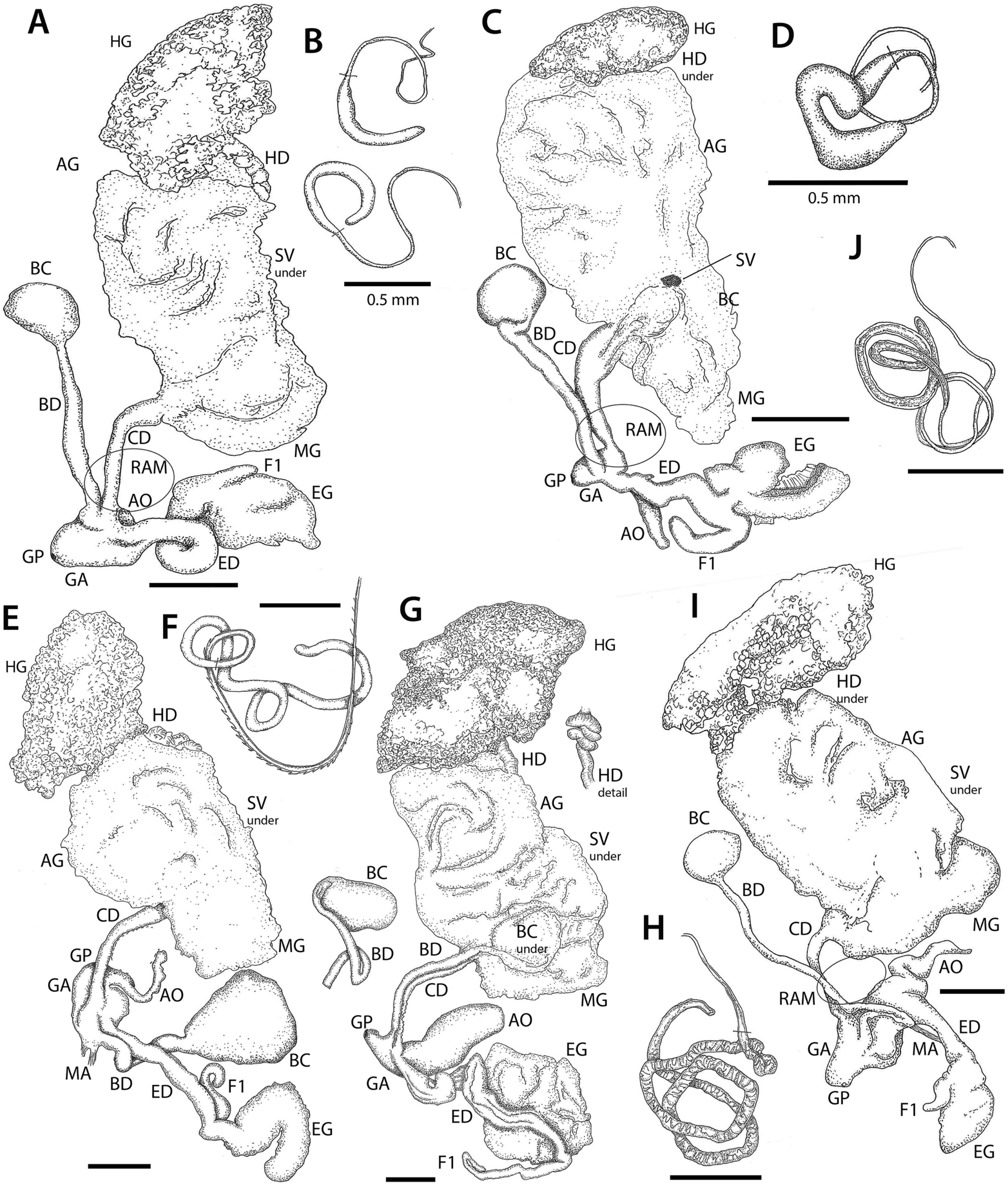

FIGURE 53. Reproductive morphology of *S. jeanae*, *S. campestra* **sp. nov.**, *S. camura* **sp. nov.**, *S. caubianensis* **sp. nov** and *S. christmasensis* **sp. nov. A–B.** *S. jeanae,* WA, Rottnest Is, AM C.585820 [SK215]. **C–D.** Holotype of *S. campestra* **sp. nov.**, Timor-Leste, Dili, AM C.584823 [M447, SK230]. **E–F.** Holotype of *S. camura* **sp. nov.**, Okinawa, Tancha Bay, AM C.585614 [M491, SK310]. **G–H.** *S. caubianensis* **sp. nov**., Philippines, Polillo Is, WAM S113803 [M600, SK557]. **I.** Holotype of *S. christmasensis* **sp. nov.**, CI, Flying Fish Cove, AM C.595957 [M298]. **J.** CI, AM C.585321 [SK083]. Scale bars = 1 mm.

to margin; siphonal groove distinct, same colour as shell margin; ADM scar distinct, CMS straight, indistinct; thickening of shell lip not observed.

Reproductive system (Fig. 53E; n = 3): positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned over BM, BC directly lodged in soft white folds of MG, BD not through

RAM as with CD (n = 2, Fig. 53E); AO small, elongated, narrow, bluntly pointed; ED broad, elongated, centrally twisted, longer than BD; ED (with outer MA) and AO each enter into top of small GA; EG relatively large with folds, often elongated; single, short, broad flagellum F1 with curled end, appears as a right-angled protrusion from end of ED at join with EG; AO, GA and ED all muscular white tissue; BD and CD join GA with swollen opposing connections close to entry of ED and AO; CD passes between inner foot wall and outside RAM connecting into large MG; BD without distal loop, longer and narrower than CD, enters MA alongside or behind ED, both ducts broad smooth; BC large, club shaped, translucent test; HD large, coiled, links soft white folds of AG to similar sized brownish finely granulated HG; SV embedded within AG, outer sides of AG and HG match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 53F). Body cylindrical, thread-like (length = 10.9 ± 3.0 mm, n = 2), test thin, translucent, smooth; head tip bluntly rounded, section containing a white gelatinous core tapers to a thinner flagellum; head section longer thicker than flagellum (head length = 6.0 ± 0.96 mm, n = 2; ~54% of SPM length, flagellum length = 4.8 ± 2.1 mm, head width = 120 ± 0 µm, flagellum width = 50 ± 0 µm, n = 2), outer ridge of mid flagellum possesses 35-17+ evenly spaced barbs pointing towards head; 2 SPM tightly coiled in white gelatinous mass in each BC of two specimens (AM C.584920, AM C.585614).

Comparative remarks. In our mitochondrial phylogeny, *S. camura* sp. nov. (unit 84) is the sister species of *S. japonica* (unit 2); both species together forming a distinctive subclade in the *Siphonaria* tree (Figs 1, 4). Both species differ form each other by COI distances of ≥ 11% (Table S2). Throughout its range, this species has been found in sympatry with five congeners: For comparisons with *S. japonica*, *S. subatra*, *S. sipho*, and *S. rucuana* refer to comparative remarks under these species. *Siphonaria tanchaensis* **sp. nov.** has a larger, taller, paler shell with greater edge scalloping, a white/brown interior and golden-brown spatula, a larger AO, longer narrower BD distal loop, smaller BC, and a longer F1.

Distribution and habitat. Recorded from Okinawa, Japan and Repulse Bay, Hong Kong (Fig. 55). In this study, found on exposed rocky shores in sheltered positions, such as rock crevices, hollows and amongst oysters, mid to upper littoral levels (Fig. 54O).

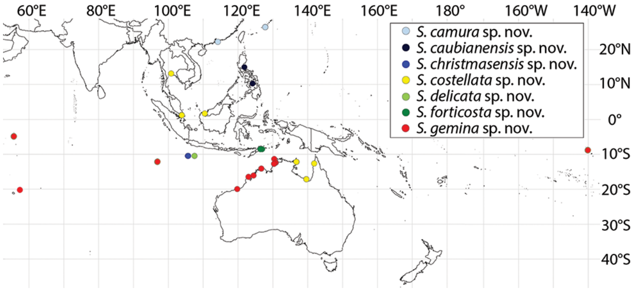

FIGURE 55. Known occurrence records of *S. camura* **sp. nov.**, *S. caubianensis* **sp. nov.**, *S. christmasensis* **sp. nov.**, *S. costellata* **sp. nov.**, *S. delicata* **sp. nov.**, *S. forticosta* **sp. nov** and *S. gemina* **sp. nov.**

Etymology. From ‘camur’ (Latin = curved, bent), referring to the slightly curved, upturned end of the siphonal ridge at the shell lip.

Siphonaria caubianensis **sp. nov.**
(Figs 53G–H, 54F–G)

Siphonaria cf *laciniosa*—Poppe 2010: 440, pl. 911, fig. 4a–c.

S. luzonica—Poppe 2010: 442, pl. 912, figs 4–5 (not *S. luzonica* Reeve, 1856).

S. subatra—Poppe 2010: 444, pl. 913, figs 5–6 (not *S. subatra* Pilsbry, 1904).

Material examined. *Type material.* Holotype, from Caubian Island, 10°17.22’N, 124°10.53’E, Bohol, Philippines (AM C.595933, Fig. 53F). Paratypes. Same data as holotype (AM C.595934 6d, Fig. 53G).

Other, non-type material. **Philippines:** Caubian Island, Bohol, 10°17.22’N, 124°10.53’E (AM C.595932 20+d, C.595935 p [SK559]); NW Polillo Is, E Quezon, Bolunga District, nr Panukalan, 14°59’N, 121°49’E (WAM S72342 10p, WAM S113803 p [SK557]).

External morphology (preserved). Foot sole and foot wall evenly cream, paler to foot edge; mantle pale, translucent, edge thick and lobed band; irregular widely spaced dark pigmentation spots on foot wall, concentrated over posterior and faintly over cephalic lobes.

Shell (Figs 54F–G; Table S9). Medium sized (max sl mean = 20.6 mm, SD = 2.1 mm, n = 20), circular ovate; height medium; apex offset weakly left and posterior, apical sides convex; protoconch direction homostrophic (n = 3), shell whorl dextral; exterior uneven, dark brown, weak radial colour banding; rib count (mean = 30, SD = 3.1, n = 20), ~14–16 primary ribs, straight to slightly bent towards shell edge, primary ribs white or dark brown, number (0–14) and position on shell extremely variable, ridges raised, rounded, broaden slightly and increasingly raised to shell edge, variably and strongly protrude beyond shell lip (often > 3 mm) to strongly and unevenly scallop shell edge; 0–4 finer secondary ribs between primary ribs, rib interstices darker; siphonal ridge formed by closely paired, often end flared, primary ribs. Interior shell dark chocolate brown, spatula white to mottled dark brown; white rays on shell margin aligned in furrows under primary ribs, may extend to spatula, siphonal groove prominent, pale white to dark chocolate brown; ADM scar indistinct, darker than margin and shell edge, CMS straight; thickening and whitening of shell lip not observed.

Reproductive system (Fig. 53G; n = 1). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts positioned over BM; GA small, with singular GP through foot wall; AO large, broad, blunt, joined to upper GA; ED long, wide, centrally twisted, joins to side of AO and GA; GA, AO, ED all white muscular fibrous tissue; EG large, soft whitish tissue, folded, joins ED with single long narrow bent flagellum (F1), appears as a narrower extension of ED; BD and CD connect juxtapose into GA/

FIGURE 54. Shells of *S. campestra* **sp. nov.**, *S. caubianensis* **sp. nov.**, *S. christmasensis* **sp. nov.** and *S. costellata* **sp. nov. A–C, M–N.** *S. campestra* **sp. nov.**, Timor-Leste, Dili. **A.** Holotype AM C.584823 [M447, SK230]. **B.** Paratype AM C.585354 [SK266]. **C.** Paratype AM C.585355 [SK267]. **M.** *In situ*. **N.** Animal. **D–E, O–P.** *S. camura* **sp. nov.**, Okinawa, Tancha Bay. **D.** Holotype AM C.585614 [M491, SK310]. **E.** Paratype AM C.584920 [M490, SK309]. **O.** *In situ*. **P.** Protoconch, AM C.585613 [SK510]. **F–G.** *S. caubianensis* **sp. nov.**, **F.** Philippines, Caubian Is., holotype AM C.595933 [SK560]. **G.** Philippines, NW Polillo Is, WAM S113803 [M600, SK557]. **H–J, Q–R.** *S. christmasensis* **sp. nov.**, CI, Flying Fish Cove. **H.** Holotype AM C.595957 [M298]. **I.** Paratype WAM S74040 [SK069]. **J.** Paratype, Ethel Bch AM C.584846 [M308]. **Q.** Protoconch AM C.585319 [SK071], **R.** CI, *in situ*. **K–L, S–T.** *S. costellata* **sp. nov. K.** Singapore, Lazarus Island, Holotype AM C.585236 [M416, SK100]. **L.** Paratype AM C.585226 [M338]. **S.** Protoconch, AM C.585233 [SK099]. **T.** *In situ*. Unlabelled scale bars 10 mm.

AO, opposing ED join, both ducts long, narrow, slightly bent, whitish, pass closely together through outer side of RAM (smooth featureless BD over wrinkled CD) into soft white folded tissues of MG; MG/AG complex large; CD connecting to ducts, BC embedded in folds close to embedded SV; BD with bursal loop; BC relatively small, elongated, thin whitish translucent test; HD long, broad, coiled, links ducts in soft white folded tissues of AG to granulated HG; outer edge of MG unlobed; AG larger than HG, sides match curvature of inner foot wall.

Spermatophore (Fig. 53H). Thread-like (length = 11.1 mm, 74 % of AL, n = 1); translucent, test thin; head section bluntly rounded, cylindrical, containing a prominent coiled white core, tapers to a thin tip; both sections smooth, featureless. Head section longer wider than flagellum (head length = 9.7 mm, mean ~ 88% of SPM length, head width = 155 µm, flagellum width = 34 µm); 1 SPM tightly folded in BC (WAM S113803).

Comparative remarks. We found this species in sympatry with four congeners on Cebu, Philippines. For comparisons with *S. sirius*, *S. bifurcata*, *S. alba*, and *S. sipho* refer to comparative remarks under these species. We have not been able to sequence material of this species.

Distribution and habitat. Recorded from Cebu and Bohol Islands, Philippines (Fig. 55). Found on rocky intertidal shores.

Etymology. For the type locality, Caubian Island, Philippines.

***Siphonaria christmasensis* sp. nov.**

(Figs 53I–J, 54H–J, Q–R)

Siphonaria 'sp. 1'—Wells & Slack-Smith 2000: 113; Tan & Low 2014: 367.

Material examined. *Type material.* Holotype, from E side Smith Point, Flying Fish Cove, 10°25.749'S, 105°39.957'E, CI; coll. B.W. Jenkins, CI01-1/2, 11 Sept 2018 (AM C.595957 [M298], Fig. 54H), 23 paratypes, same data as holotype (WAM S74040 p [SK069], Fig. 54I, WAM S74075 9p; AM C.585992 9p, AM C.584837 p [M299], AM C.584838 p [M300], AM C.584839 p [M301]); Ethel Beach, 10°27.827'S, 105°42.497'E; coll. B.W. Jenkins, CI02-1, 11 Sept 2018 (AM C.584846 p [M308], Fig. 54J).

Other, non-type material. **Australia, CI:** Off Dale 3, 10°28.52'S 105°33.503'E (AM C.595955 p [SK566]); E side Smith Point Flying Fish Cove, 10°25.749'S, 105°39.957'E CI01-1 (AM C.584836 p [SK021 protoconch A11], C.585319 p [SK071 protoconch C1], C.585321 p [SK083], C.585954 p [SK568]), CI01-2 (AM C.584729 10p); West White Beach, 10°27.748'S, 105°34.934'E CI01-3 (AM C.585922 p [SK567]); Ethel Beach, 10°27.827'S, 105°42.497'E CI02-1 (AM C.585695 8p, C.584846 p [M308]).

Taxonomic remarks. This species has previously been identified as '*Siphonaria* sp. 1' by Wells & Slack-Smith (2000: 113).

External morphology (Fig. 54R). Foot sole grey, foot wall grey to yellowish with black flecked pigmentation; edge of foot sole and foot wall yellowish to white, fading to grey at mantle join; mantle lobed, translucent, narrower than foot wall, patches of black pigmentation occur on lobes, aligning with dark shell rib interstices; cephalic folds grey with black flecks concentrating around lobe join; foot wall and pneumostome pustulose, pneumostome yellowish, wide, within mantle, between right ADMs.

Shell (Figs 54H–I, Q; Table S9). Small (max sl mean = 10.1 mm, SD = 1.4 mm, n = 11); height low to medium; ovate; apex offset posterior and left, apex cap brown, often eroded to appear white; apical sides convex, posterior concave; protoconch direction central to weakly homostrophic (n = 2; Fig. 54Q), shell whorl dextral; growth lines distinct, undulating; rib count (mean = 30.6, SD = 6.3, n = 11), 20–30 primary ribs prominent, often very broad, weakly raised, whitish, straight to weakly bent, width increases strongly to shell lip often touching to replace rib interstices and any infill of 0–1 secondary ribs, extend slightly beyond shell edge creating corrugations and weak scalloping in the uneven shell lip; rib interstices black to dark brown, siphonal ridge slightly raised, indicated by abutting paired primary ribs; segments either side of siphonal ridge often clear of primary ribs, black or brown coloured, show finer secondary ribs; interior shell margin yellowish, white under primary ribs, dark black/brown markings under rib interstices span from shell lip to spatula across the shell margin; spatula brown to dark brown; ADM scar impression distinct, same as shell margin colouring, cephalic scar convex; thickening of shell lip commonly occurs, translucent, not covering black/brown markings of rib interstices, CMS curved.

Reproductive system (Fig. 53I; n = 2). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between BM and RAM; GA small with singular GP through foot wall; AO large elongated centrally twisted, tapers to point, joined to upper GA alongside ED; ED long broad slightly centrally bent, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG large pointed soft whitish tissue, slightly folded, joins ED; single short flagellum (F1) on side. BD and CD join side-by-side into GA between AO join and GP; CD short curved smooth thickened whitish featureless; BD long, narrower than CD, with distal loop and prominent MA; both pass closely together through RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex relatively large; BC embedded in folds of AG/MG close to embedded SV; BD similar thickness to CD; BC small bulbous thin whitish translucent test; HD short narrow coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; AG larger than HG, both outer sides curved to curvature of inner foot wall.

Spermatophore (Fig. 53J). Test thin, translucent (length = 11.27 mm, n = 1, AL = 7.21 mm; possibly longer as flagellum appeared incomplete); head bulbous, tip bluntly rounded, containing a white gelatinous mass; very short taper region into the filamentous transparent flagellum; both sections smooth, featureless; head shorter and much thicker than flagellum (head length = 4.94 mm, ~ 44% of SPM length, head width = 126 µm, flagellum width = 32 µm); single SPM found in one BC (AM C.585321).

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 3), *S. christmasensis* **sp. nov.** (*plicata* group, unit 63) is the sister species of *S. delicata* **sp. nov.** (unit 62). Both species occur on CI forming a well-differentiated lineage. They differ from each other by COI distances of ≥ 10.7% (Table S7). We found this species in sympatry with five congeners on CI: For comparisons with *S. alba*, and *S. incerta* refer to comparative remarks under these species. *Siphonaria tenebrae* **sp. nov.** has a slightly larger, lower, darker shell with greater edge scalloping, a single primary rib forming the siphonal ridge, darker interior, a more pointed AO and a longer F1. *Siphonaria umbra* **sp. nov.** has a slightly larger, lower and darker shell, a larger AO and BC, and a longer F1. *Siphonaria delicata* **sp. nov.** has a smaller, taller, darker shell with less prominent ribs, darker interior, a larger AO and BC, and longer ED and F1.

Distribution and habitat. Known only from CI, Indian Ocean (Fig. 55). In this study, found in sheltered positions on moderately exposed and exposed limestone rocky shores, upper and mid littoral levels (Fig. 54R).

Etymology. For the type locality, Christmas Island, Indian Ocean.

Siphonaria costellata sp. nov.

(Figs 54K–L, S–T, 58A–B)

Siphonaria guamensis—Tan & Chou 2000: 115, fig 115; Tan & Woo 2010: 61; Tan & Yeo 2010: 294 (not *S. guamensis* Quoy & Gaimard, 1833).

Siphonaria sp.—Swennen *et al.* 2001: 142, fig. 522.

Siphonaria '*normalis* group, unit 13'—Dayrat *et al.* 2014: 259, 260, 267, fig. 3O.

Material examined. *Type material.* Holotype, from Lazarus Island, causeway 01°13.288'N, 103°51.195'E, Singapore; coll. Chim C.K. and B.W. Jenkins, SI04-3, 21 Nov 2018 (ZRC.MOL.24890 [M416, SK100], Fig. 54K). 18 paratypes, same data as holotype (AM C.585234 p [M326], AM C.585427 10p, AM C.585677 6p), paratype from Lazarus Island, 01°13.355'N, 103°51.148'E, Singapore; coll. B.W. Jenkins, SI04-2, 24 Nov 2018 (AM C.585226 p [M338], Fig. 54L).

Other, non-type material. **Australia, Qld:** Weipa, 12°37.795'S, 141°51.853'E, Q52-1 (AM C.585186 p [M075]; C.585187 p [M178]); Inspection Pt, Sweers Is, 17°08.471'S, 139°36.868'E, Q56-3 (AM C.585189 p [M147]). **NT:** Nhulunbuy, Cape Wirawawoi, 12°09.513'S, 136°46.904'E, NT05-1A (AM C.585529 20+p, C.585075 p [SK044], C.585076p [M028], C.585077 p [M092]); East Woody Islet, 12°09.695'S, 136°45.075'E, NT05-2 (AM C.585684, 7p); N Turtle Beach, 12°18.816'S, 136°55.930'E, NT04-1 (AM C.585477 17p; C.585990 10+p); Smith Pt 2, 11°07.466'S, 132°08.538'E, NT21-3 (AM C.585989 10+p). **Singapore:** Pasir Ris, seawall, 01°22.981'N, 103°56.956'E, SI01-1 (AM C.585986 10p); Fort Road, drain seawall, 01°17.605'N, 103°53.809'E, SI01-3 (AM C.585603 3p); Lazarus Island, 01°13.355'N, 103°51.148'E, SI04-2 (AM C.585988 16p); Lazarus Island causeway, 01°13.288'N, 103°51.195'E, SI04-3 (AM C.585226 p [M338], C.585233 p [SK099], C.585234 p [M326], C.585236 p [M457, SK183], C.595973 p [M327]); Lazarus Island channel headland, 01°13.085'N, 103°51.429'E, SI04-4 (AM C.585985 10p).

External morphology. Foot sole, foot wall and cephalic folds evenly dark yellowish grey, paler at foot/wall edge; foot wall and mantle more yellowish; mantle lobed with small black pigmentation at thickened edge aligning with rib interstices; translucent, as wide as foot wall, covers exposed inner shell lip; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold; two small black epithelial spots centralised on two centrally touching unpigmented cephalic folds; pneumostomal lobe relatively long, under the mantle, unpigmented, between the right ADMs.

Shell (Figs 54K–L, S; Table S9). Medium to large sized (max sl mean = 11.6 mm, SD = 1.7 mm, n = 7), ovate; medium to tall; apex offset central sightly posterior (usually eroded), apical sides strongly convex, protoconch direction heterostrophic (n = 2; Fig. 54S), shell whorl dextral; growth striae prominent in bands, shell thickness thick; rib count (mean = 45.7, SD = 5.5, n = 7), primary ribs pale white, fairly straight, increasingly raised and protrude beyond shell lip to unevenly scallop and corrugate the edge; 1–2 interspersed pale white finer secondary ribs, rib interstices darker; paired primary ribs on siphonal ridge, no more prominent than other primary ribs. Interior shell margin dark brown to tan, white rays align on shell margin under primary/secondary ribs, siphonal groove distinct, same colour as shell edge, points to right anterior; spatula dark chocolate brown to mottled tan; ADM scar distinct, CMS straight, paler than shell lip; thickening of shell lip translucent, infills and reduces lip scalloping, spatula becomes whitened.

Reproductive system (Fig. 58A; n = 1). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts positioned between RAM and BM. GA very small indistinct with singular GP through foot wall; AO small broad bluntly pointed, joined to GA; ED elongated narrow thickened, slightly centrally bent, joins to GA; GA, AO, ED all white muscular fibrous tissue; EG large, soft whitish tissue, folded, joins ED; single wide flagellum (F1) lays over BM, shorter but similar width to ED, appears as an extension of ED. BD and CD connect side-by-side to GA between AO and GP, both ducts thick short bent smooth whitish, pass together through RAM (BD over thicker CD) into soft white folded tissues of MG, BC embedded in folds close to embedded blackish SV; BD short narrow bent before BC, without distal loop or MA to inner anterior foot wall; CD shorter wider than BD; BC relatively large bulbous, thin whitish translucent test (2 SPM in brownish gelatinous mass of BC); MG/

AG complex relatively large; HD short narrow coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; AG/MG larger than HG, both outer sides curved to curvature of inner foot wall.

Spermatophore (Fig. 58B). Relatively short (length = 4.25 ± 0.196 mm, n = 2, flagellum incomplete), test thin, translucent, containing a white gelatinous core mass; over half-length comprises a translucent bulbous cylindrical head section (head length = 1.646 mm, SD = 0.213 mm, n = 2; mean ~ 39% of SPM length, SD = 3%); tip bluntly rounded, with a prominent twist before tapering into a filamentous transparent flagellum; head section much thicker than flagellum (head width = 116 ± 16 µm, flagellum width = 12 ± 0 µm, n = 2); both sections smooth, featureless; 7–8 SPM tightly coiled in one BC (AM C.585236).

Comparative remarks. In our mitochondrial tree (Figs 1, 4, Clade E), *S. costellata* **sp. nov.** (*normalis* group, unit 13) is more closely related to four species, *S. normalis*, *S. madangensis*, *S. fuliginata*, and *S. campestra*. It differs from any of these by COI distances of ≥ 7.3%. Throughout its range, this species has been found in sympatry with four congeners. Three species are sympatric in northern Australia, from N Qld to Nhulunbuy, NT: For comparisons with *S. viridis*, *S. atra*, and *S. normalis* refer to comparative remarks under these species. In Singapore the species is sympatric with *S. viridis* and *S. alba*; refer to comparative remarks under these species. *Siphonaria madangensis* **sp. nov.** differs in having a smaller, lower shell, a smaller AO, larger BC, and a more bulbous SPM. The specimen identified as '*normalis* group, unit 13' in Dayrat *et al.* (2014: 266, fig. 3O) is a member of *S. costellata*.

Distribution and habitat. Recorded from Thailand, Singapore, Malaysia and NT, Australia (Fig. 55). In this study, found in sheltered and vertical positions on moderately exposed rocky shores across upper littoral levels (Fig. 54T).

Etymology. From 'costellata' (Latin = ribbed), referring to the finely ribbed shell; adjective.

***Siphonaria delicata* sp. nov.**

(Figs 56A–C, M, 58C–D)

Material examined. *Type material.* Holotype, from Ethel Beach 10°27.827'S, 105°42.497'E, Christmas Is, Indian Ocean; coll. B.W. Jenkins, CI02-1, 11 Sept 2018 (AM C.585322 [M421, SK108], Fig. 56A).

Five paratypes, same data as holotype (AM C.585585 2p, WAM S74043 p, WAM S74041 p [M307], Fig. 56C, WAM S74042 p [M410], AM C.608199 p [SK093], Fig. 56B).

External morphology. Animal evenly pale cream without any dark/black pigmentation; paler at foot/wall edge; mantle wider than foot wall, weakly lobed, translucent, covers exposed inner shell lip, outer edge thickened; genital pore indistinct, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two centrally touching cephalic folds; pneumostomal lobe long, under the mantle, unpigmented, between the right ADMs.

Shell (Figs 56A–C; Table S9). size small (max sl mean = 8.5 mm SD = 1.0 mm, n = 4), ovate, shell thin translucent; tall, apex offset to posterior; protoconch below height of apex, direction heterostrophic (n = 2), protoconch area distinctly dark brown to black; anterior apical side convex, posterior side concave, lateral apical sides straight to weakly concave; growth lines prominent; rib count (mean = 29.3, SD = 4.8, n = 3) primary ribs pale to dark grey, weakly raised, secondary ribs not prominent, 1–2 between primary ribs, rib interstices dark brown to black; siphonal ridge not prominent, shell lip even, weakly corrugated with some primary rib ridges; interior polished, shell lip apically banded with white rays aligning with primary ribs extending and narrowing over shell margin and ADM scar to the start of dark chocolate brown spatula; CMS weakly concave, similar but darker colouration to spatula and shell margin; thickening of inner shell lip occurs in larger specimens, resulting in white coating covering the brown/black colouration of inner shell lip.

Reproductive system (Fig. 58C; n = 2). Positioned within entire right side of coelom, against foot wall on foot muscle, under the respiratory cavity occupying large proportion of animal body volume. GA, EG and ED positioned between BM and RAM. GA small, with singular GP through foot wall; AO distinct, bluntly pointed, maybe elongated, joined to upper GA alongside ED; ED long, broad, centrally bent, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG medium, soft whitish tissue, slightly folded, joins ED; single very long flagellum (F1), similar length and width to ED, appears as an extension of ED, possible F2. BD and CD with opposing connections into GA between ED join and GP, CD short,; BD long, both ducts smooth, thickened, whitish, featureless, pass closely together through RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex relatively large; BC embedded in folds close to embedded SV; BD with distal loop(s) and MA, longer thinner than CD; BC relatively large, spherical, thin whitish translucent test; HD short, wide, coiled, links ducts in soft white folded tissues of AG to small, yellowish granulated HG; outer edge of MG lobbed; AG larger than HG, both left outer sides curved to curvature of inner foot wall.

Spermatophore (Fig. 58D). Test thin, translucent (length = 5.77 ± 1.23 mm, n = 2); over half-length comprises a translucent cylindrical head section (head length = 4.73 ± 0.79 mm, ~ 49% of SPM length, n = 3); tip bluntly rounded, containing a white gelatinous core mass; tapers into a filamentous transparent flagellum; head section much thicker than flagellum (head width = 59 ± 1.2 µm, flagellum width = 11 ± 0 µm, n = 3), both sections smooth, featureless; 6 and 3 SPM each in holotype and paratype.

Comparative remarks. In our mitochondrial phylogeny, *S. delicata* **sp. nov.** (*plicata* group, unit 62) is the sister species of *S. christmasensis* **sp. nov.** (Figs 1, 3). Both differ from each other by COI distances of ≥ 10.7%

(Table S7). For comparison with *S. christmasensis* **sp. nov.** refer to comparative remarks under that species. We found this species in sympatry with four other congeners on CI: For comparisons with *S. alba*, and *S. incerta* refer to comparative remarks under these species. *Siphonaria tenebrae* **sp. nov.** has a lower, darker shell with greater edge scalloping and raised ribbing, a smaller AO and BC, and a shorter ED. *Siphonaria umbra* **sp. nov.** has a slightly larger, taller shell with a dual-ribbed siphonal ridge, a shorter ED, and a slightly shorter SPM.

Distribution and habitat. Known only from CI, Australia, and likely endemic to this island (Fig. 55). In this study, found in sheltered positions on exposed rocky shores, at upper littoral level (Fig. 56M).

Etymology. From 'delicata' (Latin = delicate) for the small, delicate shell; adjective.

Siphonaria forticosta sp. nov.

(Figs 56D–F, P, 58E–F)

Material examined. *Type material.* Holotype, from Christi Rea Beach, 8°32.072'S, 125°36.868'E, Timor-Leste; coll. B.W. Jenkins, TL01-2, 14 July 2019 (AM C.584829 p [M441, SK227], Fig. 56P). Paratype, same data as holotype (AM C.585318 p [SK546], Fig. 56E); two paratypes from Dolokoan Beach, 8°31.424'S, 125°37.091'E, N of Dili, Timor-Leste; coll. B.W. Jenkins, TL01-1, 18 July 2019 (AM C.584825 p [M445], Fig. 56F, AM C.584830 p [SK228], Fig. 56P).

Other, non-type material. Dolokoan Beach, 8°31.424'S, 125°37.091'E, N of Dili, Timor-Leste (AM C.585981 8p, C.585991 p [SK547]).

External morphology. Foot sole evenly cream; foot wall, foot edge, cephalic folds and pneumostomal lobe evenly grey cream, darker to foot edge, faint black pigmentation on foot wall; mantle thin, translucent, narrower than foot wall, edge weakly lobed, without pigmentation; cephalic folds small, pneumostome wide.

Shell (Figs 56D–F, P; Table S9). medium to large sized (max sl mean = 15.6 mm, SD = 6.1 mm, n = 2), ovate; height medium to low; apex offset sightly posterior and central (usually eroded), apical sides convex, protoconch direction homostrophic (n= 1, Fig. 56P), shell whorl dextral; growth striae indistinct, shell thick; exterior evenly brown maybe mottled, juveniles display a mix of bluish colouration; rib count (mean = 36, SD = 1.0, n = 2), primary ribs weakly bent, raised and protrude beyond shell lip (up to 1 mm) to unevenly scallop the edge; interspersed with 1–2 finer secondary ribs; single or paired primary ribs form siphonal ridge. Interior shell margin dark brown to tan, spatula dark chocolate brown, white rays aligning under primary/secondary ribs extend irregularly from shell lip over margin, siphonal groove prominent, same colour as shell margin; ADM scar distinct, CMS straight, paler than shell lip; thickening of shell margin noted forming a translucent layer.

Reproductive system (Fig. 58E; n = 2). Positioned within coelom under the respiratory cavity, hermaphroditic complex (HG, AG and MG) to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between RAM and BM; AO medium, elongated, blunt, weakly centrally bent, merges to upper part of indistinct GA, singular GP; ED short, wide, compressed in coil, longer than AO, joins to lower side of GA; GA, AO, ED all white muscular fibrous tissue; EG soft whitish, folded, smaller than AO; single very long twisted uneven thin flagellum (F1), tip of F1 tucks into gap between start of FI and EG; BD and CD jointly but opposing connections to side of GA between AO and GP; both ducts smooth and pass closely together through RAM (BD over CD); BD long narrow with prominent short distal loop without MA to inner body wall, twist immediately prior to connection to medium sized bulbous BC with thin translucent test, embedded in lower folds of MG; CD short, wider than BD; CD connects into MG; HD short, thick, brown markings, coiled, under AG, links AG to much smaller yellowish granulated HG; MG and AG folded, soft white tissue.

Spermatophore (Fig. 58F, J). Thread-like (length = 5.21 mm, 52 % of AL, n = 1); translucent, test thin; head section narrow, bluntly rounded, cylindrical, flagellum tapers to a thin tip, tip attached to inner test of BC; both sections smooth, featureless. Head section longer wider than flagellum (head length = 3.16 mm; ~ 61% of SPM length, head width = 70 μm, flagellum width = 17 μm, n = 1); 3 SPM tightly folded in yellowish gel in BC (AM C.585991).

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 2), *S. forticosta* **sp. nov.** (*atra* group, unit 71, Clade G) is the sister species of a sub-clade containing *S. sirius*, *S. recurva* **sp. nov.**, *S. incerta* **sp. nov.** and an unidentified species from Tonga. It differs from these species by COI distances of ≥ 20% (Table S3). *Siphonaria forticosta* has been found in sympatry with six congeners in TL: For comparisons with *S. javanica*, *S. viridis*, *S. campestra* **sp. nov.**, *S. alba*, and *S. atra*, refer to comparative remarks under these species. *Siphonaria planucosta* **sp. nov.** has a smaller, slightly darker shell with more prominent ribbing, weaker edge scalloping, and a smaller, narrower AO.

Distribution and habitat. Recorded from Dolokoan Beach, Timor-Leste (Fig. 55). In this study, found at mid littoral level in sheltered positions (mainly in crevices) on exposed shore boulders.

Etymology. From contraction of 'fortis' (Latin = strong, sturdy) and 'costa' (Latin = rib), referring to the sturdy primary ribs on the shell of this species.

Siphonaria gemina sp. nov.

(Figs 56G–T, 57A–B, 58G–J, 59A–D)

Siphonaria cf *normalis*—Maes 1967: 119, pl. 14, fig. l; Wells 1994: 19; Tan & Low 2014: 367 (not *S. normalis* Gould, 1846).

Siphonaria normalis—Willan *et al.* 2015: 330 (not *S. normalis* Gould, 1846 (not 1856)).

Siphonaria sp.—Wells & Bryce 1995: 113; 1996: 63.

Siphonaria '*atra* group, unit 51'—Ossenbrügger *et al.* 2023: 38, fig. 2a–b.

Material examined. *Type material.* Holotype, from Nightcliff 12°22.836'S, 130°50.402'E, Darwin, NT; coll. B.W. Jenkins, NT23-1, 8 Sept 2017 (AM C.585485 [M088, SK089], Fig. 56G). Paratype, from Cox Peninsula 2, 12°25.558'S, 130°44.593'E; coll. B.W. Jenkins, NT25-2, 10 Sept 2017 (AM C.585487 p [M089], Fig. 56H), 2 paratypes, from Native Point oyster reef, Dundee Beach 12°42.906'S, 130°20.653'E, NT; coll. B.W. Jenkins, NT26-6, 11 Sept 2017 (AM C.585096 p [M140], AM C.585099 p [M141]).

Other, non-type material. **Australia, Qld:** Sweers Is, 12°03.456'S, 96°52.329'E, Q56-2 (AM C.585188p [M091]). **NT:** Luxmore Hd, Melville Is, 11°20.639'S, 130°23.149'E, NT24-1 (AM C.585336 p); Nightcliff, Darwin, 12°22.836'S, 130°50.402'E NT23-1 (AM C.585090 p [SK078 protoconch C5], C.585091 p [SK089]); Cox Peninsula 2, 12°25.558'S, 130°44.593'E NT25-2 (AM C.585092 p [M144], C.585093 p [M145], C.585094 p [M090, SK091], C.585098 p [M143]); N of Native Point, Dundee Beach, 12°42.182'S, 130°20.881'E NT26-1 (AM C.585095 p [SK103], C.585337 p [SK088]); Native Point oyster reef, Dundee Beach, 12°42.906'S, 130°20.653'E NT26-6 (AM C.585097 p [M094]); Native Point reef, Dundee Beach, 12°42.981'S, 130°20.807'E NT26-3 (AM C.585488 p [M146]). **WA:** Tait Point, Mission Bay, 14°05.442'S, 126°41.143'E, WA04-1 (AM C.584669 p [SK246]; Raft Point Collier Bay, 16°04.045'S, 124°26.814'E, WA17-2 (AM C.584668 p [M464, SK199]); Catamaran Bay, 16°27.622'S, 123°00.242'E, WA22-3 (AM C.585301 p [M071, SK090], C.585302 p [M072], C.585303 p [M043]); Cape Keraudren, 19°57.393'S, 119°46.358'E, WA29-2 (AM C.585308 p [M032]). **Mauritius:** Nth Albion Is, Mauritius, 20°12.258'S, 57°24.252'E, MRU2-2 (AM C.584971 [M249], Fig. 56I, C.585976 20p, AM C.584972 p [M250], Fig. 56J). **Australia, CKI:** E coast of Home Is, 12°06.917'S, 96°53.835'E, CKI04-1 (WAM S74044 [M317, SK255], Fig. 56K, AM C.608183 15p, C.584666 p [M318], C.584667 p [M319]); S coast of West Is, 12°12.210'S, 96°50.372'E, CKI02-2 (AM C.584849 p [M315], Fig. 56L, C.584850 p [M316]); West Island, N point (Trannies), 12°08.540'S, 96°49.013'E, CKI01-1 (AM C.585372 10p); S coast of West Is, 12°12.210'S, 96°50.372'E, CKI02-2 (AM C.585373 10p, C.584665 p [M314], C.585933 p [SK092], C.585942 p [SK086]); N coast Direction Is, 12°03.456'S, 96°52.329'E, CKI03-1 (AM C.585374 10p, C.585941 p [SK535]). **Marquesas Islands:** Nuku Hiva, Baie des Controleurs, 08°53.92'S, 140°02.92'W, MQ7-M (MNHN IM-2013-74895 [M574], Fig. 57A), Baie d'Hakatea, 08°56.53'S, 140°09.69'W, MQ25-M, (MNHN IM-2013-74904 p [M566], Fig. 57B; IM-2013-74902 p [M571], IM-2013-74900 p [M576], IM-2013-74903 p [M572], MNHN IM-2013-74901 p [M573]), Baie des Controleurs, 08°53.92'S, 140°02.92'W, MQ7-M (MNHN IM-2013-67892p [M578], IM-2013-74894 p [M575], IM-2013-74896 p [M564]).

External morphology (Fig. 56M). Foot sole and foot wall evenly pale yellowish grey, paler at foot/wall edge; foot wall and mantle more yellowish, without black pigmentation; mantle strongly lobed, translucent, as wide as foot wall, covers exposed inner shell lip; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two centrally touching unpigmented cephalic folds; pneumostomal lobe long, under the mantle, unpigmented, between the right ADMs.

Shell (Fig. 56G–T, 57A–B; Table S9). Shell ribbing and colouration variable; small sizing (max sl mean = 9.3 mm, SD = 1.7 mm, n = 8); ovate to elongate, height medium; apex often tall, pointed (protoconch very tall when intact), slightly offset posteriorly and left; protoconch direction heterostrophic (n = 2; Fig. 56T) to upright (n = 2; Fig. 56Q), shell whorl dextral; apical sides weakly convex, posterior concave; protoconch area distinctly darker brown, growth lines usually distinct undulating; rib count (mean = 28, SD = 5.3, n = 8), primary ribs white, curved, wavy, moderately flare at and extend beyond shell edge, rib ridges rounded, rib interstices dark brown/black; paired primary ribs form siphonal ridge, extend well beyond line of shell lip, strongly to weakly flared upwardly at shell edge; none to one secondary ribs between primary ribs, either side of siphonal ridge the number of secondary ribs greater; interior shell lip uneven, corrugated to no corrugations, shell lip with white blotches or rays under primary ribs, dark brown/black under rib interstices; white rays may extend over shell margin; spatula usually evenly dark brown/black but may be white to dull white; siphonal groove usually white, may be dark brown/black, bounded on either side by prominent dark brown/black axial patches aligning with primary rib interstices. WA and NT specimens often with heavy and strongly raised ribbing with corrugations on shell lip, CKI specimens possess flatter ribs and few to no corrugations on shell lip; thickening of inner shell lip and spatula not observed.

Reproductive system (Fig. 58G, I, 59A; n = 5). Positioned within coelom under the respiratory cavity, occupies the entire right side of coelom, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between BM and RAM; GA small, with singular GP through foot wall; AO very small, bluntly pointed, joined to upper GA alongside ED; ED short, broad, slightly bent (without prominent MA), joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG large, soft whitish tissue, slightly folded, joins ED; single narrow flagellum (F1; possible 2nd flagellum), similar length and width to ED, appears as a continuous extension of ED to EG, laid over BM, often centrally bent; BD and CD connect together into GA between ED/AO joint and GP, both ducts short, straight, smooth, thickened, whitish, featureless, pass closely together through RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex relatively large; BC embedded in folds of AG/MG close to embedded SV; BD on posterior side only, unlooped, similar thickness to CD; BC relatively large, spherical, thin translucent test; HD short, not thickened, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobbed; AG much larger than HG, sides match curvature of inner foot wall.

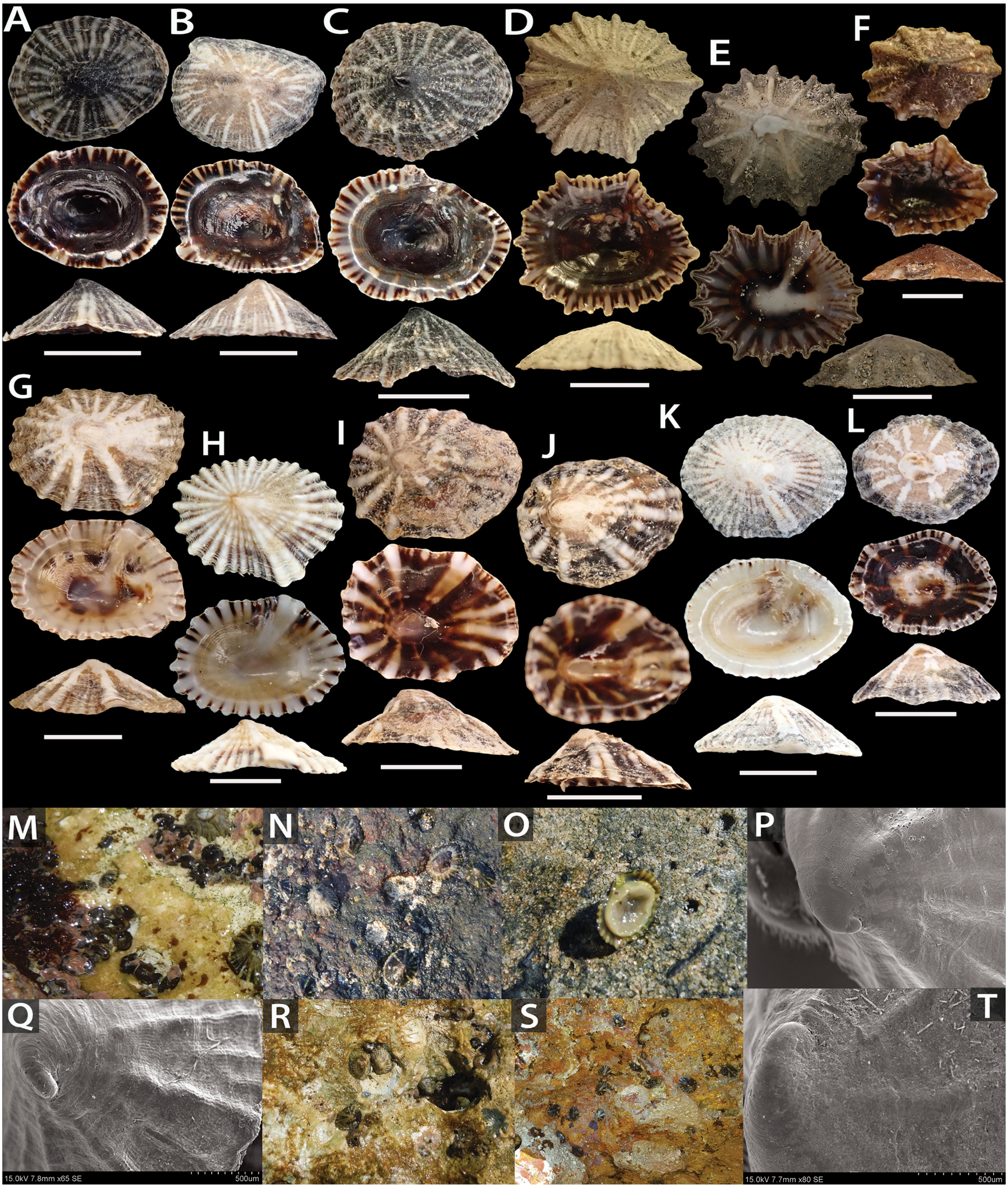

FIGURE 56. Shells of *S. delicata* **sp. nov.**, *S. forticosta* **sp. nov.**, *S. gemina* **sp. nov. A–C, M.** *S. delicata* **sp. nov**., CI, Ethel Beach. **A.** Holotype AM C.585322 [M421, SK108]. **B.** Paratype AM C608199 [SK093]. **C.** Paratype WAM S74041 [M307]. **M.** *In situ*. **D–F, P.** *S. forticosta* **sp. nov.**, Timor-Leste, Dili. **D.** Holotype AM C.584829 [M441]. **E.** Paratype AM C.585318 [SK546]. **F.** Paratype AM C.584825 [M445]. **P.** Protoconch, AM C.584830 [SK228]. **G–T.** *S. gemina* **sp. nov. G.** NT, Darwin, holotype AM C.585485 [M088]. **H.** NT, Cox Peninsula, paratype AM C.585487 [M089]. **Q.** NT, protoconch, AM C.585337 [SK088]. **S.** Darwin, animal. **T.** Darwin, *in situ*. **I–J, N.** Mauritius, North Albion. **I.** AM C.584971 [M249]. **J.** AM C.584972 [M250]. **N.** *In situ*. **K–L, O, R.** CKI. **K.** WAM S74044 [M317]. **L.** AM C.584849 [M315]. **O.** Animal. **R.** *In situ*. Scale bars 5 mm.

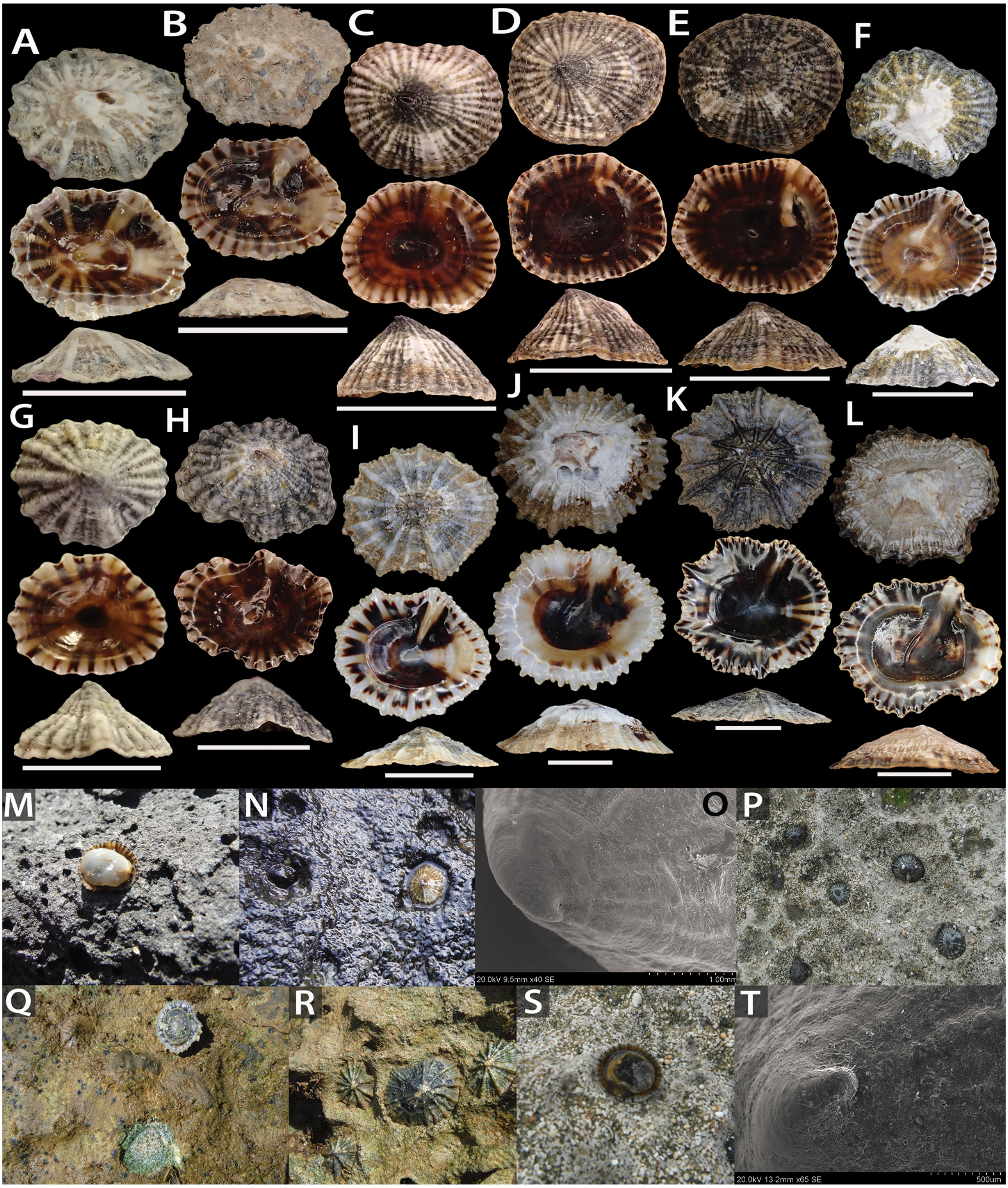

FIGURE 57. Shells of *S. gemina* **sp. nov.**, *S. griffithsorum* **sp. nov.**, *S. tongatapuensis* **sp. nov.** and *S. hienghenensis* **sp. nov. A–B.** ***S.*** *gemina* **sp. nov.**, Marquesas, Nuku Hiva. **A.** IM-2013-74895 [M574]. **B.** IM-2013-74904 [M566]. **C–E, M–N, T.** *S. griffithsorum* **sp. nov.**, Mauritius, Souillac. **C.** Holotype AM C.584963 [M256]. **D.** Paratype AM C.584966 [M257]. **E.** Paratype AM C.585909 [SK389]. **M.** Animal**. N.** *In situ*. **T.** Protoconch, AM C.585909 [SK389]. **F–H, O–P, S.** *S. tongatapuensis* **sp. nov.**, Tongatapu, Halafuoleva Bch. **F.** Holotype AM C.585279 [M420, SK107]. **G.** Paratype AM C.585281 [SK224]. **H.** Paratype AM C.585911 [SK387]. **O.** Protoconch, AM C.585282 [SK222]. **P.** *In situ*. **S.** Animal. **I–L, Q–R.** *S. hienghenensis* **sp. nov.**, NC, Ponerihouen. **I.** Holotype AM C.584989 **[**SK127]. **J.** Paratype AM C.584985 [M355]. **K.** Ouassé, paratype AM C.584990 [SK170]. **L.** Ouassé paratype AM C.584805 [M375]. **Q.** Ponerihouen, animal. **R.** Ponerihouen, *in situ*. Scale bars = 10 mm.

Spermatophore (Fig. 58H, J, 59B). Broad head with short flagellum (length = 4.0 ± 2.9 mm, 64% of AL, n = 4), head section cylindrical, bulbous, centrally bent, rounded tip; test thin, smooth, featureless, translucent encasing a white opaque central core; short tapering section merges head to filamentous flagellum; head shorter, wider than translucent flagellum (head length = 1.8 ± 0.18 mm, ~ 82% of SPM length, head width = 171 ± 14.8 µm, flagellum width = 24 ± 1.3 µm, n = 4); 1 SPM coiled in one BC (AM C.585488). The SPM of specimens from Mauritius differs somewhat in having a shorter flagellum (Fig. 58J, length = 4.34 ± 3.42, n = 3, AM C.584971). Specimens from the Cocos (Keeling) Islands have a broad head with short flagellum (length = 5.8 ± 3.2 mm, n = 2), head section cylindrical, bulbous, centrally bent, rounded tip; test thin, smooth, featureless, translucent encasing a white opaque central core; short tapering section merges head to filamentous flagellum; head shorter, wider than translucent flagellum (length = 4.0 ± 2.1 mm, ~ 69% of SPM length, head width = 249 ± 20.2 µm; flagellum width = 29 ± 2.1 µm, n = 4); 1–2 SPM in each of two BC (WAM S74044, AM C.585942).

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 4), *S. gemina* populations from north-western Australia, CKI, Mauritius, and the Marquesas Islands form a clade with little apparent genetic differentiation between them (*normalis* group, unit 78). COI sequences of this unit differ from each other by genetic distances of up to 6.2% (Table S8). We observed minor, yet consistent morphological differences between populations from mainland Australia, Mauritius, the Marquesas Islands, and the Cocos Keeling Islands in features of the shell, BC, and SPM. However, we consider these differences to represent intraspecific morphological variation. *Siphonaria gemina* **sp. nov.** is the sister species of an unidentified *Siphonaria* sp. (unit 11, from NT, Australia and Yap Is). These two clades differ by COI distances of ≥ 14.1% (Table S8). Throughout its range in tropical WA, we found *S. gemina gemina* in sympatry with five congeners: For comparisons with *S. alba*, *S. normalis*, *S. zelandica*, and *S. viridis* refer to comparative remarks under these species. *Siphonaria restis* **sp. nov.** has a larger, lower, sturdier shell with a less prominent siphonal ridge, stronger edge scalloping, a larger AO and BC, longer ED and BD, and a shorter SPM. Specimens figured as '*Siphonaria* unit 51' by Ossenbrügger *et al.* (2023) belong to the same MOTU, unit 78 and correspond well with specimens examined here.

Distribution and habitat. *Siphonaria gemina* has a wide distribution spanning Mauritius, the Seychelles, the Cocos (Keeling) Islands, Tropical Australia, between Cape Keraudren in northern WA and the Sweers Is, Gulf of Carpentaria, Qld, to the Marquesas Islands (Fig. 55). In this study, found on moderately exposed rocky shores, in upper littoral level (Fig. 56S).

Etymology. From 'geminus' (Latin = paired), referring to the prominence of paired siphonal primary ribs accentuated by dark flanking bands on the shell of this species; adjective.

Siphonaria griffithsorum sp. nov.

(Figs 57C–E, M–N, T, 59E–F)

Siphonaria '*laciniosa* group, unit 25'—Dayrat, *et al.* 2014: 261 (in part).

Material examined. *Type material.* Holotype, from Souillac 20°31.519'S, 57°31.633'E, Mauritius; coll. B.W. Jenkins, MRU01-1, 9 Aug 2018 (AM C.584963 [M256], Fig. 57A). Six paratypes, same data as holotype (AM C.585910 4p), Souillac 20°31.467'S, 57°31.582'E, Mauritius; coll. B.W. Jenkins, MRU01-2, 9 Aug 2018 (AM C.584966 p [M257], Fig. 57B; AM C.585909 p [SK389], Figs 57C, T).

Other, non-type material. **Mauritius:** Isle de la Passe 20°24'S, 57°46.133'E (WAM S72343 7p).

External morphology (Fig. 57M). Foot sole, foot wall, cephalic folds and pneumostomal lobe evenly cream, foot edge and mantle paler; mantle narrow, edge lobed, thickened, faint grey banding aligning with shell rib interstices; faint grey pigmentation over cephalic lobes.

Shell (Figs 57C–E; Table S9). small sized (max sl mean = 9.3 mm, SD = 0.5 mm, n = 2), ovate, height medium; apex offset weakly posterior and to left; apical sides convex, posterior concave to straight; protoconch direction weakly heterostrophic to central (n = 1, Fig. 57T), area black colouration, shell whorl dextral; growth striae weak; shell thickness thin; colouration uneven with some radial banding; rib count (mean = 41.5, SD = 1.5, n = 2); slightly raised, pale white, fairly straight, faintly protrude beyond shell lip; predominantly primary ribs, finer secondary ribs interspersed, develop between primary ribs with shell growth, rib interstices darker; siphonal ridge formed by paired primary ribs, protrudes past shell edge, otherwise indistinct. Interior evenly dark brown to black from margin to spatula, paler on shell lip aligning under rib ends, siphonal groove clear; ADM scar indistinct, CMS weakly convex; No evidence of growth variations in shell thickness or shell margin colouration.

Reproductive system (Fig. 59E; n = 1): Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts lay over BM and to side of RAM, F1 folded over back of BM. ED distinct entry to top of GA; AO large, elongated, bluntly pointed hook, centrally bent, attached to top of large, bulbous GA; ED thick, elongated, centrally bent, twisted; AO, GA and ED all muscular white tissue; EG large, folded, soft white tissue; single elongated, centrally looped, broad, blunt flagellum F1 appears as extension of ED at EG join; BD and CD connect into GA in opposing directions close to ED attachment, both ducts smooth, short, thick, slightly bent, pass together between RAM and inner foot wall (BD over CD) connecting into MG, BD with coiled distal loop; BC white opaque test, relatively large, bulbous, embedded along with part of BD in soft white folds of MG, inner edge of MG lobed; HD narrow, coiled, links soft white folded AG to small yellowish granulated HG; AG larger than HG, both with outer sides curved

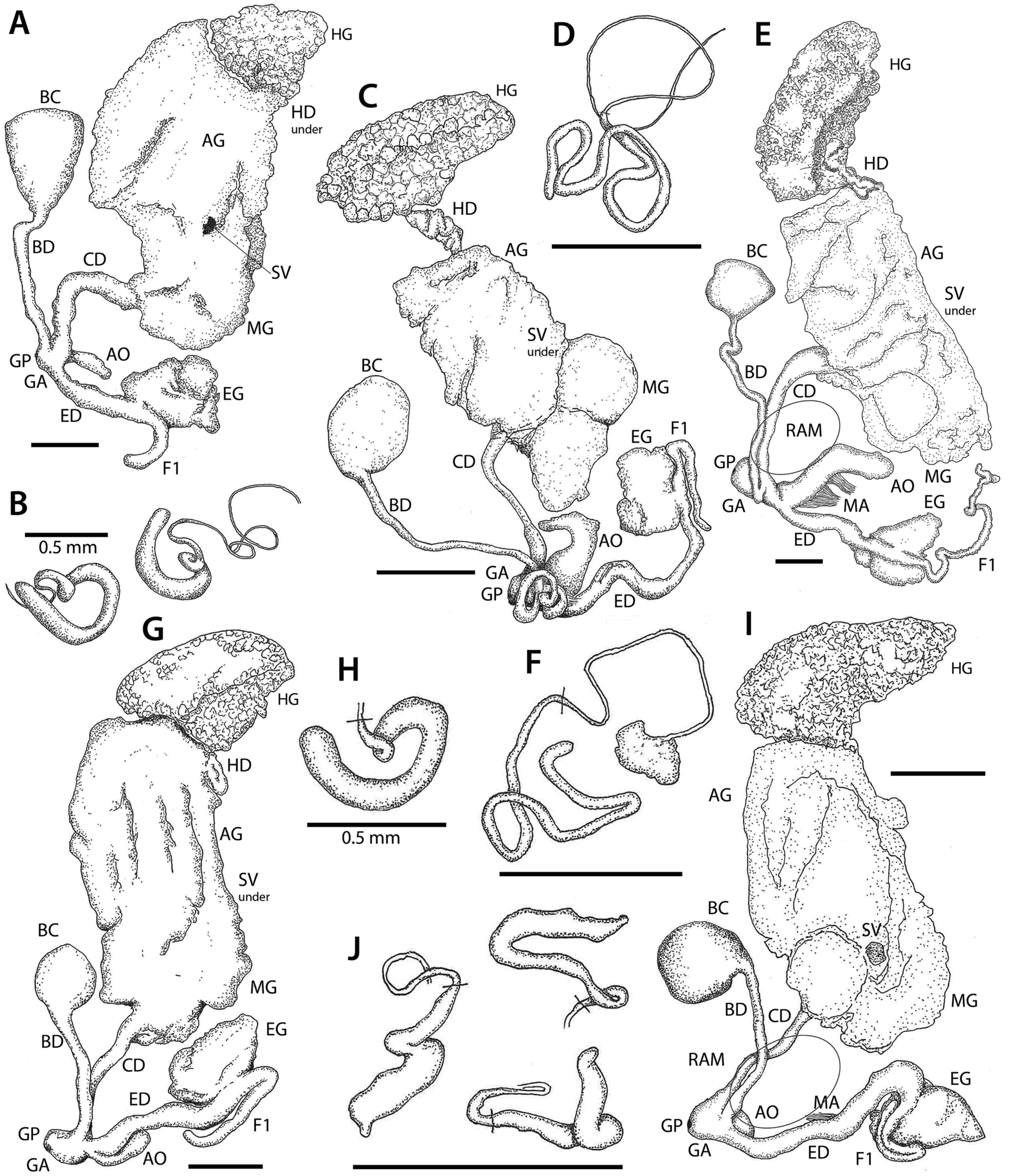

FIGURE 58. Reproductive morphology of *S. costellata* **sp. nov.**, *S. delicata* **sp. nov.**, *S. forticosta* **sp. nov.** and *S. gemina* **sp. nov.** **A–B.** Holotype of *S. costellata* **sp. nov.** ZRC.MOL.24890 [M416, SK100], Singapore, Lazarus Is. **C–D.** Paratype of *S. delicata* **sp. nov.** AM C.608199 [SK093], CI. **E.** Holotype of *S. forticosta* **sp. nov.** AM C.584829 [M441, SK227], Timor-Leste, Dili. **F.** *S. forticosta* **sp. nov.**, AM C.585991 [SK547]. **G–H.** Holotype of *S. gemina* **sp. nov.** AM C.585485 [M088], NT, Darwin. **I–J.** *S. gemina* **sp. nov.**, Mauritius AM C.584971 [M249]. Unlabelled scale bars 1 mm.

reflecting the close positioning to curvature of inner foot wall at right posterior quarter of coelom; SV embedded in AG close to BC.

Spermatophore (Fig. 59F). Thread-like (length = 8.98 mm, n =1), translucent, test thin; head section bluntly rounded, evenly cylindrical, containing a core white gelatinous mass, tapers along the transparent flagellum to a thin tip; keel as high as body width occurs along mid ¾ of head section; both sections smooth, featureless. Head section longer wider than flagellum (head length = 6.89

mm, ~ 77 % of SPM length, flagellum length = 2.08 mm, head width = 103 µm, flagellum width = 17 µm, n = 1). 3 SPM tightly coiled embedded in whitish gelatinous mass in BC (AM C.584966).

Comparative remarks. *Siphonaria griffithsorum* **sp. nov.** (*plicata* group, unit 64) is well-individualised genetic lineage within the pectinate group. It represents the sister lineage of the species pair *S. delicata* **sp. nov.** and *S. christmasensis* **sp. nov.** (Figs 1, 3). It differs from other species by COI distances of ≥ 23.7% (Table S7). We found *S. griffithsorum* **sp. nov.** in sympatry with two congeners: For a comparison with *S. plana* and *S. incerta* refer to comparative remarks under these species. *Siphonaria griffithsorum* **sp. nov.** closely resembles *S. lirata* from Guam by having a heterostrophic protoconch.

Distribution and habitat. Recorded as endemic to Mauritius, Indian Ocean (Fig. 60). In this study, found in sheltered positions on exposed rocky shores, upper and mid littoral levels (Fig. 57N).

Etymology. For Mary-Ann and Owen Griffiths, Mauritius, in recognition of their hospitality and selfless assistance with collecting provided to the first author whilst visiting Mauritius.

Siphonaria tongatapuensis sp. nov.

(Figs 57F–H, O–P, S, 59G–H)

Material examined. *Type material.* Holotype, from Halafuoleva Beach, 21°12.021'S, 175°14.680'W, S coast of Tongatapu, Tonga; coll. B.W. Jenkins, TO03-1-2, 23 May 2019 (AM C.585279 [M420, SK107], Fig. 57F). Paratypes, same data as holotype (AM C.585540 20+p; AM C.585281 p [SK224], Fig. 57G; AM C.585911 p [SK387], Fig. 57H).

Other, non-type material. **Tonga:** Halafuoleva Beach, S coast Tongatapu, 21°08.358'S, 175°02.443'W, TO03-1-2 (AM C.586002 3p, C.585282 p [SK222]).

External morphology (Fig. 57P). Foot sole dark grey; foot edge and cephalic folds cream; foot wall, mantle and pneumostomal lobe evenly grey, darker to foot edge, some irregular blotches of black pigmentation on foot wall; mantle thin, translucent, narrower than foot wall, edge thickened, lobed, with weak black banding aligning with rib interstices, pneumostome wide.

Shell (Figs 57F–H, O, P; Table S9). Small sized (max sl mean = 11.1 mm, SD = 1.5 mm, n = 2), circular ovate; height medium; apex offset central, apical sides convex, protoconch direction central to homostrophic (n=1, Fig. 57O); shell whorl dextral; initial growth profile very tall, profile flattens with maturity, exterior pale blue/grey uneven, protoconch area darker, shell thick, growth striae prominent; rib count (mean = 34.5, SD = 7.5, n = 2), primary ribs pale grey, fairly straight, ridges rounded, increasingly raised to and extend beyond uneven shell lip to unevenly scallop the lip; two prominent primary ribs extending strongly beyond shell edge form the siphonal ridge. Interior tan to golden brown, shell lip white with dark chocolate brown rays extending over shell margin and ADM to spatula, aligning under rib interstices; siphonal groove prominent; ADM scar distinct, CMS convex; no thickening of shell lip noted.

Reproductive system (Fig. 59G; n = 1). Positioned within right coelom under the respiratory cavity, hermaphroditic complex (HG, AG and MG) to posterior against right foot wall and over foot sole, epiphallic parts to anterior between RAM and BM; AO medium, broad, blunt, weakly centrally bent, side MA, merges to upper part of indistinct GA, singular GP; ED short, wide, compressed in coil, longer than AO, joins to lower side of GA; GA, AO, ED all white muscular fibrous tissue; EG soft whitish, folded, slightly smaller than AO; single twisted thin flagellum (F1) lays over MG; BD and CD join closely but with opposing connections to side of GA between AO and GP; both ducts smooth and pass closely together through RAM (BD over CD); BD long very narrow with prominent short distal loop with MA to inner body wall, connected to small sized bulbous BC with thin translucent test, positioned in folds of AG; CD short, wider than BD; CD connects into MG; HD short, thick, brown markings, coiled, under AG, links AG to much smaller yellowish granulated HG; MG and AG folded, soft white tissue. Several parasite eggs were found on the EG and AG of holotype (Halafuoleva Beach, S coast Tongatapu, Tonga).

Spermatophore (Fig. 59H). Thread-like (length = 5.64 mm, n =1), translucent, test thin; head section bluntly rounded, evenly cylindrical, containing a core white gelatinous mass, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless. Head section longer wider than flagellum (head length = 3.36 mm, ~ 64% of SPM length, n = 1; flagellum length = 1.98 mm, head width = 45 µm, flagellum width = 11 µm). 2 SPM tightly coiled, embedded in purple/brown gelatinous mass in one BC (AM C.585281).

Comparative remarks. In our mitochondrial phylogeny (Figs 1–4), *S. tongatapuensis* **sp. nov.** (*plicata* group, unit 69) is a well-individualized lineage that represents the sister group of a clade comprising *S. guamensis*, an unidentified species from Rarotonga ('unit 17' in Dayrat *et al.* 2014), and *S. nusalikensis* **sp. nov.** It differs from other species by COI distances of ≥ 26% (Table S7). We found *S. tongatapuensis* **sp. nov.** in sympatry with *S. plicata*; for comparative remarks refer to that species. While both species have a similar RS structure, in particular size and shape of the epiphallic parts and SPM, they clearly differ in shell sculpture, colouration, and absence of a prominent multi-ribbed siphonal ridge. *Siphonaria tongatapuensis* **sp. nov.** differs from other species of the *plicata* group, such as *S. nuttallii*, *S. lirata*, and *S. monticulus* particularly in size and shape of AO, ED, and HD. The SPM shape of these species is generally similar. *Siphonaria nuttallii* has the most similar RS.

Distribution and habitat. Recorded exclusively from Halafuoleva Beach, Tonga (Fig. 60). In this study, found in sheltered positions (mainly in rock hollows) on exposed rocky shores, mid and upper littoral levels (Fig. 57P).

Etymology. For Tongatapu, Tonga, where this species is found.

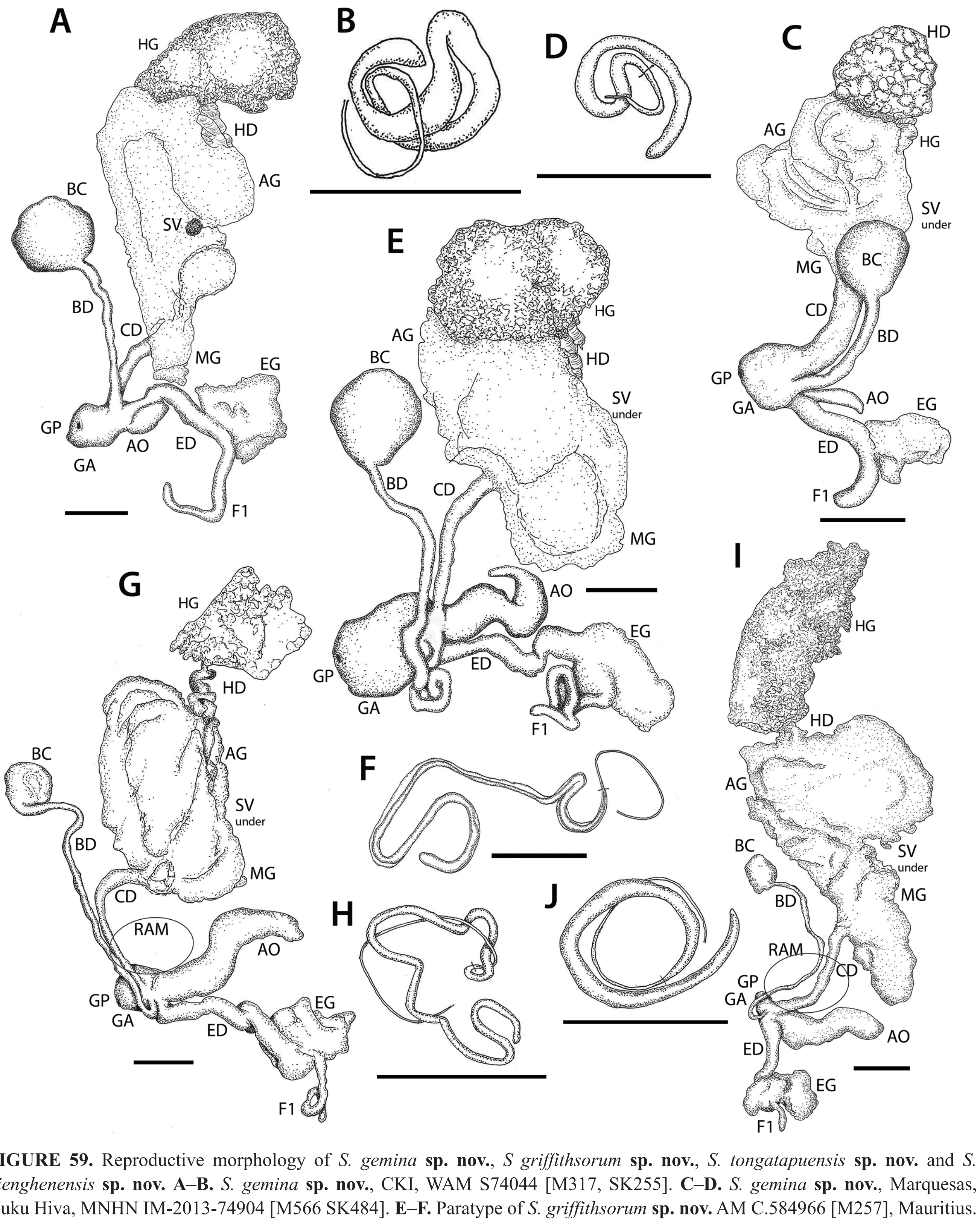

FIGURE 59. Reproductive morphology of *S. gemina* **sp. nov.**, *S griffithsorum* **sp. nov.**, *S. tongatapuensis* **sp. nov.** and *S. hienghenensis* **sp. nov.** **A–B.** *S. gemina* **sp. nov.**, CKI, WAM S74044 [M317, SK255]. **C–D.** *S. gemina* **sp. nov.**, Marquesas, Nuku Hiva, MNHN IM-2013-74904 [M566 SK484]. **E–F.** Paratype of *S. griffithsorum* **sp. nov.** AM C.584966 [M257], Mauritius. **G–H.** Holotype of *S. tongatapuensis* **sp. nov.** AM C.585279 [M420, SK107], Tongatapu, Halafuoleva Beach. **I–J.** Holotype of *S. hienghenensis* **sp. nov.** AM C.584989 [SK127], NC, Ponerihouen. Scale bars = 1 mm.

Siphonaria hienghenensis sp. nov.

(Figs 57I–L, Q–R, 59I–J)

Siphonaria '*atra* group, unit 40'—Dayrat *et al.* 2014: 264 (in part)

Material examined. *Type material.* Holotype, from Ponerihouen, 21°05.644'S, 165°26.646'E, NC; coll. B.W. Jenkins, NC03-1, 23 Oct 2018 (AM C.584989 [SK127], Fig. 57I). 27 paratypes, same data as holotype

(AM C.585524 20+p, C.584985 p [M355], Fig. 57J, C.584986 p [M357], C.584987 p [M358], C.584988 p [M378], C.584990 p [SK170], Fig. 57K, C.584991 p [SK362]); paratye from Ouassé nr Canala, 21°30.346'S, 166°03.732'E, NC; coll. B.W. Jenkins, NC02-1, 22 Oct 2018 (AM C.584805 p [M375], Fig. 57L).

Other, non-type material. **NC:** Hienghène, 20°41.210'S, 164°59.108'E NC04-1 (AM C.584808 p); Ouassé nr Canala, 21°30.346'S, 166°03.732'E, NC02-1 (AM C.585968 10+p); S of Pouebo NC04-2 (AM C.585399 7p); Presqu'ile de Ouano La Foa 20°51.434'S, 165°48.479'E NC06-4 (AM C.584816 3p); Presq'ile Ducos Baie des Dames Noumea 22°14.170'S, 166°24.524'E NC01-1 (AM C.584803 16p).

External morphology (Fig. 57Q). Foot sole, foot wall, mantle evenly pale grey, paler to foot edge; no pigmentation; mantle covers shell lip, wide, edge thickened lobed, paler grey; pneumostome lobe large, under mantle.

Shell (Figs 57I–L; Table S9). Medium sized (max sl mean = 19.8 mm, SD = 1.9 mm, n = 7), ovate to elongate; height medium to low; apex offset central, apical sides strongly convex, protoconch direction undetermined, shell whorl dextral; growth striae prominent in bands, shell thickness thick; 3 radial band layers: whitish protoconch, mid shell dark brown band, and mid shell to edge pale brown/grey band; growth lines indistinct; rib count (mean = 45, SD = 6.5, n = 7), primary ribs pale white, fairly straight, ridges rounded, increasingly raised to and slightly protrude beyond uneven shell lip; shell lip scalloped between primary ribs; paired primary ribs form siphonal ridge which protrudes up to 1 mm beyond shell lip; secondary ribs similar to primary ribs, rib interstices slightly darker, indistinct. Interior margin irregular brown patterns; underside of primary ribs furrowed, white to cream rays, rib interstices marked with dark brown rays, some rays extend from spatula to shell lip; spatula dark chocolate brown, maybe white in smaller/juvenile specimens; siphonal groove distinctly furrowed, fairly straight bounded by dark brown patches; ADM scar distinct white to brown, paler than spatula and margin, CMS straight, paler than shell lip; Internal shell thickening occurs in larger/more mature specimens; shell lip thickens, whitens with yellow tinge, infills and reduces lip scalloping, spatula becomes whitened, distinct dark brown patches remain prominent on both sides of the siphonal groove. Significant colour and sculpture variation exists in the shell of this species.

Reproductive system (Fig. 59I; n = 5). Overall very small; hermaphroditic (HG, AG and MG) complex (AL=12.52mm) on right side within coelom against inside of foot muscle and foot wall under the respiratory cavity and intestine; epiphallic parts beside BM and RAM; GA very small; AO very large, elongated, bluntly bulbous, joins to GA, singular GP; ED relatively short, broad, smaller than AO, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG soft whitish, slightly folded, smaller than AO, single short blunt flagellum (F1); BD and CD jointly but opposing connections to GA between ED, AO and GP; BD narrow short with a prominent distal loop without any MA; CD broad short; both ducts smooth and pass closely together through RAM (BD over much broader CD); CD connects into MG; BD connects to small BC with thick white test, embedded in mid folds of MG/AG close to SV; HD short, narrow, coiled, links AG to a larger yellowish granulated HD; MG and AG small, folded, soft white tissue. Spermatophore (Fig. 59J). Relatively short (length = 5.69 ± 0.99 mm, n = 2) and narrow; test thin, translucent, containing a white gelatinous core mass; over half-length comprises a translucent bulbous cylindrical body section (head length = 3.01 ± 1.18 mm, ~ 63% of SPM length, n = 3), tip bluntly pointed, tapering into a filamentous transparent flagellum; head section much thicker than flagellum (head width = 72 ± 29 µm, n = 3; flagellum width = 13 ± 3 µm), both sections smooth, featureless; 2 SPM tightly coiled in single BC (AM C.584989).

Comparative remarks. In our mitochondrial tree (Figs 1, 2, Clade G), unit 40 (*atra* group) is the sister lineage of *S. atra* (unit 41). Unit 40 contains *S. hienghenensis* **sp. nov.** and sequences from Qld and PNG that probably represent an undescribed species. These sequences are excluded from *S. hienghenensis* **sp. nov.** delimited here. *Siphonaria hienghenensis* **sp. nov.** differs from *S. atra* by COI distances of ≥ 8.3%. The next more closely related species is *S. alba* (unit 39), which differs by COI distances of ≥ 13% (Table S3). *Siphonaria hienghenensis* **sp. nov.**, considered to be endemic to New Caledonia, has been found in sympatry with four species in NC: For comparisons with *S. monticulus* and *S. normalis* refer to comparative remarks under these species. *Siphonaria ouasseensis* **sp. nov.** has a smaller, taller, darker shell with more raised and broader ribbing, BD with a bursal loop and a narrower F1. *Siphonaria bourailensis* **sp. nov.** has a smaller, taller, paler shell with more uneven ribbing, darker interior, a larger pointed AO, and a shorter SPM. Six are sympatric on NC. *Siphonaria caledonica* **sp. nov.** has a smaller, taller, darker shell with stronger edge scalloping and darker interior, and a larger pointed AO and ED. *Siphonaria poindimiensis* **sp. nov.** has a smaller, taller, darker shell with stronger edge scalloping and darker interior, and a larger pointed AO. *Siphonaria namukaensis* **sp. nov.** has a smaller, slightly darker shell with more raised ribbing, weaker edge scalloping, and a smaller, narrower AO, *Siphonaria poindimiensis* **sp. nov.** has a taller shell with stronger edge scalloping, wider ribs, fused dual siphonal ridge ribs, patterned interstices, a larger AO, and a longer ED. For comparisons with *S. viridis* and *S. atra* refer to comparative remarks under these species.

Distribution and habitat. Recorded as endemic to NC and Lifou (Fig. 60). In this study, found on exposed to sheltered rocky boulder and platform shores, mid and upper littoral levels (Fig. 57R).

Etymology. Named after Baie de Hienghène, immediately north of the type location of Ponerihouen, west coast of NC, Pacific Ocean.

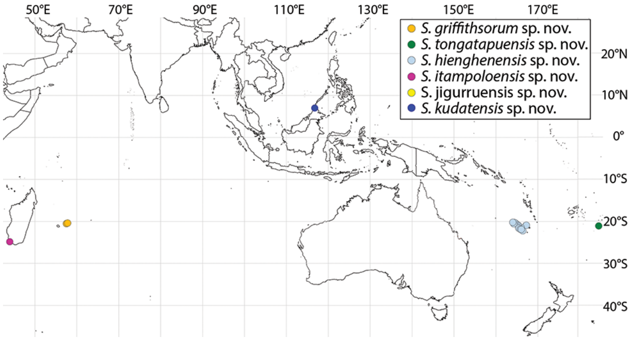

FIGURE 60. Known occurrence records of *S. griffithsorum* **sp. nov.**, *S. tongatapuensis* **sp. nov.**, *S. hienghenensis* **sp. nov.**, *S. itampoloensis* **sp. nov.**, *S. jiigurruensis* **sp. nov.** and *S. kudatensis* **sp. nov.**

Siphonaria itampoloensis sp. nov.

(Figs 61F–G, 62A)

Siphonaria '*laciniosa* group, unit 25'—Dayrat *et al.* 2014: 261 (in part).

Material examined. *Type material.* Holotype, from Itampolo, SW Madagascar; coll. O. Griffiths, MA09_1b, July 2018 (AM C.584955 [M273], Fig. 61F). Paratype, same data as holotype (AM C.584956 p [M274], Fig. 61G).

External morphology. Foot sole, foot wall, cephalic folds and pneumostomal lobe evenly cream in colour, paler to foot edge; mantle thin, translucent, wider than foot wall, strongly lobed with thickened edge, faint brown pigmentation on mantle edge; no black pigmentation; pustules prominent on foot wall; two black 'Eye' spots prominent centrally on thickened cephalic lobes; pneumostome fold prominent.

Shell (Figs 61F–G; Table S9). Small sized (max sl mean = 9.07 mm, SD = 0.35 mm, n = 2), circular ovate; height tall; apex offset central, apical sides convex, protoconch direction central to weakly homostrophic (n = 1), shell whorl dextral; growth striae distinct, exterior uneven, shell thickness thick; rib count (mean = 25, SD = 1.0, n = 2), predominance of pale white primary ribs, crooked, often discontinuous to shell lip, single secondary ribs may develop between primary ribs, rib interstices dark brown, ridges rounded, increasingly raised and protrude slightly beyond uneven weakly scalloped and strongly corrugated shell edge; siphonal ridge indistinct. Interior shell lip and margin dark chocolate brown with white rays aligning under primary/secondary ribs, fading to prominent thin ADM scar; spatula whitish to golden tan; siphonal groove indistinct, CMS convex; thickening or whitening of shell lip not observed.

Reproductive system (Fig. 62A; n = 2). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts lay over BM to side of RAM. ED distinct entry to top of GA; AO indistinct, part of GA, GA/AO large, elongated, weakly bent; ED thick, elongated, slightly twisted; AO, GA and ED all muscular white tissue; EG large, folded, soft white tissue; single looped thick blunt flagellum F1 appears as extension of ED at EG join; BD and CD with bulbous ends connect side by side into GA, both ducts smooth, short, broad, slightly bent, pass together through RAM (BD over CD) connecting into MG; BC white opaque test, relatively small, bulbous, embedded along with part of BD in soft white folds of MG; HD long, narrow, coiled, links soft white folded AG to small yellowish granulated HG; AG larger than HG, both with outer sides curved reflecting the close positioning to curvature of inner foot wall at right posterior quarter of coelom; SV embedded in AG close to BC.

Comparative remarks. In our mitochondrial phylogeny, *S. itampoloensis* **sp. nov.** (*pectinata* group, unit 81) is the sister species of *S. carbo* (Figs 1, 4) Both species differ from each other by COI distances of ≥ 5.1% (Table S8). Morphologically, *S. carbo* has a darker, more finely ribbed, grey/brown shell, a longer, wider BD and larger BC. We have found *S. itampoloensis* **sp. nov.** in sympatry with two congeners in Madagascar: *Siphonaria striata* **sp. nov.** has a lower shell with more raised ribs, a prominent siphonal ridge and posteriorly offset apex, a larger AO, a longer BD with distal and bursal loops, and a shorter F1. For comparison with *S. madagascariensis* refer to comparative remarks under that species. *Siphonaria itampoloensis* **sp. nov.** differs from other members of the *pectinata* group, such as *S. asghar*, *S. capensis*, and *S. pectinata* (unit 4), by having a taller shell, more prominent shell ribbing, distinct shell interior colouration, and larger and thicker epiphallic parts.

Distribution and habitat. Recorded exclusively from Madagascar, Indian Ocean (Fig. 60). In this study, found on intertidal rocks, on inner lagoon shores.

Etymology. Named after the type location of Itampolo, SW Madagascar, Indian Ocean.

Siphonaria jiigurruensis sp. nov.

(Figs 61A–E, 62B–C)

Siphonaria '*laciniosa* group, unit 21'—Dayrat *et al.* 2014: 267, fig. 4C.

Material examined. *Type material.* Holotype, from Lizard Island 14°40.908'S, 145°27.007'E, Qld, Australia; coll. B.W. Jenkins, Q40-1, 29 June 2017 (AM C.584789 [M423, SK114 (RS, SPM)], Fig. 61A). Five paratypes, same data as holotype (AM C.585641 4p, C.585496 p [M398], Fig. 61C); two paratypes from Freshwater Beach, Lizard Is, Qld; coll. P.H. Colman, 2 Dec. 1974 (AM C.585032 p [SK264], Fig. 61B, C.608197 p [SK400], Fig. 61E). *Other, non-type material.* Australia, Qld: Freshwater Beach, Lizard Is, 14°39.922'S, 145°26.854'E (AM C.585943 20+p).

External morphology. Foot sole, foot wall, cephalic folds and pneumostomal lobe evenly light grey; foot sole darker to centre, paler to edge; fringing mantle narrow translucent at foot wall gradually becoming opaque with a thickened paler grey band at the lobed mantle edge, black pigmentation markings on band aligning with rib interstices; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two thick centrally touching dark grey cephalic folds; thin pale grey pneumostomal lobe part of the mantle, between the right ADMs, closes the pneumostome and anus at the mantle edge.

Shell (Figs 61A–C, E; Table S9). Small sized (max sl mean = 15.3 mm, SD = 2.7 mm, n = 3), elongate ovate; height tall; apex offset central weakly posterior, apical sides weakly convex, protoconch direction homostrophic (n = 1, Fig. 61E), shell whorl dextral; growth striae prominent, 3 prominent coloured bands—protoconch area whitish, mid dark brown/black, margin and shell lip light brown; shell thick; rib count (mean = 43, SD = 5.0, n = 3), 8–10 primary ribs whitish, ridge rounded, fairly straight raised, weakly extend beyond slightly scalloped corrugated uneven shell lip; paired primary ribs on siphonal ridge, no more prominent than other primary ribs; few secondary ribs, rib interstices darker. Interior even white rays align on shell margin under primary/secondary ribs, brown rays under rib interstices, spatula dark brown or whitish; dark brown shell margin dark brown to tan, siphonal groove distinct, same colour as shell edge, points to right anterior; spatula dark chocolate brown to mottled tan even whitish; ADM scar distinct, CMS weakly convex. Degree of intra-specific variability low. Conchologically very similar to *S. viridis* in northern Qld to WA, Australia.

Reproductive system (Fig. 62B; n = 1). Positioned within coelom under the respiratory cavity, occupies the right side of coelom, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between BM and RAM; GA medium, with singular GP through foot wall; AO large, elongated, broad, rounded point, joins next to ED to upper GA; ED short, broad, coiled; GA, AO, ED all white muscular fibrous tissue; EG reasonably large, soft whitish tissue, slightly folded, joins ED; single elongated narrow flagellum (F1), appears as an extension of similar length and broader ED. BD and CD connect side-by-side into GA between ED/AO joint and GP, both ducts smooth, thickened, whitish, featureless, pass closely together through RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex relatively large; BC embedded in folds of AG/MG close to embedded SV; BD with distal loop, posteriorly short and without prominent MA, similar thickness to CD; BC relatively large, bulbous, thin whitish translucent test; HD short, narrow, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobbed; AG larger than HG, sides match curvature of inner foot wall.

Spermatophore (Fig. 62C). Thread-like (length = 6.73 mm, n =1), translucent, test thin; head section bluntly rounded, evenly cylindrical, containing a white gelatinous core, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless. Head section longer wider than flagellum (head length = 4.15 ± 0.34 mm, n = 2; ~ 58% of SPM length, head width = 85 ± 24 µm, n = 2, flagellum width = 34 ± 16 µm); 5 SPM tightly coiled embedded in brown gelatinous mass in single BC (AM C.584789).

Comparative remarks. In our molecular phylogeny (Figs 1, 3), *S. jiigurruensis* **sp. nov.** (*laciniosa* group, unit 21) forms a well-differentiated lineage. The species differs from other species by COI distances of ≥ 23% (Table S6). We found *S. jiigurruensis* **sp. nov.** in sympatry with four congeners on Lizard Island, Qld: For comparisons with *S. normalis*, *S. oblia*, *S. atra*, and *S. viridis* refer to comparative remarks under these species. The specimen figured as '*laciniosa* group, unit 21' in Dayrat *et al.* (2014: 262, fig. 4C) corresponds well with *S. jiigurruensis* **sp. nov.**

Distribution and habitat. Recorded exclusively from Lizard Island, northern Qld, Australia (Fig. 60). In this study, found on granite boulder/platform exposed rocky shores, mid to upper littoral levels (above barnacle zone) (Fig. 61D).

Etymology. For Jiigurru, the name of Lizard Island in the language of the Dingaal people, traditional custodians of the land.

***Siphonaria kudatensis* sp. nov.**

(Figs 61H, 62D)

Material examined. *Type material.* Holotype, from Bak Bak Beach, Kudat, Sabah, 07°00′ N, 116°46′ E, E Malaysia; coll. P.H. Colman, 31 March, 1984, HWL on rocks on beach (AM C.585938 [SK522], Fig. 61H).

External morphology (preserved). Foot sole, foot wall, cephalic folds and pneumostome evenly cream, paler to foot edge; mantle edge thickened strongly lobed without darker pigmentation on mantle edge or cephalic folds.

Shell (Fig. 61H; Table S9). Small sized (max sl = 12.8 mm, n = 1), circular ovate, height tall; apex weakly offset to posterior and centrally left, apical sides weakly convex except posterior which is straight; protoconch direction heterostrophic (n = 1), shell whorl dextral; growth striae clear; exterior pale brown, radial colour bands indistinct; rib count (38, n = 1), primary ribs fewer than secondary, very prominent, strongly raised, off white and rounded, broaden to shell edge; paired primary ribs form siphonal ridge, ribs ends protrude weakly at shell lip, shell edge weakly scalloped and corrugated, few secondary ribs, rib interstices indistinct, darker. Interior shell margin to spatula mottled dark chocolate brown; outer shell margin paler with white rays aligning under ribs; siphonal groove distinct, same colour as spatula, darker than margin; ADM scar indistinct, CMS convex; no thickening of shell lip noted.

Reproductive system (Fig. 62D; n = 1). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts positioned between RAM and BM. GA small, with singular GP through foot wall; AO large, elongated, broad, tip bluntly pointed, weakly centrally bent, merges to upper part of GA, singular GP; ED long, wide, upper twist, shorter than AO, joins to lower side of GA; GA, AO, ED all white muscular fibrous tissue; EG soft whitish, folded;

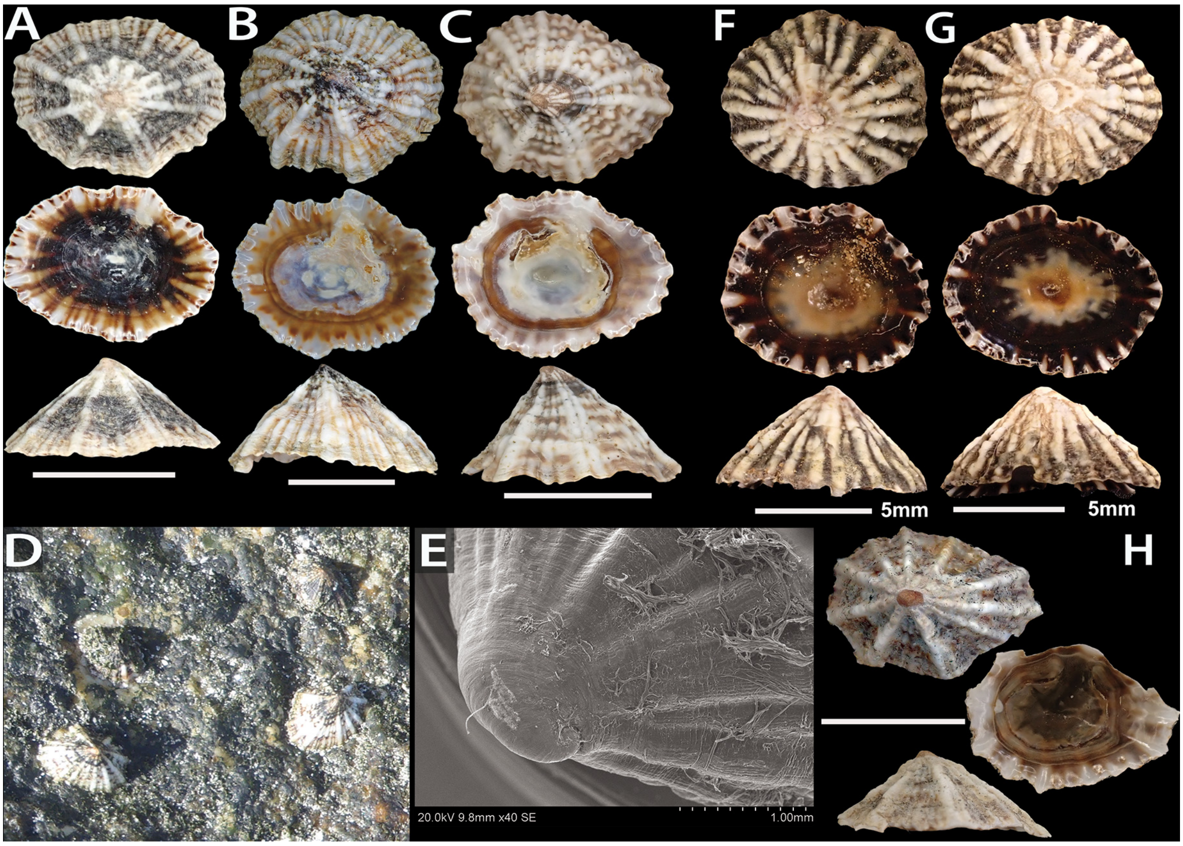

FIGURE 61. Shells of *S. jiigurruensis* **sp. nov.**, *S. itampoloensis* **sp. nov.** and *S. kudatensis* **sp. nov. A–E.** *S. jiigurruensis* **sp. nov.**, Qld, Lizard Is. **A.** Holotype AM C.584789 [M423]. **B.** Paratype AM C.585032 [SK264]. **C.** Paratype AM C.585496 [SK398]. **D.** *In situ*. **E.** Protoconch, AM C.608197 [SK400]. **F–G.** *S. itampoloensis* **sp. nov.**, SW Madagascar, Itampolo. **F.** Holotype AM C.584955 [M273]. **G.** Paratype AM C.584956 [M274]. **H.** Malaysia, Sabah, holotype of *S. kudatensis* **sp. nov.** AM C.585938 [SK522]. Unlabelled scale bars 10 mm.

twisted narrow flagellum (F1) lays over MG, possible second shorter flagellum (F2); BD and CD join closely but with opposing connections to side of GA between AO and GP; both ducts long, featureless, smooth and pass outside RAM (BD over CD); BD with prominent short distal loop and MA attached to inner body wall, connected to small sized bulbous BC with thin translucent test, positioned in folds of AG; CD connects into soft white folded tissues of small MG/AG complex; BC relatively small, elongate, thin whitish translucent test, embedded in MG/AG folds close to large embedded SV; outer edge of MG lobed; HD large, coiled, links ducts in soft white folded tissues of AG to yellowish finely granulated HG; AG larger than HG, sides match curvature of inner foot wall.

Comparative remarks. We have found *S. kudatensis* **sp. nov.** (*laciniosa* group) in sympatry with two congeners at Kudat, Sabah. *Siphonaria radiata* has a lower, broader shell with a less offset apex, less prominent ribbing and siphonal ridge, a smaller AO, shorter BD without a distal loop and a larger BC. *Siphonaria radians* has a lower, broader shell with a less offset apex, finer ribbing and a less prominent siphonal ridge, a smaller AO, AG and HD, larger HG, and a longer F1. We have been unable to sequence mtDNA markers from specimens of this species.

Distribution and habitat. Recorded exclusive from Sabah, Malaysia (Fig. 60). Found on rocky shores, intertidal.

Etymology. Named after the type locality of Kadat, Sabah, E Malaysia.

Siphonaria madangensis **sp. nov.**

(Figs 63A–B, 64C–D)

Material examined. *Type material.* Holotype, from S Dumduman Is, Rempi Area, Madang, PNG Coll. PNG 2013, PM12, 9 Nov. 2012 (MNHN IM-2013-12006 [M550], Fig. 63A). Paratype, from Sek Island 05°04,7'S, 145°48,9'E, Madang, PNG; coll. PNG 2013, PM22, 14 Nov. 2012 (MNHN IM-2013-13132 p [M552], Fig. 63B).

External morphology (preserved). Foot sole grey, paler to foot edge; foot wall, mantle and cephalic lobes darker grey; mantle edge band pale grey with darker markings aligning under rib interstices.

Shell (Figs 63A–B; Table S9). Circular ovate, small sized (max sl mean = 12.1 mm, SD = 1.8 mm, n = 2); shell thin, height low to medium; apex offset central, apical sides straight to weakly convex, protoconch

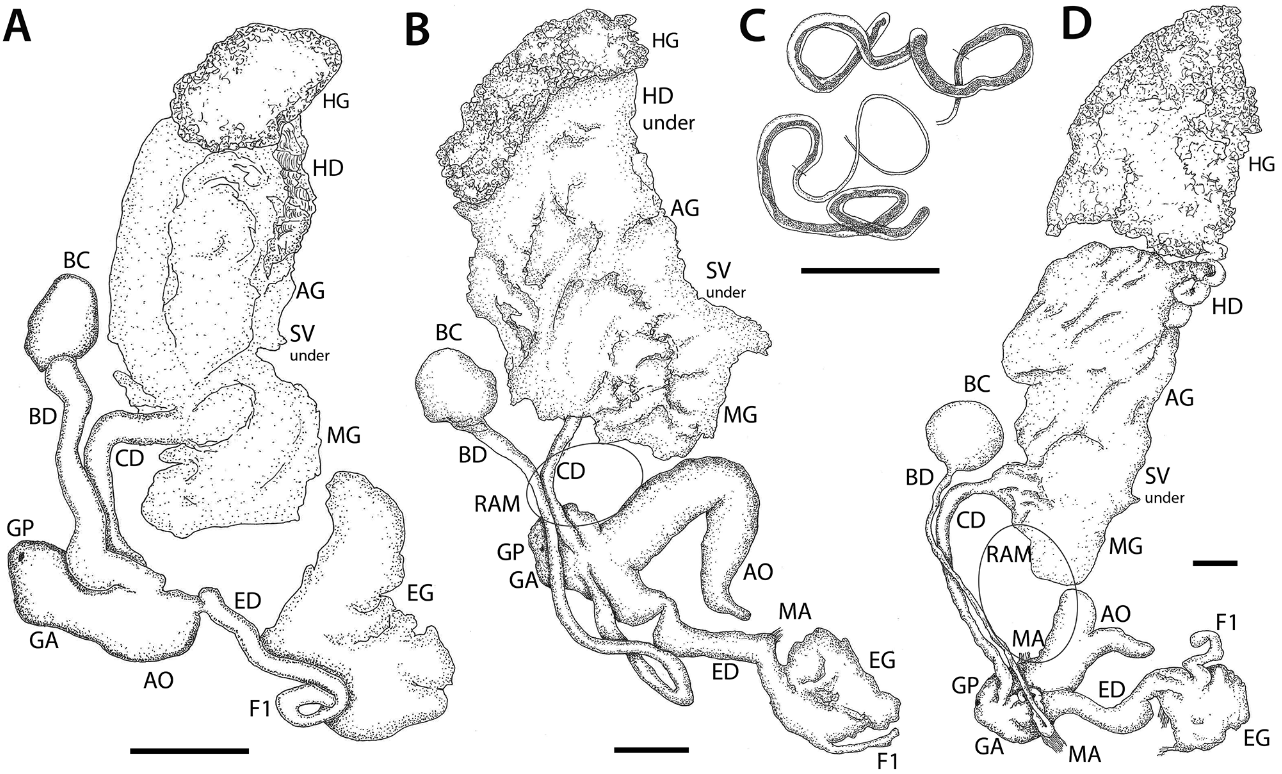

FIGURE 62. Reproductive morphology of *S. itampoloensis* **sp. nov.**, *S. jiigurruensis* **sp. nov.** and *S. kudatensis* **sp. nov. A.** Holotype of *S. itampoloensis* **sp. nov.** AM C.584955 [M273]. **B–C.** Holotype of *S. jiigurruensis* **sp. nov.** AM C.584789 [M423, SK114]. **D.** Holotype of *S. kudatensis* **sp. nov.** AM C.585938 [SK522]. Scale bars = 1 mm.

direction undetermined, shell whorl dextral; growth striae indistinct, radial banding apparent, shell edge even thin, weakly scalloped; rib count (mean = 55.5, SD = 2.5, n = 2), ribs white, straight, fairly even, weakly raised to unraised, interstices dark brown; siphonal ridge clear, formed by dual split primary ribs, extends beyond shell edge; 0 to 2 secondary ribs between primary ribs; interior golden brown, dark brown rays aligned under rib interstices, span from shell edge to ADM scar, spatula golden brown to chocolate brown, siphonal groove clear, shallow; CMS weakly convex; no whitening or thickening of shell lip observed.

Reproductive system (Fig. 64C; n = 1). Positioned within coelom under the respiratory cavity, occupies the right side of coelom, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between BM and RAM; GA small, with singular GP through foot wall; AO indistinct; ED short, broad, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG small, soft whitish tissue, slightly folded, joins ED; single short broad flagellum (F1), similar length and width to ED, appears as an extension of ED. BD and broader CD with juxtapose connections into GA between ED/AO joint and GP, both ducts smooth, broad, whitish, featureless, pass closely together through outer side of RAM (BD over CD) into soft white folded tissues of MG; BD without distal loop or prominent MA, centrally twisted; BC embedded in folds of small MG close to small pale embedded SV; BC medium sized, elongated, whitish translucent test; MG/AG complex relatively small; outer edge of MG lobbed; HD elongated, narrow, coiled, links ducts in soft white folded tissues of AG to small granulated HG; AG larger than HG, side reflects curvature of inner foot wall.

Spermatophore (Fig. 64D). Wide thread-like (length = 1.08 mm, n = 3), translucent, test thin; head section looped, pointed to bluntly rounded, bulbous cylindrical, containing a white gelatinous core, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless, head section longer wider than flagellum (head length = 0.82 ± 0.14 mm, ~ 77% of SPM length, head width = 92 ± 10 µm, flagellum width = 17 ± 0 µm, n = 3). 4 SPM tightly coiled in brown gelatinous mass in single BC (MNHN IM-2013-13132).

Comparative remarks. In our mitochondrial tree (Figs 1, 4), *S. madangensis* **sp. nov.** (*normalis* group, Clade E, unit 88) is most closely related to *S. fuliginata* (unit 80) from Rodrigues. Both species differ by COI distances of ≥ 5.9%. *Siphonaria madangensis* differs from *S. normalis* by COI distances of ≥ 5.6%. *Siphonaria fuliginata* has a paler shell with weaker scalloped edge, white to golden brown interior, a larger AO, a wider BD with bursal loop, and a thinner SPM. We found *S. madangensis* **sp. nov.** in sympatry with three congeners in northern PNG. For comparisons with *S. atra*, *S. viridis*, and *S. normalis* refer to comparative remarks under these species.

Distribution and habitat. Recorded from S

Dumduman and Sek Islands, Madang area, northern PNG (Fig. 67). In this study, found on limestone shores, intertidal.

Etymology. Named after the type locality of Madang, northern PNG.

Siphonaria maloensis sp. nov.

(Figs 63C–F)

Material examined. *Type material.* Holotype, from N coast of Malo Is, 15°37.7'S, 167°11'E, Vanuatu; coll. Marine Biodiversity Survey, 18 Sept. 2006 VM16, sand and coral (MNHN IM-2006-31454 p [M545] Fig. 63C). Paratype, same data as holotype (MNHN IM-2006-31358 p [M546], Fig. 63D); two paratypes, from Palikulo Peninsula, 15°28.8'S, 167°15.3'E, Vanuatu; coll. Marine Biodiversity Survey, 14 Sept. 2006 VM11, hard bottom (MNHN IM-2006-31355 p [M547], Fig. 63E; IM-2006-31353 p [M548], Fig. 63F).

External morphology (preserved). Foot sole, foot wall, cephalic folds and pneumostome cream, paler to foot edge; mantle translucent, edge thickened strongly lobed with dark/black pigmentation on mantle edge aligning with rib interstices, faint pigmentation over cephalic folds.

Shell (Figs 63C–F; Table S9). Ovate, small to medium sized (max sl mean = 17.9 mm, SD = 2.3 mm, n = 4); apex offset central and weakly to left, apical sides strongly convex, height tall; protoconch direction undetermined, shell whorl dextral; exterior uneven without prominent radial colour bands; growth striae distinct, shell thickness thick; rib count (mean = 45.5, SD = 2.3, n = 4), ribs fairly even, primary ribs pale grey, wavy, slightly broaden and increasingly raised to shell edge, ridges rounded narrow; edge finely scalloped and unevenly corrugated; siphonal ridge clear, formed by 2–3 primary ribs; few finer secondary ribs, rib interstices darker grey with irregular red/brown markings; interior shell margin white, red brown rays aligned under rib interstices, from shell lip over shell margin to spatula, siphonal groove distinct, same colour as shell margin; spatula dark brown; ADM scar distinct, darker brown, CMS convex; thickening and whitening of shell lip occurs (Fig. 63C).

Comparative remarks. In our molecular phylogeny (Figs 1, 2), *S. maloensis* **sp. nov.** (*laciniosa* group, unit 87) is the sister species of *S. caledonica* **sp. nov.** (unit 23) from New Caledonia. Both species differ from each other by 16S distances of ≥ 9.7%. *Siphonaria maloensis* differs from *S. normalis* by 16S distances of ≥ 10%. Morphologically, *S. caledonica* **sp. nov.** has a smaller, thinner, taller, darker shell, with more prominent primary ribbing, and a less scalloped edge. We found *S. maloensis* **sp. nov.** in sympatry with *S. viridis* in Vanuatu; refer to comparative remarks under that species.

Distribution and habitat. Recorded exclusively from Malo Island, Vanuatu, Pacific Ocean (Fig. 67). In this study, found on hard substrate, sand and coral, intertidal.

Etymology. Named after the type locality of Malo Island, Vanuatu, Pacific Ocean.

Siphonaria mauiensis sp. nov.

(Figs 63G–K, 64A–B)

Material examined. *Type material.* Holotype, from Hanakao'o Beach 20°54.586'N, 156°41.338'W, Maui, Hawaii; coll. B.W. Jenkins, HA03-2, 23 June 2018 (AM C.584888 [M297], Fig. 63G). Six paratypes, same data as holotype (AM C.584890 p [SK245], Fig. 63I, C.584891 p [SK207], Fig. 63H, C.585586 3p, C.584921 p [SK206]).

External morphology (Fig. 63K). Foot sole grey; foot wall, mantle, cephalic folds, pneumostome evenly yellowish/green; irregular blotches of black pigmentation on foot wall, concentrated over cephalic lobes and posterior; mantle translucent narrower than foot wall, covers exposed inner shell lip, wider at anterior, mantle edge thickened white band lobed with even black pigmentation rays aligned with shell rib interstices; genital pore indistinct, located on foot wall to right anterior of right cephalic fold; small black epithelial eye spot centralised on each of centrally touching cephalic folds; pneumostomal lobe under mantle between the right ADMs.

Shell (Figs 63G–I; Table S9): small sized (max sl mean = 11.93 mm, SD = 1.16 mm, n = 3), circular ovate; height tall; apex offset central, apical sides convex uneven, protoconch direction homostrophic to central (n=1), shell whorl dextral, apex weakly hooked; growth striae distinct, 2–3 discontinuous bands of blue/grey radial shading, protoconch area dark brown, shell thin; rib count (mean = 60, SD = 4.3, n = 3), ribs white/grey, rib interstices narrow brown/black, difference between primary and secondary ribs indistinct, narrow, crooked, weakly raised, slightly broaden to and weakly protrude beyond uneven shell lip; siphonal ridge indistinct formed by 3–4 ribs. Interior shell margin mottled brown, shell lip dark brown with uneven white rays extending to shell margin under ribs; siphonal groove distinct, same colour as shell edge but maybe white; spatula dark chocolate brown; ADM scar distinct, CMS straight; thickening of shell lip occurs in mature specimens, infills and reduces scalloping of lip, spatula becomes whitened.

Reproductive system (Fig. 64A; n = 1). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; RS very large proportion of animal size compared to other species; epiphallic parts (GA, EG and ED) positioned over back of BM, F1 long, draped over BM; GA small, with singular GP through foot wall; AO medium, bluntly rounded, joined at base to upper GA, rests against MG; ED long broad, centrally bent, joins to posterior side of GA; GA, AO, ED all white muscular fibrous tissue; EG very large, soft whitish tissue, folded, joins ED; single long broad flagellum (F1) centrally looped, appears as an extension of wider ED; BD and CD connect closely in opposite directions into GA between ED join and GP, both ducts whitish curved, pass closely together around outside of RAM (BD over CD) into soft white folded tissues of MG/AG complex; outer edge of CD lobed, broadens to connection with AG ducts, BC long with distal loop and MA to inner foot wall in front of BM, initially broader

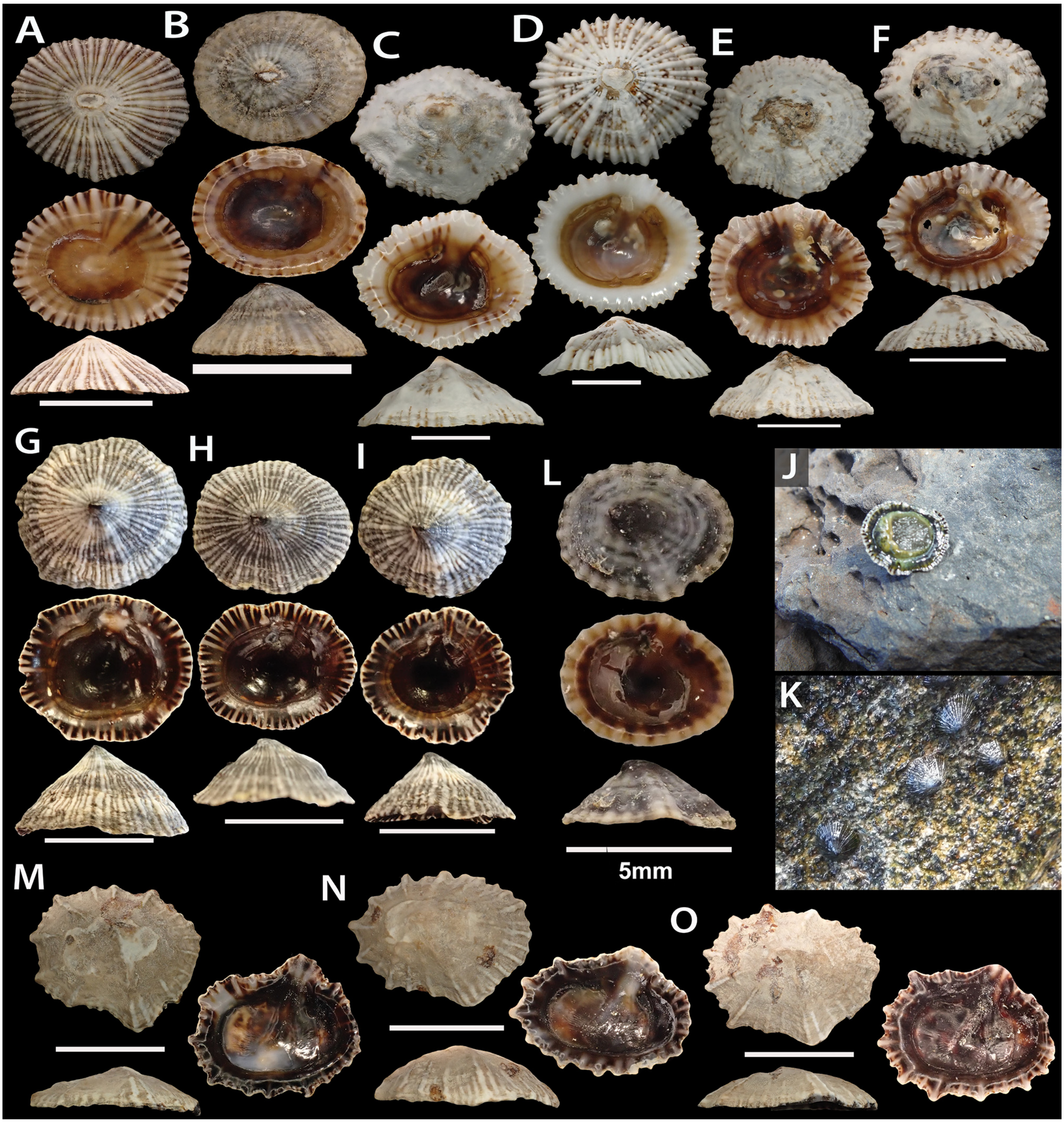

FIGURE 63. Shells of *S. madangensis* **sp. nov.**, *S. maloensis* **sp. nov.**, *S. mauiensis* **sp. nov.**, *S. nusalikensis* **sp. nov.** and *S. cacao* **sp. nov. A–B.** *S. madangensis* **sp. nov. A.** Holotype MNHN IM-2013-12006 [M550]. **B.** Paratype IM-2013-13132 [M552]. **C–F.** *S. maloensis* **sp. nov. C.** Holotype IM-2007-31454 [M545]. **D.** Paratype IM-2007-31358 [M546], Sek Is. **E.** Paratype IM-2007-31355 [M547], Palikulo Peninsula. **F.** Paratype IM-2007-31353 [M548], Palikulo Peninsula. **G–K.** *S. mauiensis* **sp. nov.**, Maui, Hanakao'o Beach. **G.** Holotype AM C.584888 [M297, SK208]. **H.** Paratype AM C.584891 [SK207]. **I.** Paratype AM C.584890 [SK245]. **J.** Animal. **K.** *In situ.* **L.** Holotype of *S. nusalikensis* **sp. nov.** IM-2013-55334 [M532]. **M–O.** *S. cacao* **sp. nov.**, French Polynesia, Tubuai. **M.** Holotype IM-2007-35319 [SK506]. **N–O.** Paratypes IM-2007-35317/18. Unlabelled scale bars = 10 mm.

than CD, narrows to embed in folds of AG; BC relatively large bulbous thin whitish translucent test, 2 SPM in BC (n=1); HD short broad coiled, links ducts in soft white folded tissues of AG to orange granulated small HG; outer edge of MG lobbed; AG much larger than HG, outer sides of both reflect curvature of inner foot wall.

Spermatophore (Fig. 64B). Relatively long and thin; test thin, translucent, comprises a translucent cylindrical body section containing a white gelatinous thread-like core, tapers into a filamentous transparent flagellum (head length = 24.56 mm, n = 1; flagellum incomplete), head section thicker than flagellum (head width = 148 µm, flagellum width = 74.1 µm, n = 1); head tip bluntly rounded; both sections smooth, featureless; 2 SPM tightly

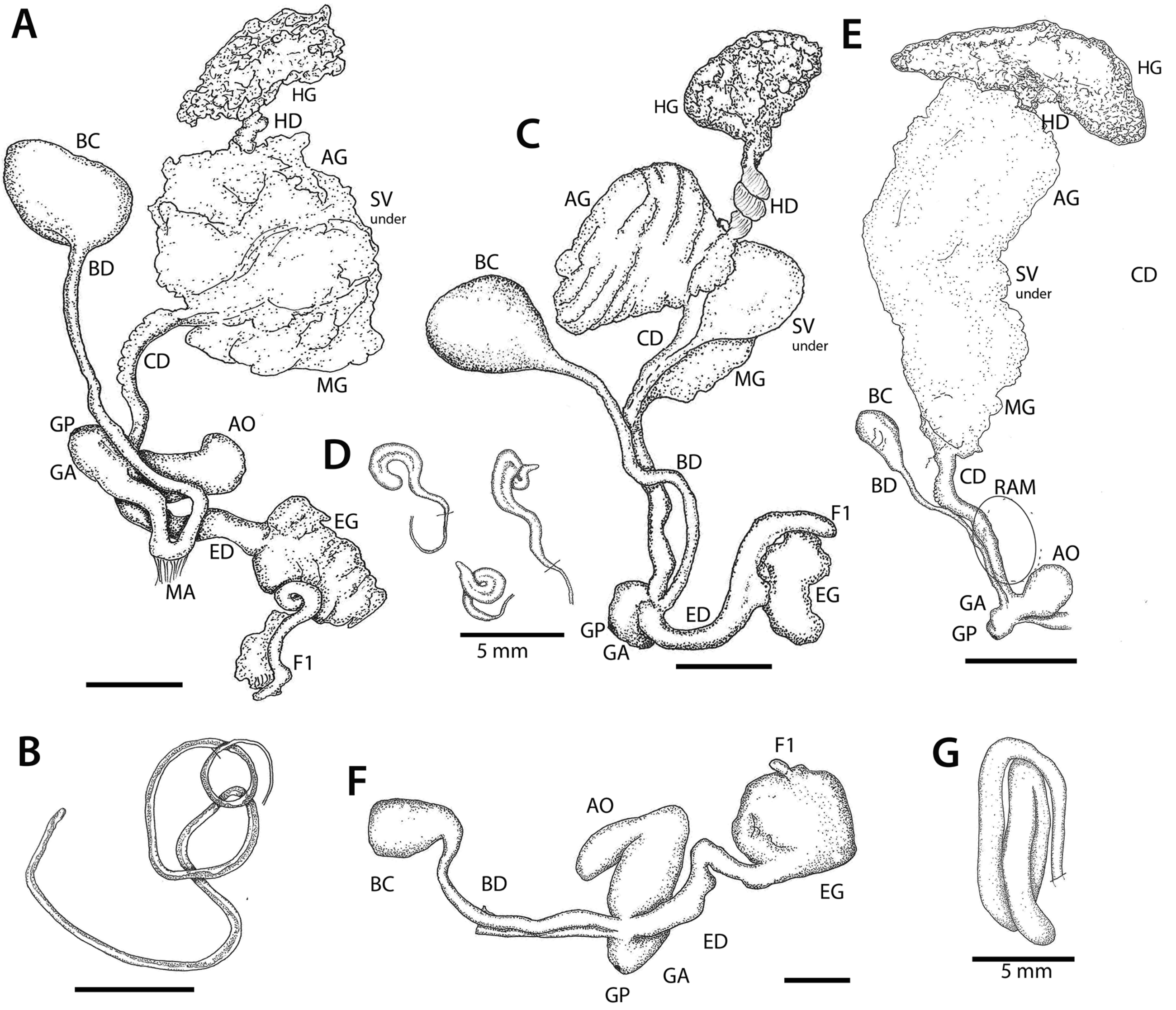

FIGURE 64. Reproductive morphology of *S. mauiensis* **sp. nov.**, *S. madangensis* **sp. nov.**, *S. nusalikensis* **sp. nov.** and *S. cacao* **sp. nov. A–B.** Holotype of *S. mauiensis* **sp. nov.** AM C.584888 [M297, SK208]. **C–D.** *S. madangensis* **sp. nov.** Paratype MNHN IM-2013-13132 [M552, SK507], PNG, Sek Is. **E.** Holotype of *S. nusalikensis* **sp. nov.** MNHN IM-2013-55334 [M532]. **F–G.** Holotype of *S. cacao* **sp. nov.** MNHN IM-2007-35319 [SK506, EPI part only). Unlabelled scale bars = 1 mm.

coiled, embedded in brown gelatinous mass within BC (AM C.584888).

Comparative remarks. *Siphonaria mauiensis* **sp. nov.** (*plicata* group, unit 60) forms a well-differentiated lineage in the mitochondrial tree (Figs 1, 3). It differs from other species by COI distances of ≥ 29.6% (Table S7). We found *S. mauiensis* **sp. nov.** in sympatry with two congeners in Hawaii. For comparisons with *S. normalis* and *S. nuttallii* refer to comparative remarks under these species. Along with the latter, *S. undans* **sp. nov.** (unit 61) and *S. waikoloaensis* **sp. nov.** (unit 55) are other Hawaiian species of the *plicata* group, but they are genetically highly distinct. The shell of *S. mauiensis* **sp. nov.** resembles that of *S. lirata* from Guam, but has a consistently darker interior.

Distribution and habitat. Recorded exclusively from Hanakao'o Beach, Maui, Hawaii, USA (Fig. 67). In this study, found in sheltered positions (mainly rock crevices) on moderately exposed fine-algal covered rocky basalt shores, upper littoral level (Fig. 63K).

Etymology. Named after the type locality's island of Maui, Hawaii.

Siphonaria namukaensis sp. nov.

(Figs 65A–F, M–N, P; 66A–D)

Siphonaria '*laciniosa* group, unit 22'—Dayrat *et al.* 2014: 261 (in part).

Material examined. *Type material.* Holotype, from Namuka Bay, 18°08.094'S, 177°23.490'E, Viti Levu, Fiji; coll. B.W. Jenkins, FI02-2, 23 Aug 2018 (AM C.585826 [M282], Fig. 65A). 25+ paratypes, same data as holotype (AM C.585893 20+p, C.584857 p [M278], C.584858

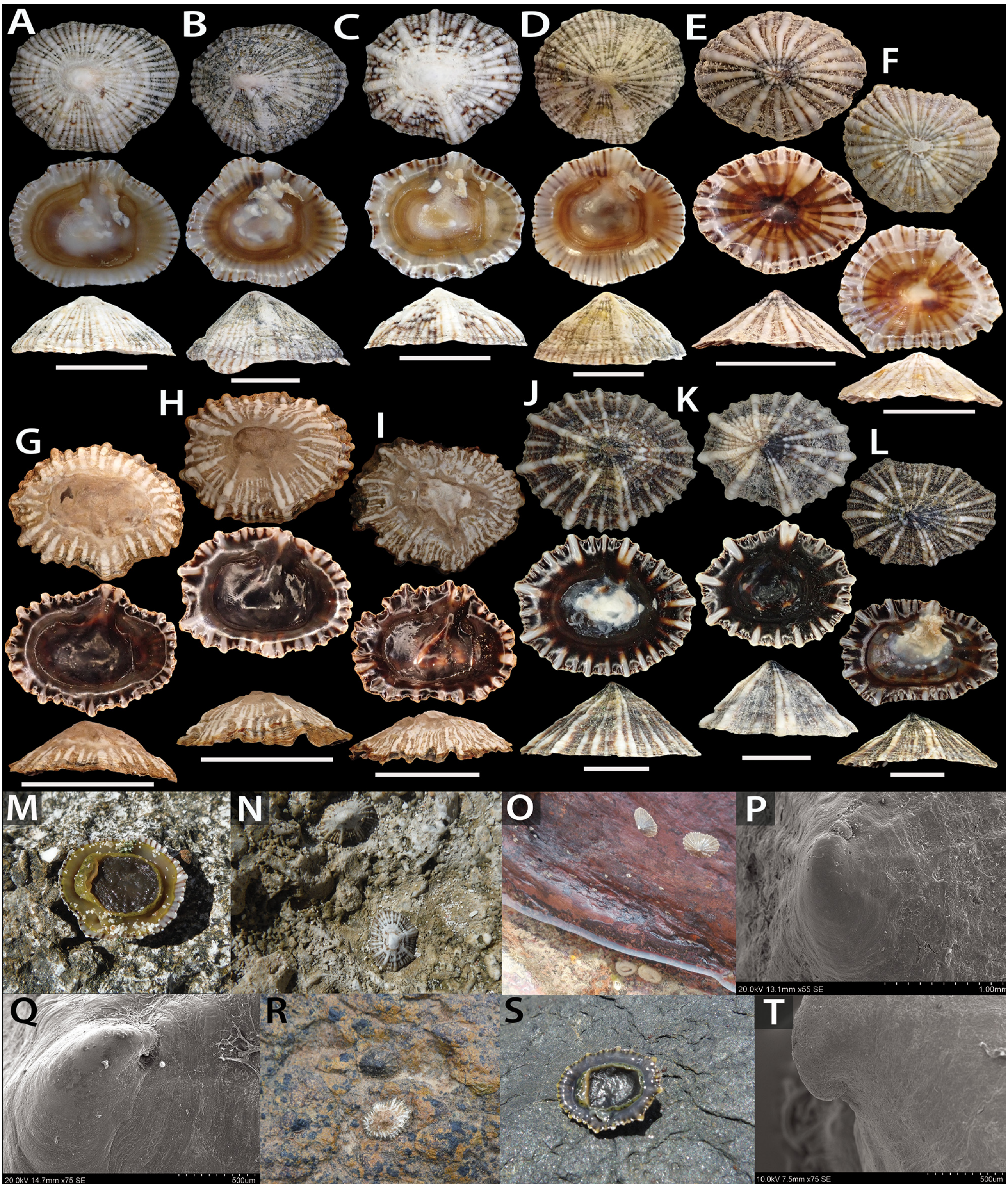

FIGURE 65. Shells of *S. namukaensis* **sp. nov.**, *S. ouasseensis* **sp. nov.** and *S. caledonica* **sp. nov. A–F, M–N, P.** *S. namukaensis* **sp. nov. A–E, M–N, P.** Fiji. **A.** Holotype AM C.585826 [M282]. **B.** Paratype AM C.584858 [SK109]. **C.** Paratype AM C.585824 [M280]. **D.** Paratype AM C.585825 [M281]. **E.** Tagaqa, AM C.585822 [M276]. **F.** NC, Poindimie, AM C.585000 [M461, SK194]. **M.** Animal. **N.** *In situ*. **P.** Protoconch, Vuda Point, AM C.584864 [M422, SK110]. **G–I, Q–R.** *S. ouasseensis* **sp. nov.**, NC, Ouassé. **G.** Holotype AM C.584786 [M377]. **H.** Paratype AM C.584800 [SK344]. **I.** Paratype AM C.585923 [SK346]. **Q.** Protoconch, AM C.585993 [SK347]. **R.** *In situ.* **J–L, O, S–T.** *S. caledonica* **sp. nov. J.** Holotype AM C.584788 [M364], NC, Tiari. **K.** Paratype AM C.585015 [M366], La Roche Percee. **L.** Paratype AM C.585838 [M362]. **O.** *In situ*, Tiari. **S.** Animal. **T.** Protoconch, AM C.585839 [M363]. Unlabelled scale bars = 10 mm.

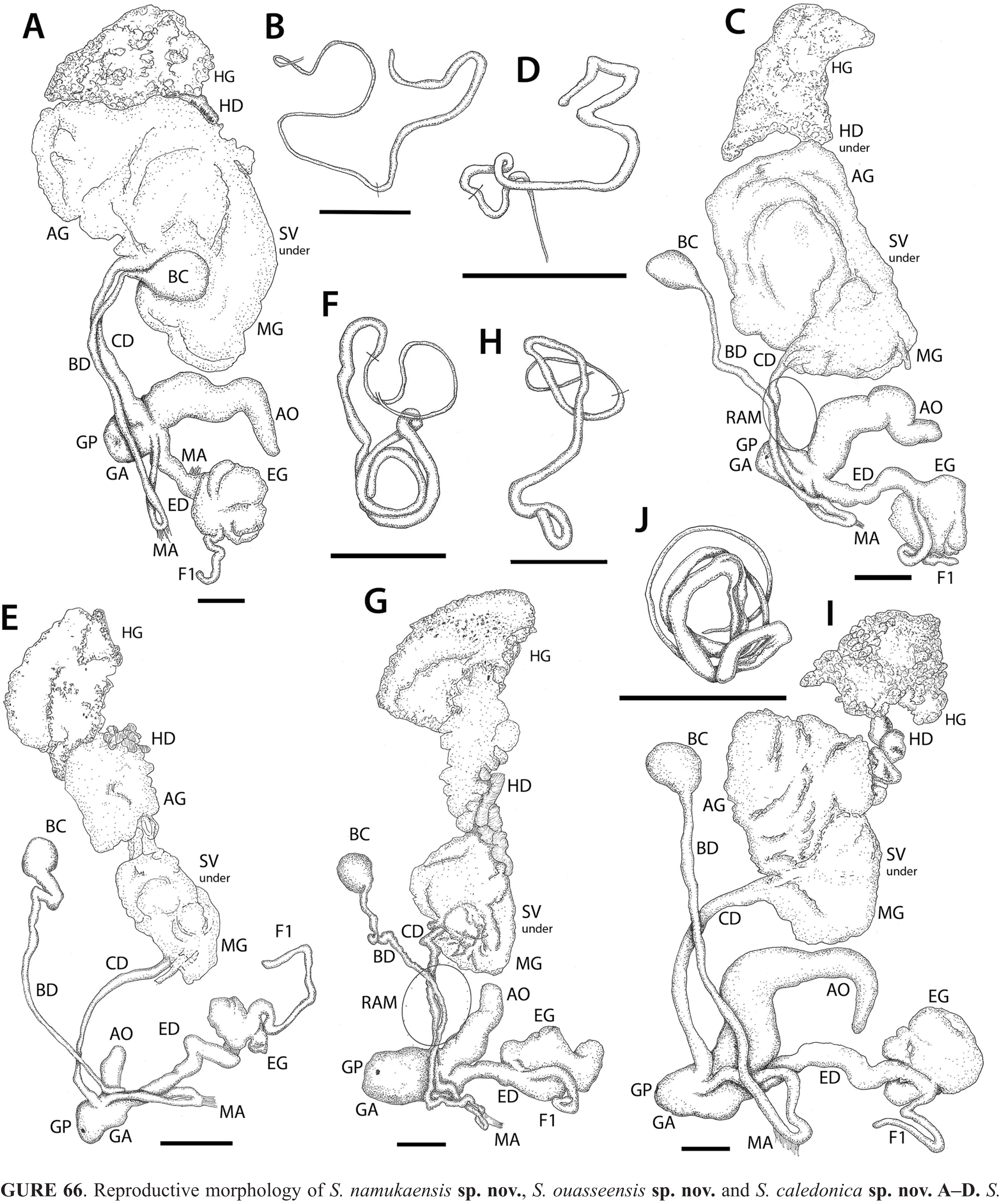

FIGURE 66. Reproductive morphology of *S. namukaensis* **sp. nov.**, *S. ouasseensis* **sp. nov.** and *S. caledonica* **sp. nov. A–D.** *S. namukaensis* **sp. nov. A.** Paratype AM C.584858 [SK109], Fiji. **B.** Holotype AM C.585826 [M282], Fiji. **C–D.** NC, Poindimie, AM C.584994 [M455, SK193]. **E–H.** *S. ouasseensis* **sp. nov.**, NC, Ouassé. **E.** Paratype AM C.585924 [SK342]. **F.** Paratype AM C.595984 [SK351]. **G–H.** AM C.585732 [SK343]. **I–J.** Holotype of *S. caledonica* **sp. nov.** AM C.584788 [M364, SK130]. Scale bars = 1 mm.

p [SK109], Fig. 65B, C.585823 p [M279], C.585824 p [M280], Fig. 65C; C.585825 p [M281], Fig. 65D).

Other, non-type material. **Fiji, Viti Levu:** Vuda Point Marina seawall, 17°40.878'S, 177°23.009'E, FI03-2 (AM C.585391 10+p, C.585696 8p, C.585828 p [M283], C.585829 p [M284], C.585830 p [M285], C.585831 p [M422], C.584864 p [M422, SK110], C.584865 p [SK116]); Heal of foot First Landing, 17°40.753'S, 177°23.006'E, FI03-1 (AM C.585827 p [M290]); Namuka Bay 18°08.094'S, 177°23.490'E, FI02-2 (AM C.586006 20+p, C.584856 p [M277], C.584858 p [SK109]); nr Tagaqa, S. coast of Viti Levu, 18°11.802'S, 177°38.640'E FI02-1 (AM C.585822 p [M276]). **NC:** Poindimie 21°55.901'S, 165°19.672'E, NC03-2 (AM C.584994 p [M455, SK193], C.585000 p [M461, SK194], Fig. 65F); Poum 2, 20°13.754'S, 164°01.699'E, NC05-3 (AM C.585999 5p).

External morphology (Fig. 65M). Foot sole evenly dark grey; foot edge, foot wall, cephalic folds and pneumostomal lobe yellow grey; mantle wider than foot wall, thin translucent, edge thickened, weakly lobed, yellow band; irregular blotches of dark pigmentation on foot wall, cephalic folds, fading to mantle join; pneumostome elongated.

Shell (Figs 65A–F, P; Table S9). Small to medium sized (max sl mean = 14.6 mm, SD = 3.7 mm, n = 7), circular ovate; height medium; apex offset central, apical sides convex, protoconch direction homostrophic (n = 2, Fig. 65P), shell whorl dextral; growth striae prominent; rib count (mean = 52.4, SD = 6.5, n = 7), ribs fairly straight, rib ridges slightly raised, rounded, align with uneven and weakly scalloped shell edge; interstices narrow, black; primary and secondary ribs white, very similar in size, brown flecks and 1–2 secondary ribs in spaces between primary ribs; siphonal ridge sole rib fold, formed by 3–4 close primary ribs. Interior shell lip tan to whitish, shell margin golden dark brown to tan, white rays align on shell margin under primary/secondary ribs, prominent siphonal groove and spatula pale tan to whitish; ADM scar prominent, darker than shell lip, margin and shell edge; CMS straight; thickening and whitening of shell lip occurs.

Reproductive system (Figs 66A, C; n = 5). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts positioned over BM. GA small, with singular GP through foot wall; AO large, broad, bent, bluntly pointed, joined to lower ED and upper GA; ED very short, very broad, centrally bent, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG very large, soft whitish tissue, slightly folded, joins ED; extension joins in parallel to single narrow flagellum (F1), similar width to ED, appears as an extension of ED, possible F2 narrow short; BD and CD connect in opposing directions closely into GA between ED join and GP, both ducts short, slightly bent, smooth, thickened, whitish, featureless, pass closely together inside outer RAM (BD over wider CD) into soft white folded tissues of MG; MG/AG complex large; CD connecting to ducts, BC embedded in folds close to embedded SV; BD with distal loop and MA; BC relatively small, spherical, thin whitish translucent test; HD short, narrow, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobbed; AG larger than HG, sides match curvature of inner foot wall.

Spermatophore (Figs 66B, D). Long, thread-like (length = 8.76 mm, n =1), translucent, test thin; head section bluntly rounded, evenly cylindrical, centrally bent, contains a core white gelatinous mass, tapers along the transparent and narrower flagellum (head length = 3.66 mm 42% of total length; head width = 103 µm, flagellum width = 17 µm, n = 1); both sections smooth, featureless. SPM tightly coiled embedded in purple/brown gelatinous mass in BC (3 SPM in AM C.585826, Fig. 66B, 1 SPM in AM C.585822, 5 SPM in AM C.585831, 1 SPM in AM C.584994, Fig. 66D).

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 3), *S. namukaensis* **sp. nov.** (*laciniosa* group, unit 22) is the sister species of *S. yagasaensis* **sp. nov.** (unit 67). Both species are well-differentiated from each other by COI distances of ≥ 17%. From all other congeners *S. namukaensis* differs by COI distances of ≥ 18% (Table S6).

Throughout its range, we found *S. namukaensis* **sp. nov.** in partial sympatry with six congeners. For comparisions with *S. atra* and *S. normalis* refer to comparative remarks under these species. *Siphonaria vudaensis* **sp. nov.** has a larger, lower, darker shell with stronger edge scalloping, and darker interior, a blunter AO. *Siphonaria poindimiensis* **sp. nov.** has a smaller taller darker shell with stronger edge scalloping, a larger AO and ED. *Siphonaria tagaquensis* **sp. nov.** has a smaller taller darker shell, a longer ED. *Siphonaria poindimiensis* **sp. nov.** has a taller, darker shell with broader ribs and stronger edge scalloping, and wider ribs, a larger BC and a longer, wider ED.

Distribution and habitat. Recorded from Viti Levu, Fiji and E coast NC, Pacific Ocean (Fig. 67). In this study found at sheltered positions on exposed and moderately exposed rocky shores, upper and mid littoral (Fig. 65N).

Etymology. Named after the type locality of Namuka Bay, Viti Levu, Fiji.

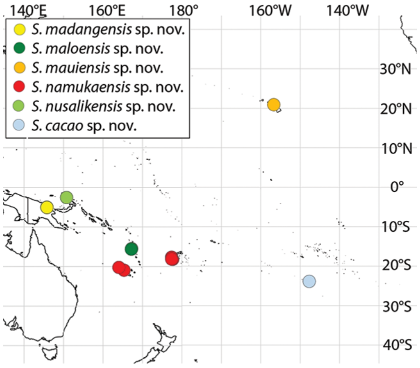

FIGURE 67. Known occurrence records of *S. madangensis* **sp. nov.**, *S. maloensis* **sp. nov.**, *S. mauiensis* **sp. nov.**, *S. namukaensis* **sp. nov.**, *S. nusalikensis* **sp. nov.** and *S. cacao* **sp. nov.**

***Siphonaria nusalikensis* sp. nov.**
(Figs 63L, 64E)

Material examined. *Type material.* Holotype, from NW side of Big Nusa Island, 02°34,1'S, 150°46,7'E, New Ireland, PNG; coll. KAVIENG 2014 expedition, KM21, 28 Jun. 2014 (MNHN IM-2013-55334 [M532], Fig. 63L).

External morphology (preserved). Foot sole, foot wall, cephalic folds and pneumostome cream, paler to foot edge; mantle translucent, edge thickened strongly lobed with dark/black pigmentation on mantle edge aligning with rib interstices, faint pigmentation over cephalic folds.

Shell (Fig. 63L; Table S9). Small sized (max sl = 4.76 mm, n = 1), circular ovate, height tall; apex weakly offset to posterior and left, apical sides convex except posterior which is concave; protoconch hooked to posterior, direction heterostrophic (n = 1), shell whorl dextral, shell thin; growth striae indistinct; multiple radial colour bands, protoconch area dark brown, central bands pale to dark, shell fringe pale brown; rib count (29, n = 1), predominance of primary ribs, few secondary ribs, weakly raised, off white and rounded, broaden to shell edge; paired primary ribs form siphonal ridge, ribs ends protrude weakly at shell lip, shell edge weakly scalloped and corrugated; rib interstices indistinct, darker. Interior shell margin to spatula mottled dark chocolate brown; outer shell margin paler with light brown rays aligning under ribs; siphonal groove distinct, same colour as spatula, darker than margin; ADM scar indistinct, CMS convex; no thickening of shell lip noted.

Reproductive system (Fig. 64E; n = 2). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts positioned between RAM and BM. GA small, with singular GP through foot wall; AO small, bulbous, tip blunt, joined to upper GA; ED (incomplete) broad, joins to side of AO and GA; GA, AO, ED all white muscular fibrous tissue; BD and CD connect closely together into GA below AO junction, both long, narrow, slightly bent, pass closely together outside RAM (BD over CD) into soft white folded tissues of MG; BD smooth, featureless; CD with short lobed mid-section; CD connecting to large MG/AG complex; BC relatively small, elongate, thin whitish translucent test, embedded in MG/AG folds close to embedded SV; BD without distal loop or MA; HD small, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobed; AG larger than HG, sides match curvature of inner foot wall.

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 3), *S. nusalikensis* **sp. nov.** (*plicata* group, unit **89**) is the sister species of a clade comprising *S. guamensis* (unit **70**) and an unidentified species from Rarotonga known only from one DNA sequence (unit **17**). *Siphonaria nusalikensis* differs from these species by genetic distances in COI of 11% (*S. guamensis*) and 13.3% (unit **17**) (Table S7). We found *S. nusalikensis* **sp. nov.** in sympatry with three congeners at New Ireland, PNG: For comparisons with *S. normalis* and *S. viridis* refer to comparative remarks under these species. *Siphonaria recurva* **sp. nov.** differs in having a larger shell with a less offset apex, a more prominent siphonal ridge and stronger edge scalloping, a similar BD, but with distal loop and a larger BC.

Distribution and habitat. Recorded as exclusive to Nusalik Island (Big Nusa Island), Kavieng, PNG (Fig. 67). In this study, found on rocky shores, intertidal.

Etymology. Named after the type locality of Nusalik Island (Big Nusa Island), Kavieng, PNG.

***Siphonaria cacao* sp. nov.**
(Figs 63M–O, 64F–G)

Material examined. *Type material.* Holotype, from Island of Tubuai, Austral Islands, 23°52'S, 147°41'E, IRD-MNHN Stn. X02 (MNHN IM-2007-35319 p [SK506], Fig. 63M). Two paratypes, same data as holotype (MNHN IM-2007-35317 p [SK564], Fig. 63N; IM-2007-35318 p [SK565], Fig. 63O).

Other, non-type material. **Austral Islands:** Tubuai, 23°52'S, 147°41'E, X02 (MNHN IM-2007-35316 p).

External morphology (preserved). Animal exterior evenly cream, foot sole grey, paler to foot edge; mantle translucent, irregular widely spaced pigmentation spots on foot wall, concentrated over posterior and centre of cephalic folds.

Shell (Figs 63M–O; Table S9). Small (max sl mean = 15.5 mm, SD = 0.5 mm, n = 3), circular ovate; height low; apex offset weakly left and strongly to posterior, apical sides straight to weakly convex; shell edge uneven; protoconch direction undetermined, shell whorl dextral; growth striae indistinct, exterior grey to pale brown and usually eroded, radial colour banding indistinct; shell thickness medium; rib count (mean = 38, SD = 1.6, n = 3), ~ 12 distinct uneven primary ribs, white to pale, fairly straight, rib growth uneven, ridges rounded, broaden to scallop and protrude beyond shell edge; 2–3 interspersed pale white finer secondary ribs, rib interstices darker; paired primary ribs form siphonal ridge, more prominent and extend shell edge further than at other primary ribs. Interior shell dark chocolate brown, shell lip thickened; paler uneven rays extend from the shell lip over the shell margin, align under primary/secondary ribs; spatula dark chocolate brown, maybe mottled blueish; siphonal groove clear, similar colour to margin and spatula; ADM scar distinct, CMS convex.

Reproductive system (Fig. 64F; n = 1). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior tightly between RAM and over back of BM. Join of AO, ED and GA together at top of GA, AO larger than GA, elongated, bluntly pointed, centrally bent, thicker than ED; ED wide, centrally bent, shorter and narrower than AO; AO, GA and ED all muscular white tissue; EG folded, block-like, flagellum F1 small indistinct; BD and CD similar in thickness, connect side-by-side into GA, directly opposite to ED; both ducts smooth and pass together through outer side of RAM connecting into MG (BD over CD), BC bulbous, embedded in MG/AG; hermaphroditic glands inaccessible.

Spermatophore (Fig. 64G). Thread-like, test thin, translucent (incomplete); head section cylindrical (head length = 2.1 mm, n = 1), tip bulbous bluntly rounded, containing a white gelatinous core, smooth, featureless; 1 SPM tightly coiled embedded in white gelatinous mass in single BC.

Comparative remarks. *Siphonaria cacao* **sp. nov.** (*atra* group) is the only species found in Tubuai in this study. We were unable to sequence COI or 16S from the available samples.

Distribution and habitat. Recorded exclusively from Austral Islands, French Polynesia, Pacific Ocean (Fig. 67). In this study, found on sheltered rocky shores (harbour at Island of Tubuai), intertidal.

Etymology. For the dark, chocolate-brown interior of the shell in this species; noun in apposition.

Siphonaria ouasseensis sp. nov.

(Figs 65G–I, Q–R, 66E–H)

Material examined. *Type material.* Holotype, from Ouassé, nr Canala, 21°30.346'S, 166°03.732'E, NC; coll. B.W. Jenkins, NC02-1, 22 Oct 2018 (AM C.584786 p [M377, SK328], Fig. 65G). Six paratypes, same data as holotype (AM C.584800 p [SK344], Fig. 65H, C.584908 p [SK341], C.585732 p [SK343], C.585923 d [SK346], Fig. 65I, C.585924 p [SK342], C.585993 p [SK347], Fig. 65Q).

External morphology. Foot sole, foot wall, cephalic folds and pneumostome cream, paler to foot edge; mantle translucent narrow, wider anteriorly, edge thickened strongly lobed with cream/white band; faint dark/black pigmentation on mantle edge aligning with rib interstices, dark pigmentation over centre of cephalic folds.

Shell (Figs 65G–I, Q; Table S9): Small (max sl mean = 13.5 mm, SD = 1.02 mm, n = 6); ovate, often elongated, shape irregular, height medium; apex weakly offset sightly posterior and left, apical sides convex, protoconch direction weakly heterostrophic (n = 1, Fig. 65Q), shell whorl dextral; growth striae indistinct, shell thick; rib count (mean = 35, SD = 2, n = 6), exterior uneven, radial shading bands faint, protoconch area pale; primary ribs white, secondary ribs darker, variably raised, crooked and bent, narrow and uneven in width, ridge rounded, extend unevenly slightly beyond shell lip to scallop and corrugate the shell edge; ribs unevenly spaced, 2–3 primary ribs form raised siphonal ridge; variable number secondary ribs between primary ribs, most rib interstices dark brown. Interior evenly dark, chocolate-brown, sometimes mottled paler in places, short white rays on shell margin align under primary/secondary ribs, siphonal groove distinct; ADM scar distinct, CMS straight, thickening and whitening of shell lip apparent in some specimens.

Reproductive system (Figs 66E, G; n = 3). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity and digestive glands; epiphallic parts all white muscular fibrous tissue, reduced in size and positioned over BM (F1 looped over front of BM), singular GP through foot wall; GA small indistinct; AO relatively small broad, bluntly pointed (embedded in folds of MG), joined to upper GA; ED elongated broad thickened, centrally twisted, joins to upper GA; EG small, soft whitish tissue, folded joins ED; single long narrow bent flagellum (F1) as an extension of ED, of similar length. BD and CD connect in opposing directions into GA between ED join and GP, both ducts very narrow long straight smooth whitish, pass together through RAM (BD over thicker CD) into soft white folded tissues of MG; BC embedded in folds of AG/MG; BD with prominent distal twisted loop with MA attached to inner anterior foot wall above BM, bent immediately before BC; BC small bulbous, thin whitish translucent test; MG/AG complex relatively large, often separated (Fig. 66E, G); HD thickened, brown markings, small coils, links ducts in soft white folded tissues of AG to yellowish granulated reddish spotted HG; HG larger than AG/MG.

Spermatophore (Fig. 66F, H). Test thin, translucent (length = 9.62 ± 0.08 mm, n = 2), head evenly cylindrical, tip bluntly rounded, containing a white gelatinous core, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless; head wider and longer than flagellum (head length = 6.06 ± 1.11 mm, ~ 72% of SPM length, head width = 103 ± 0 µm, flagellum width = 17 ± 0 µm, n = 2). 5 SPM tightly coiled and embedded in dark brown gelatinous mass in one BC.

Comparative remarks. In our mitochondrial tree (Figs 1, 2), *S. ouasseensis* **sp. nov.** (*atra* group, Clade H, unit 48) forms a clade with *S. bourailensis* **sp. nov.** (unit 49), *S. pravitas* **sp. nov.** (unit 51) and *S. scabra* (unit 50) (Figs 1, 2). It differs from *S. bourailensis* **sp. nov.** by COI distances of ≥ 11.8% and from other species by COI distances of ≥ 24% (Table S4). We have found this species in sympatry with three congeners in NC: *Siphonaria bourailensis* **sp. nov.** has fewer and broader ribs, a more prominent siphonal ridge, a larger, wider and pointed AO, and a larger ED. For comparisons with *S. hienghenensis* **sp. nov.** and *S. atra* refer to comparative remarks under these species.

Distribution and habitat. Known only from NC (Fig. 70). In this study, found at Ouassé nr Canala in sheltered positions on exposed and sheltered rocky boulder and platform shores, mid to upper littoral level (Fig. 65R).

Etymology. Named after the type locality of Ouassé near Canala, NC.

Siphonaria caledonica sp. nov.

(Figs 65J–L, O, S–T, 66I–J)

Siphonaria '*laciniosa* group, unit 23'—Dayrat *et al.* 2014: 261, fig. 4 E.

Material examined. *Type material.* Holotype, from Tiari, 20°15.692'S, 164°24.664'E, NC; coll. B.W. Jenkins, NC04-3, 25 Oct 2018 (AM C.584788 [M364, SK130 (RS

+ SPM)], Fig. 65J). Paratype, same data as holotype (AM C.585838 p [M362], Fig. 65L); seven paratypes, from Bonhomme de Bourail, La Roche Percee, 21°36.487'S, 165°27.423'E, NC; coll. B.W. Jenkins, NC06-3, 28 Oct 2018 (AM C.584799 5p, C.585015 p [M366], Fig. 65K, C.585016 p [M367]).

Other, non-type material. **NC:** Tiari, 20°15.692'S, 164°24.664'E NC04-3 (AM C.585969 20p, AM C.584787 p [SK060], C.585839 p [M363, SK131], C.585840 p [M365], C.585841 p [M459]); Bonhomme de Bourail, La Roche Percee, 21°36.487'S, 165°27.423'E NC06-3 (AM C.584798 15p); Presqu'ile de Ouano La Foa, 20°51.434'S, 165°48.479'E NC06-4 (AM C.595910 12p).

External morphology (Fig. 65S). Foot sole, foot wall, cephalic folds and pneumostome pale grey, paler to foot edge; mantle translucent narrow, edge thickened, weakly lobed with black pigmentation bands aligning with rib interstices; black pigmentation more intense and darkest over centre of cephalic folds.

Shell (Figs 65J–L, T; Table S9). medium sized (max sl mean = 17.5 mm, SD = 3.7 mm, n = 8);ovate, often elongated, shape irregular, height tall; apex offset slightly posterior and left, apical sides convex, posterior side straight to slightly concave, protoconch direction homostrophic (n = 1, Fig. 65T), shell whorl dextral; growth striae prominent in bands, shell thick; rib count (mean = 44.4, SD = 5, n = 8), radial shading bands occur, protoconch area dark; primary ribs white, fairly straight often bent, narrow and uneven in width, ridge rounded, extend slightly beyond shell lip to scallop and corrugate the edge; ribs may be fairly evenly spaced, paired primary ribs forming siphonal ridge bounded with a wide interstice either side; 0–4 secondary ribs between primary ribs, most secondary ribs and rib interstices dark brown, smaller ribs occur in growth interstitial areas. Interior shell margin dark brown to tan, white rays align on shell margin under primary/secondary ribs, siphonal groove distinct, same colour as shell edge, points to right anterior; spatula dark chocolate brown to mottled tan even whitish; ADM scar distinct, CMS straight, paler than shell lip; thickening of shell lip translucent, infills and reduces lip scalloping, spatula becomes whitened.

Reproductive system (Fig. 66I; n = 2). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity and digestive glands; epiphallic parts positioned over BM, with singular GP through foot wall; GA very small indistinct; AO relatively large elongated broad centrally bent bluntly pointed (embedded in folds of MG), joined to upper GA; ED elongated broad thickened, centrally bent, joins to lower side of GA; GA, AO, ED all white muscular fibrous tissue; EG large, soft whitish tissue, folded, joins ED and single narrow bent flagellum (F1) as an extension of ED, shorter length. BD and CD connect in opposing directions into GA between ED join and GP, both ducts narrow long straight smooth whitish, pass together through RAM to outerside (BD over thicker CD) into soft white folded tissues of MG; BC embedded in folds of AG/MG; BD long narrow with prominent distal loop with MA connected to inner anterior foot wall above BM; BC medium bulbous, thin whitish translucent test; MG/AG complex relatively large; HD thickened coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; AG/MG larger than HG.

Spermatophore (Fig. 66J). Test thin, translucent (length = 8.93 mm, n = 1); head evenly cylindrical, bulbous, tip bluntly rounded, containing a white gelatinous core, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless; head much wider and similar length to flagellum (head length = 4.65 mm, 52% of SPM length, head width = 124 µm, flagellum width = 22 µm). 2 SPM tightly coiled embedded in brown gelatinous mass in one BC (AM C.584788).

Comparative remarks. In our mitochondrial phylogeny, *S. caledonica* **sp. nov.** (*laciniosa* group, unit 23) is the sister species of *S. maloensis* (see comparative remarks under this species) (Figs 1, 3). It differs from other species by COI distances of ≥ 19% (Table S6). We found *S. caledonica* **sp. nov.** in sympatry with five congeners on the E coast of NC: For comparisons with *S. atra*, *S. hienghenensis* **sp. nov.**, and *S. normalis* refer to comparative remarks under these species. *Siphonaria bourailensis* **sp. nov.** has a shell with slightly more raised ribbing, greater edge scalloping, a paler spatula, and a shorter ED. *Siphonaria poindimiensis* has a shell with a more central apex, greater edge scalloping, paler spatula, a blunt AO, and a longer ED. The RS resembles that of *S. atra* and *S. viridis*. Specimens figured as '*laciniosa* group, unit 23' in Dayrat *et al.* (2014: 262) belong to this species.

Distribution and habitat. Recorded from E and W coasts of NC (Fig. 70). In this study, found on exposed to sheltered rocky boulder and platform shores, mid to upper littoral level (Fig. 65O).

Etymology. For New Caledonia, where this species has been found; adjective.

***Siphonaria perexigua* sp. nov.**

(Figs 68A–C, K, 69A–B)

Siphonaria '*laciniosa* group, unit 10'—Dayrat *et al.* 2014: 261, fig. 3L.

Material examined. *Type material.* Holotype, from Clifton Beach, Karachi, 24°45.500'N, 67°05.968'E, Pakistan; coll. S. Mushtaq, S. Amir and B.W. Jenkins, PA02-1, 4 July 2018 (AM C.585859 [M233], Fig. 68A). Paratypes: same data as holotype (AM C.585891 17p, C.585104 p [M232], Fig. 68C, C.585105 p [M234], Fig. 68B); French Beach Karachi, Pakistan; coll. S. Mushtaq, S. Amir and B.W. Jenkins, 24°50.367'N, 66°49.387'E PA01-1 4 July 2018, (AM C.585183 p [SK187]).

Other, non-type material. **Pakistan:** Karachi, Clifton Beach 24°45.500'N, 67°05.968'E PA02-1, 4 July 2018 (AM C.595985 [SK569]); French Beach 24°50.367'N, 66°49.387'E PA01-1 (AM C.585894 3p, C.595949 p [SK376]).

Taxonomic remarks. Sequences of a specimen of 'unit 10' from Hikman Peninsula, Oman first published in

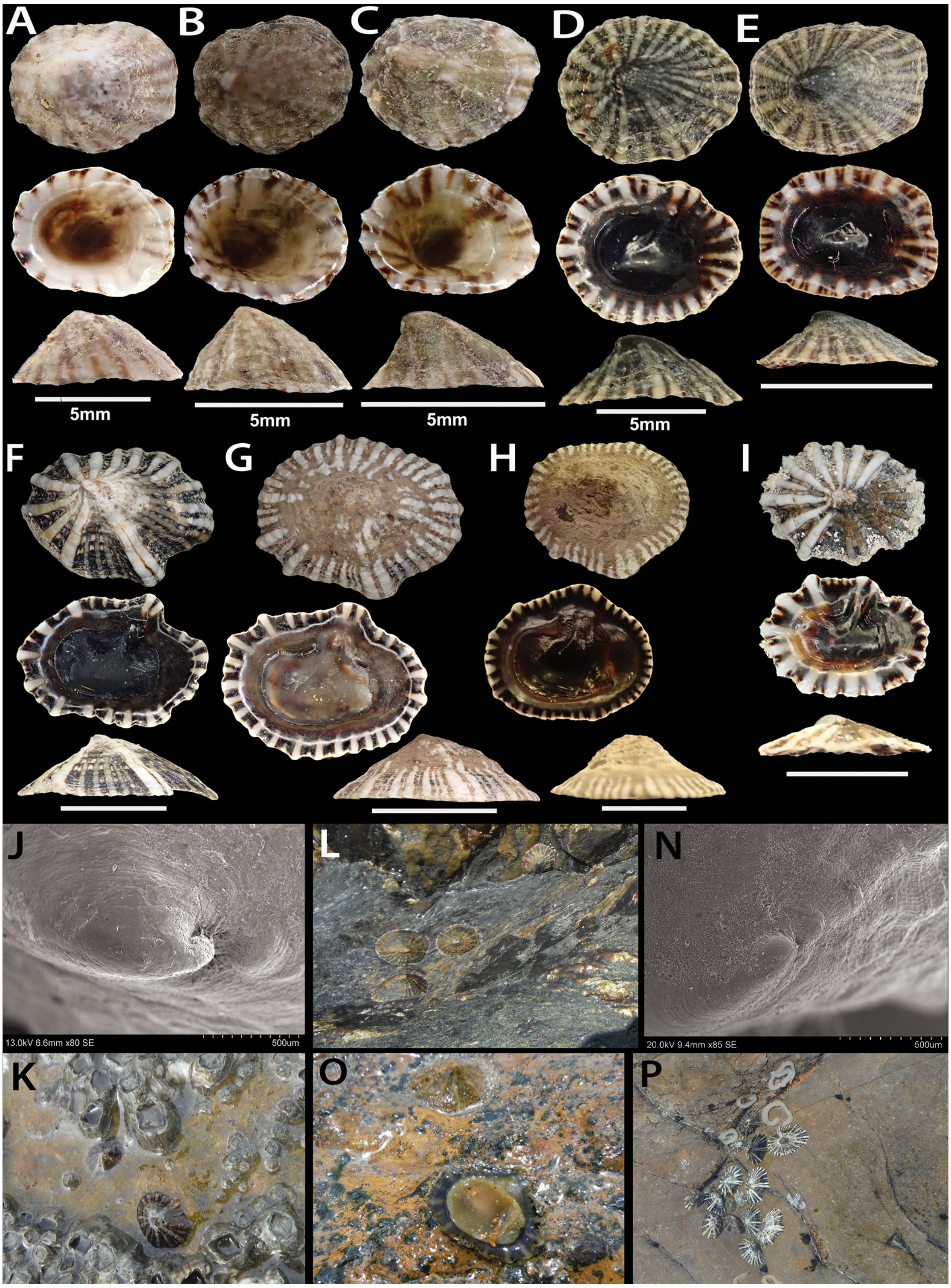

FIGURE 68. Shells of *S. perexigua* **sp. nov.**, *S. planucosta* **sp. nov.** and *S. bourailensis* **sp. nov. A–C, K.** *S. perexigua* **sp. nov.**, Pakistan, Karachi. **A.** Holotype AM C.585859 [M233]. **B.** Paratype AM C.585105 [M234]. **C.** Paratype AM C.585104 [M232]. **K.** *In situ*. **D–E, L–N.** *S. planucosta* **sp. nov.**, Timor-Leste, Dili. **D.** Holotype AM C.584826 [M446, SK229]. **E.** Paratype AM C.585442 [M451, SK165]. **L.** *In situ*. **N.** Protoconch, AM C.585925 [SK231]. **F–J, O–P.** *S. bourailensis* **sp. nov.**, NC, La Roche Percee. **F.** Holotype AM C.585017 [M368]. **G.** Paratype AM C.608182 [SK126]. **H.** Paratype AM C.585466 [M372]. **I.** Paratype AM C.585438, Lifou, Chateaubriand [M390]. **J.** Protoconch, AMS C.585331 [SK125]. **O.** NC, Poum, animal. **P.** Poum, in situ. Unlabelled scale bars = 10 mm.

Dayrat *et al.* (2014) have subsequently been referenced by Gonzàlez-Wevar *et al.* (2018) as '*Siphonaria* sp. (Caroline Island)' under an identical GenBank registration number.

External morphology. Foot sole, foot wall, cephalic folds and pneumostome evenly cream, without dark pigmentation; mantle narrower than foot wall, edge thickened, weakly lobed.

Shell (Figs 68A–C; Table S9). Small sized (max sl mean = 4.6 mm, SD = 0.58 mm, n = 4), elongate ovate; height tall, medium thickness; apex offset strongly posterior and left, apical sides very flat to weakly convex, protoconch direction homostrophic (n = 2), apex curled to posterior, shell whorl dextral; growth striae indistinct; rib count (mean = 21, SD = 0.43, n = 4), primary ribs indistinct, pale white, slightly bent, broaden to shell lip; shell lip weakly corrugated, uneven; no distinct secondary ribs, rib interstices darker brown; siphonal ridge indistinct, radial shading bands absent. Interior shell lip white, pale to dark brown rays on shell margin to spatula align under primary/secondary ribs, siphonal groove indistinct, same colour as shell edge, points to right anterior; spatula golden brown to mottled brown; ADM scar distinct, CMS concave, paler than shell lip; thickening of shell lip occurs in some specimens; infills and reduces lip corrugations.

Reproductive system (Fig. 69A; n = 3). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity and intestine; epiphallic parts positioned between BM and RAM. GA very small with singular GP through foot wall; AO small, narrow, bluntly pointed, joined to inner side of GA; ED short, elongated, centrally bent, joins to outer side of GA; GA, AO, ED all white muscular fibrous tissue; EG medium, soft whitish tissue, slightly folded, joins ED; single centrally folded broad flagellum (F1), shorter but similar width to ED, appears as an extension of ED; BD and CD connect closely but in opposing directions into GA between ED join and GP; CD short, broad, slightly bent, smooth, whitish, featureless; BD long, narrow, featureless; both ducts pass closely together through outer side of RAM (BD over CD); MG/AG complex medium; CD connecting to ducts, BC embedded in folds of AG/MG; BD without distal loop and MA; BC relatively large, spherical, thin whitish translucent test; HD short, thickened, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobbed; AG/MG larger than HG, sides match curvature of inner foot wall.

Spermatophore (Fig. 69B). Thread-like (length = 3.07 ± 0.03 mm, n =2), translucent, test thin; head section bluntly rounded, evenly cylindrical, containing a core white gelatinous mass, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless. Head section longer wider than flagellum (head length = 1.47 ± 0.06 mm, ~ 48% of SPM length, head width = 69 ± 0 μm, flagellum width = 17 ± 0 μm, n = 2); 2 SPM tightly coiled embedded in whitish gelatinous mass in BC [SK562].

Comparative remarks. *Siphonaria perexigua* **sp. nov.** (*normalis* group, unit 10) forms a well-differentiated lineage in the mitochondrial tree (Clade E, Figs 1, 4). It differs from other species by COI distances of ≥ 18% (Table S8). Specimens from Pakistan examined and sequenced herein form a sub-clade with an unidentified species from Oman (*Siphonaria* sp. 'unit 10') published by Dayrat *et al.* (2014). We have not examined the specimen from Oman but presume that it is conspecific based on the close genetic relationships with the samples from Pakistan. In Pakistan, we found *S. perexigua* **sp. nov.** in sympatry with four other congeners: For comparisons refer to comparative remarks under these species (*S. asghar*, *S. belcheri*, *S. kurracheensis*, and *S. crenata*). Bosch *et al.* (1995: 185) identified individuals of this species as *S. compressa* Allanson, 1958. However, *S. compressa* (not reviewed herein) differs in shell geometry (fragile shell, apex weakly offset, not overlapping posterior shell edge; see Chambers & McQuaid, 1994a: 266, fig. 1A) and distribution (west coast of S. Africa; Chambers & McQuaid, 1994a) from the the specimens figured in Bosch *et al.* (1995: fig. 861).

Distribution and habitat. Recorded from Karachi, Pakistan and Hikman Peninsula, Oman (Fig. 70). In this study, found in sheltered positions on moderately exposed rocky shores, mid littoral level, amongst small barnacles (Fig. 68K).

Etymology. From 'perexiguus' (Latin = very small), for the very small shell size of this species; adjective.

Siphonaria planucosta sp. nov.

(Figs 68D–E, L–N, 69C–D)

Material examined. *Type material.* Holotype, from Dolokoan Beach, 8°31.424'S, 125°37.091'E, N of Dili, Timor-Leste; coll. B.W. Jenkins, TL01-1, 14 July 2019 (AM C.584826 [M446, SK229 (RS + SPM)], Fig. 68D). Paratypes: same data as holotype (AM C.585443 10+p, C.585442 p [M451, SK165], Fig. 68E).

Other, non-type material. **Timor-Leste:** Dolokoan Beach N of Dili, 8°31.424'S, 125°37.091'E TL01-1, (AM C.585925 p [SK231]).

External morphology. Foot sole dark grey, foot edge cream; foot wall, cephalic folds and pneumostomal lobe evenly grey; black pigment shading at join of foot wall and mantle, concentrated over cephalic folds; mantle thin, narrower than foot wall, edge lobed with black bands aligning with shell rib interstices and interstice width; pneumostome under mantle between right adductor muscles.

Shell (Figs 68D–E, L; Table S9). Small sized (max sl mean = 8.3 mm, SD = 0.47 mm, n = 2), ovate; low, fragile, thin; apex offset strongly posterior and to left, apical sides strongly convex, protoconch direction weakly homostrophic to central (n = 1, Fig. 68L), below apex, curls to posterior, shell whorl dextral; growth striae indistinct, shell edge uneven, faintly scalloped; rib count (mean = 33, SD = 4, n = 2), primary ribs flat, pale white, fairly straight bent in places, broaden to shell lip, 2–3 secondary ribs between primary ribs, interstices dark brown; paired primary ribs form siphonal ridge, usually not prominent, may appear raised, protoconch area darker; Interior shell

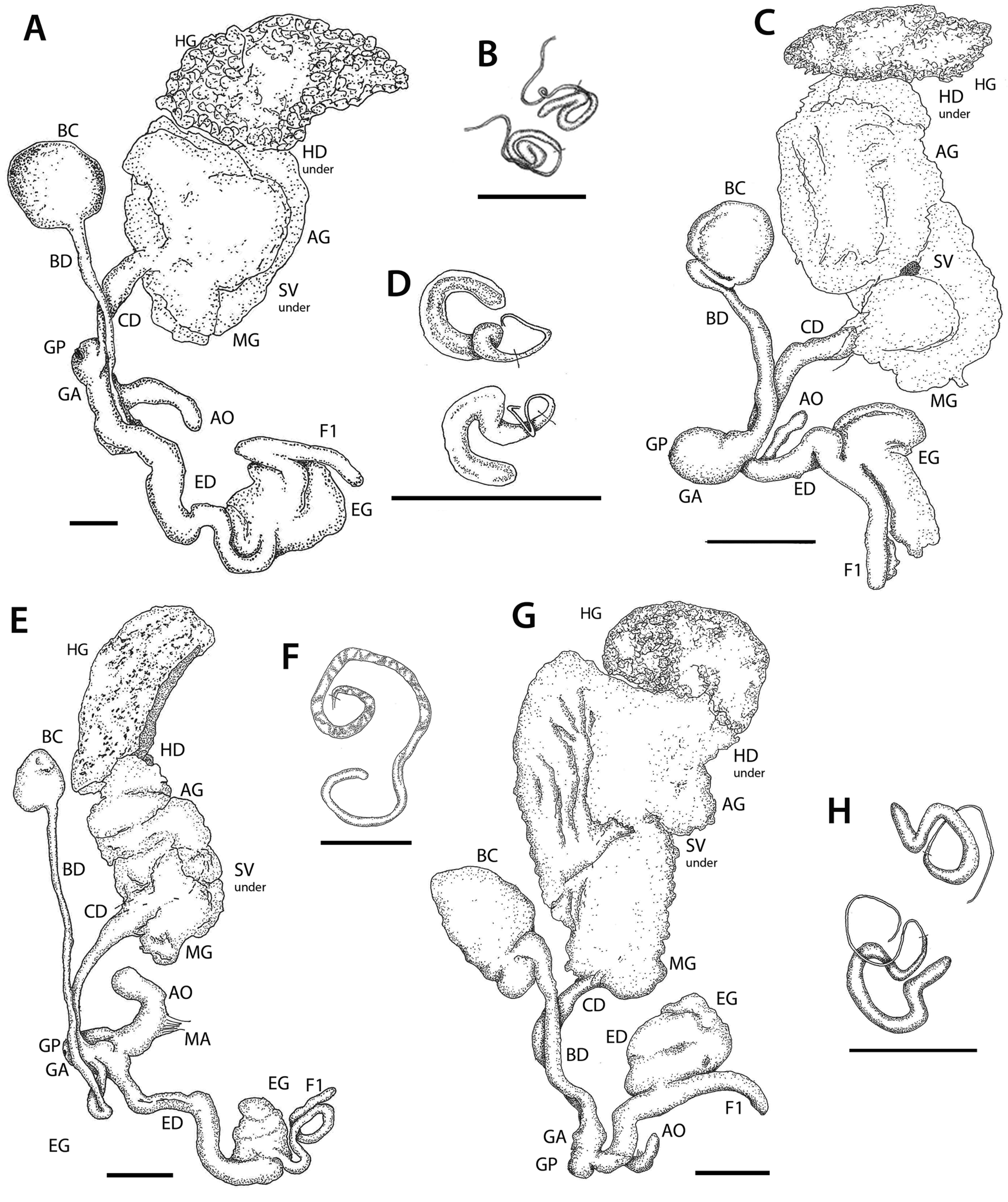

FIGURE 69. Reproductive morphology of *S. perexigua* **sp. nov.**, *S. planucosta* **sp. nov.**, *S. bourailensis* **sp. nov.** and *S. pravitas* **sp. nov. A–B.** Paratype of *S. perexigua* **sp. nov.** AM C.585183 [SK187]. **C–D.** Holotype of *S. planucosta* **sp. nov.** AM C.584826 [M446, SK229]. **E–F.** Holotype of *S. bourailensis* **sp. nov.** AM C.585017 [M368]. **G–H.** Holotype of *S. pravitas* **sp. nov.** AM C. 585040 [M192, SK118]. Scale bars = 1 mm.

margin white, dark chocolate brown rays extend from shell lip to spatula appearing paired, aligning under rib interstices; spatula and indistinct siphonal groove evenly dark chocolate brown; ADM scar indistinct, CMS convex; thickening of shell lip occurs, infills and reduces lip scalloping. Shell resembles other small dark *normalis* group.

Reproductive system (Fig. 69C; n = 2). Positioned within entire right side of coelom, against foot wall on foot muscle, under the respiratory cavity and intestine occupying large proportion of animal body volume; epiphallic parts positioned over BM. GA medium, with singular GP through foot wall; AO very small, narrow, bluntly pointed, joined to lower ED and upper GA; ED very short, broad, centrally bent, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG very large, soft whitish tissue, slightly folded, joins ED; single very broad flagellum (F1), similar length and width to ED, appears as an extension of ED, EG and F1 joined in parallel; BD and CD connect side-by-side into GA between ED join and GP, both ducts short, slightly bent, smooth, thickened, whitish, featureless, pass closely together between outside RAM and inner foot wall (BD over CD) into soft white folded tissues of MG; MG/AG complex medium in size; CD connecting to ducts, BC embedded in folds close to embedded blackish SV; BD without distal loop and MA, with loop immediately prior to BC; BC relatively large, spherical, thin whitish translucent test, (4 SPM in holotype AM C.584826 TL01-1 [M446, SK229]); HD short, narrow, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobbed; AG larger than HG, sides match curvature of inner foot wall.

Spermatophore (Fig. 69D). Broad head with short flagellum (length = 1.71 ± 0.08 mm, n = 2); head section cylindrical, bulbous, rounded tip; test thin, smooth, featureless, translucent encasing a white opaque central core; short looped tapering section merges head to filamentous flagellum; head slightly shorter, wider than translucent flagellum (head length = 1.16 ± 0.17 mm, flagellum length = 0.55 ± 0.088 mm, ~ 68% of SPM length, head width = 119 ± 8 µm, flagellum width = 11 ± 0 µm, n = 2); 4 SPMs tightly coiled in BC (AM C.584826 holotype [M446, SK229]).

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 4), *S. planucosta* **sp. nov.** (*normalis* group, unit 79) is the sister species of *S. radiata* (unit 12). *Siphonaria planucosta* **sp. nov.** differs from *S. radiata* by COI distances of ≥ 18.4% (Table S8).

We found *S. planucosta* **sp. nov.** in sympatry with five congeners in TL. For comparisons with *S. forticosta* **sp. nov.**, *S. alba*, *S. javanica*, *S. viridis*, and *S. campestra* **sp. nov.** refer to comparative remarks under these species.

Distribution and habitat. Recorded from Dolokoan Beach, N of Dili, Timor-Leste (Fig. 70). In this study, found at sheltered positions (mainly in crevices) on exposed shore boulders, at mid littoral levels (Fig. 68L).

Etymology. From 'planus' (Latin = level, even), for the level, even primary ribs on the shell of this species; adjective.

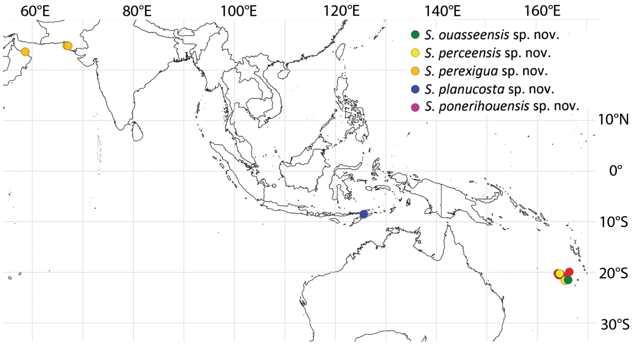

FIGURE 70. Known occurrence records of *S. ouasseensis* **sp. nov.**, *S. caledonica* **sp. nov.**, *S. perexigua* **sp. nov.**, *S. planucosta* **sp. nov.** and *S. bourailensis* **sp. nov.**

Siphonaria bourailensis sp. nov.

(Figs 68F–J, O–P, 69E–F)

Material examined. *Type material.* Holotype, from Bonhomme de Bourail, La Roche Percee, 21°36.487'S, 165°27.423'E, NC; coll. B.W. Jenkins, NC06-3, 28 Oct 2018 (AM C.585017 [M368], Fig. 68F). Paratypes: same data as holotype (AM C.608182 p [SK126], Fig. 68J, C.585466 p [M372] Fig. 68H); We Baie de Chateaubriand, East coast Lifou, Loyalty Islands, NC, 20°54.779'S, 167°15.636'E; coll. B.W. Jenkins, LFU01-1, 22 Oct 2018 (AM C.585438 p [M390], Fig. 68I).

Other, non-type material. **NC:** Poum 2, 20°13.754'S, 164°01.699'E, NC05-3 (AM C.586000 4p); Ponerihouen, 21°05.644'S, 165°26.646'E, NC03-1 (AM C.584807 p [M360]); Bonhomme de Bourail, La Roche Percee, 21°36.487'S, 165°27.423'E, NC06-3 (AM C.585331 p [SK125 protoconch I2]); Presq'ile Ducos Baie des Dames, Noumea, 22°14.170'S, 166°24.524'E, NC01-1 (AM C.584804 4p).

External morphology (Fig. 68O). Foot sole and foot wall evenly cream, without black pigmentation, paler to foot edge and mantle edge; even black-pigmented shading along mantle and foot wall join, black pigmentation darkest over centre of cephalic folds; mantle narrow, edge thickened, weakly lobed without black pigmentation; pneumostomal lobe under mantle, narrow and unpigmented.

Shell (Figs 68F–J; Table S9). Small to medium sized (max sl mean = 15.1 mm, SD = 2.4 mm, n = 5), ovate; height low to medium; apex offset strongly posterior and left pointing to posterior, apical sides convex, protoconch direction homostrophic (n=3, Fig. 68J), shell whorl dextral; growth striae notable uneven, shell thin, rib count (mean = 41, SD = 5.7, n = 5), primary ribs white, fairly straight, increasingly widen to shell lip, weakly extend beyond shell lip; interstices pale brown to black,; secondary ribs indistinct and fewer than primary; paired primary ribs on siphonal ridge, more prominent than other primary ribs; dark patches with 3–4 secondary ribs either side of siphonal ridge. Interior shell margin and spatula dark chocolate brown to black, primary and secondary ribs marked by short white rays often extending over shell margin, siphonal groove distinct and weakly bent; shell edge scalloped, not corrugated, swollen rounded; ADM scar distinct, CMS straight, paler than shell lip. Thickening and dark brown /black of shell lip common.

Reproductive system (Fig. 69E; n = 1). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts lie over back of BM; GA very small, singular GP through foot wall; AO very small elongate, tip blunt; ED relatively large, broad, bent, joins to side of GA; single flagellum (F1) long broad, as long as ED, appears as an extension of ED; GA, AO, ED all white muscular fibrous tissue; EG large, soft whitish tissue, slightly folded; BD and CD short, broad, jointly connect into upper end of GA; BD without any distal loop, longer slightly narrower than CD; both ducts smooth featureless, pass closely together through outer side of RAM (BD over CD) into folded, soft white tissues of large MG complex; BC very large, bulbous, thin translucent test, embedded in MG folds close to embedded SV; HD large, coiled, links AG to small yellowish granulated HG; AG larger than HG, sides match curvature of inner foot wall.

Spermatophore (Fig. 69F). Body cylindrical, relatively short (length = 3.68 ± 0.87 mm, n = 2); test thin, translucent; head bulbous, tip bluntly rounded, wide, evenly cylindrical, containing a core white gelatinous mass, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless. Head section slightly shorter but much wider than flagellum (head length = 1.95 ± 0.37 mm, ~ 55% of SPM length; head width = 119 ± 8 µm, flagellum width = 13 ± 0.0 µm, n = 2); 6 SPM tightly coiled in one bursa embedded in brown gelatinous mass.

Comparative remarks. In our mitochondrial phylogeny, *S. bourailensis* **sp. nov.** (*atra* group, unit 49) is the sister species of *S. ouassensis* **sp. nov.**; for comparison refer to comparative remarks under that species. We found *S. bourailensis* **sp. nov.** in sympatry with seven congeners in NC and on Lifou, Loyalty Islands: For comparison with *S. atra* (unit 41), *S. hienghenensis* **sp. nov.** (unit 40), *S. monticulus* (unit 57), *S. normalis* (unit 14), *S. ouasseensis* **sp. nov.** (unit 48), *S. caledonica* **sp. nov.** (unit 23), and *S. viridis* (unit 25) refer comparative remarks under these species. Specimens of *S. bourailensis* **sp. nov.** on Lifou slightly differ from those on NC in having a smaller shell with wider and fewer primary ribs and a golden-brown internal colouration.

Distribution and habitat

Recorded as endemic to NC and Lifou (Fig. 70). In this study, found on exposed to sheltered rocky boulder and platform shores, mid to upper littoral levels (amongst and above oysters) (Fig. 68P).

Etymology

Named after type locality of Bonhomme du Bourail, NC.

***Siphonaria pravitas* sp. nov.**

(Figs 69G–H, 71A–B, M–N, S)

Material examined. *Type material.* Holotype, from Laings Point, 33°50.419'S, 151°16.638'E, Sydney Harbour, NSW, Australia; coll. B.W. Jenkins, NSW06-3, 19 April 2018 (AM C.585040 [M192], Fig. 71A [SK118 (RS and SPM)], Fig. 69G). Paratypes same data as holotype (AM C.585334 p; C.585038 p [M153], Fig. 71B; C.585039 p [M166]).

Other, non-type material. **Australia, LHI:** Signal Point, 31°31.501'S, 159°03.580'E, LHI2017Apr04-099 (AM C.608190 p [M010]), LHI2017Apr04-104 (AM C.585939 p). **NSW:** Sydney, Spit Bridge, 33°48.198'S, 151°14.860'E (AM C.546769 4p, C.546766 p [SK432 protoconch I4]); Laings Point, 33°50.419'S, 151°16.638'E, NSW06-3 (AM C.585033 p [M191]); Spit Bridge 2, 33°48.270'S, 151°14. 520'E (AM C.546764 p; C.546767 2p; C.608191 p, C.595942 p [SK186 protoconch I3]); 100 m NW of Spit Bridge, 33°48.210'S, 151°14.664'E (AM C.608194 p).

External morphology (Fig. 71N). Foot sole, foot wall and mantle smooth, evenly cream to yellow, paler at foot edge; regular vertical uneven bands/stripes on foot wall, roughly align with rib interstices, fades to none at join of foot wall and mantle; narrow cream pneumostomal lobe under mantle; black pigmentation heavy dark over front of cephalic folds; foot wall shows black blotches; fringing mantle translucent, narrow, covers shell mantle, outer edge thickened, lobed, none to slight black pigmentation aligning with rib interstices; pneumostomal lobe within mantle between the right ADMs, closes the pneumostomal and anal openings at the mantle edge; two small black epithelial eye spots centralised on two thick brownish yellow centrally touching cephalic folds; genital pore inconspicuous, located on foot wall to right anterior of right cephalic fold.

Shell (Figs 71A, B, S; Table S3). Size medium (max sl mean = 18.03, SD = 0.87, n = 5), elongate ovate; low; apex offset central sightly to left, apical sides straight, posterior concave; protoconch direction homostrophic (n = 3; Fig. 71S), shell whorl dextral, growth striae uneven, distinct, protoconch area dark brown; shell thick; rib count (mean = 38.8, SD = 3.3, n = 5), 12–16 primary ribs pale white, bent, crooked to shell lip, rib ridges rounded, increasingly raised and broaden to shell edge, weakly protrude beyond shell lip to unevenly scallop and corrugate the edge; 3-4 interspersed pale white less raised secondary ribs, rib interstices brown; paired primary ribs on siphonal ridge. Interior shell margin dark to golden brown, white/cream rays under primary and secondary ribs, extend to dark chocolate brown blotched white spatula; siphonal groove distinct, whitish; ADM scar distinct, chocolate brown to whitish, CMS straight; no thickening of shell lip noted; pale variety may occur.

Reproductive system (Fig. 69G; n = 2). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between BM and RAM. Join of AO and GA indistinct, AO elongated, bluntly pointed, centrally bent with MA, much larger than GA, much thicker than ED; ED relatively long, slightly twisted, narrow; EG white, folded, elongated; single flagellum F1 on EG, long, looped, narrow; AO, GA and ED all muscular white tissue; BD and CD with opposing connections to GA between ED, AO and GP; BD slightly longer and thinner than CD with a prominent loop on anterior side, both ducts smooth and pass together through RAM connecting into MG (BD above CD), BC translucent, white test, mid-sized and bulbous; HD short, coiled, links AG to a small elongated narrow brownish finely granulated HG, inner edge firmly moulded; MG and AG small, folded, soft white tissue; purple SV embedded on left side of AG, AG larger than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 69H). Long cylindrical, body long; test thin, short tapering section merging head with filamentous flagellum; head bluntly rounded, central whitE, WAvy core, longer thicker than translucent flagellum (head length = 7.09 mm, head width = 160 µm n = 1; flagellum incomplete); 2 tightly coiled SPMs in bursa of one specimen (AM C.585040).

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 2), *S. pravitas* **sp. nov.** (*atra* group, unit 51) is the sister species of *S. scabra* (unit 50). Both species differ by COI distances of ≥ 8.2%. From any other species *S. pravitas* differs by COI distances of ≥ 23.5% (Table S4). *Siphonaria scabra* differs by having a higher shell with less raised ribs and less developed edge scalloping, a larger AO, longer ED, smaller BC, a longer, narrower BD with distal loop, a longer SPM. We found *S. pravitas* **sp. nov.** in sympatry with eight congeners throughout its range. Six congeners are sympatric in Sydney Harbour, NSW: For comparisons with *S. stowae*, *S. denticulata*, *S. diemenensis*, *S. funiculata*, *S. scabra*, and *S. zelandica* refer to comparative remarks under these species. Two congeners are sympatric in LHI: Refer to comparative remarks under *S. lentula* and *S. exulum*.

Distribution and habitat. Recorded as endemic to SE Australia (Fig. 73). In this study, found on sheltered rocky shores, at upper to mid littoral levels (Fig. 71M).

Etymology. From ‘pravitas’ (Latin = ‘crookedness, inequality, irregularity or deformity’) referring to the crooked waviness of the radial ribs on the shell of this species; noun in apposition.

Siphonaria recurva sp. nov.

(Figs 71C, 72A)

Siphonaria ‘*atra* group, unit 32’—Dayrat *et al.* 2014: 264, fig. 5I.

Material examined. *Type material.* Holotype, from NW side of Big Nusa Is., 02°34.1’S, 150°46.7’E, New Ireland, PNG; coll. KAVIENG 2014 expedition, KM21, 28 Jun. 2014 (MNHN IM-2013-55336 [M534], Fig. 71C).

External morphology (preserved). Animal exterior evenly cream, foot sole darker, paler to foot edge; irregular black pigmentation on foot wall.

Shell (Fig. 71C; Table S9). Small sized (max sl = 15.3 mm, n = 1), circular ovate, height tall; apex noticeably offset to posterior and left, hooked to posterior, apical sides convex, posterior straightening, protoconch direction homostrophic (n = 1, MNHN IM-2013-55336 holotype), shell whorl dextral, shell thin; growth striae prominent and slightly raised; multiple radial colour bands, protoconch area dark brown, central band pale, shell fringe dark brown; rib count (35, n = 1), primary ribs far more prominent than secondary ribs; ~ 17 pale brown to off white primary ribs, ridges raised and rounded, broaden to shell edge; paired primary ribs form siphonal ridge, most primary ribs protrude strongly beyond shell lip with ends slightly raised to strongly scallop and corrugate shell edge; 0–3 finer secondary ribs between primary ribs, rib interstices darker. Interior shell margin and spatula dark chocolate brown; off white to cream rays on shell margin align under ribs, siphonal groove distinct, same colour as spatula, paler than margin; ADM scar distinct, CMS convex; no thickening of shell lip noted.

Reproductive system (Fig. 72A; n = 1). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts lie over back of BM; GA medium, singular GP through foot wall; AO bulbous wide, tip blunt; ED short, wide, bent, joins to side of GA; single flagellum (F1) short, twisted, as long as ED, appears as an extension of ED; GA, AO, ED all white muscular fibrous tissue; EG small, soft whitish tissue, slightly folded; BD and CD long, narrow, jointly connect into upper end of GA; BD with distal loop and MA, longer, centrally narrower than CD but wider at GA and MG junctions; both ducts smooth featureless, pass closely together through RAM (BD over CD) into folded, soft white tissues of large MG/AG complex; BC large, bulbous, thin translucent test, embedded in MG folds close to embedded SV; HD small, lobed, coiled, links AG to small yellowish granulated HG; AG larger than HG, sides match curvature of inner foot wall.

Comparative remarks. In our mitochondrial tree (Figs 1, 2), *S. recurva* **sp. nov.** (*atra* group, unit 32) is the sister species of *S. incerta* (unit 72). Both species differ by COI distances of ≥ 16.7%. From other species *S. recurva* differs by distances of ≥ 23.3% (Table S3). We found *S. recurva* **sp. nov.** in sympatry with two congeners in New Ireland, PNG. For comparisons with *S. nusalikensis* **sp. nov.** and *S. normalis* refer to comparative remarks under these species. The specimen figured as ‘*atra* group, unit 32’ in Dayrat *et al.* (2014: fig. 5I) is conspecific.

Distribution and habitat. Recorded from Big Nusa Island, Kavieng, New Ireland, PNG and Tutuila, American Samoa, Western Pacfic Ocean (Fig. 73). Found on intertidal platforms and limestone cliffs.

Etymology. Derived from Latin adjective “recurvus” meaning ‘curving back, crooked’ referring to the shape of the shell’s prominent protoconch.

***Siphonaria restis* sp. nov.**

(Figs 71D–H, O–P, 72B–D)

Siphonaria kurracheensis—Knox 1955: 88; Roberts & Wells 1981: 72, pl. 30, figs 142, 143; Black & Johnson 1981: 79; Jenkins 1983: 28; 1984: 117; Wells 1984: 54; Johnson & Black 1997: 104; Chim & Tan 2009: 269; Willan *et al.* 2015: 330 (not *S. kurracheensis* Reeve, 1856).

Siphonaria luzonica—Hubendick 1955: 3, fig 3; Hodgkin *et al.* 1966: 27, pl. 8, fig. 3 (not *S. luzonica* Reeve, 1856).

Siphonaria sp.—Verco 1912b: 205; Wells & Bryce 1997: 379.

Material examined. *Type material.* Holotype, from Chinamans Rock, 27°42.776’S, 114°09.361’E, Kalbarri, WA; coll. B.W. Jenkins, WA52-1, 20 Nov 2017 (WAM S74049 [M400], Fig. 71D).

Paratypes same as holotype (WAM S74079 6p, S74048 p [M100], Fig. 71E, AM C.584731 11p, C.585200 p [M313], Fig. 71F, C.585919 p [SK150], Fig. 71G).

Other, non-type material. **Australia, WA:** Chinamans Rock, Kalbarri, 21°54.739’S, 113°58.706’E; coll. B.W. Jenkins, WA52-1, 20 Nov 2017 (WAM S74047 p [M099], Fig. 54D, S4078 p [SK050]); Thompson Bay, Rottnest Is, RI012 (AM C.585201 p [SK381], Fig. 54E, C.585202 d [SK382], C.595909 d [R2004]); Tantabiddi, 21°54.739’S, 113°58.706’E, WA42-1 (AM C.585656 5p, WAM S74045 p [SK036]); Cape Latouche Treville nr Gourdon Bay, 18°27.101’S, 121°48.911’E, WA27-2 (AM C.584687 5p, WAM S74135 5p); 18°27.457’S, 121°48.725’E, WA27-1 (AM C.584711 5p, WAM S74136 2p); Cape Keraudren, 19°57.393’S, 119°46.358’E, WA29-2 (AM C.584704 5p, WAM S74138 2p); Withnell Bay Dampier, 20°35.106’S, 116°47.252’E, WA33-1 (AM C.584752 5p, WAM S74141 5p); Point Samson, 20°36.655’S, 117°11.472’E, WA32-2 (AM C.584781 8p, WAM S74140 8p); 20°36.684’S, 117°11.303’E, WA32-1 (AM C.584751 5p, WAM S74139 5p); Dampier Hbr, 20°39.920’S, 116°42.134’E, WA33-3 (AM C.585575 3p); Gnoorea Point, 1 20°50.560’S, 116°21.804’E, WA36-1 (AM C.584689 3p, WAM S74142 2p); Beardon Pt Onslow, 21°37.860’S, 115°06.573’E, WA37-1 (AM C.584722 5p, WAM S74143 4p); NW Cape Exmouth, 21°48.360’S, 114°07.665’E, WA41-1 (AM C.584698 6p, WAM S74144 3p); Fly Island, Great Sandy Islands, 21°48’19.548‘‘S, 114°33’9.36‘‘E (WAM S97276 p); Tantabiddi, 21°54.739’S, 113°58.706’E, WA42-1 (AM C.584690 5p, d; WAM S74145 2p); Pt S of Bruboodjoo Pt Bateman Bay, 23°02.991’S, 113°49.371’E, WA43-1 (AM C.584732 12p, WAM S74146 5p); Point Maud, 23°08.322’S, 113°46.294’E, WA44-1 (AM C.584753 5p, C.585919 p [SK150], WAM S74147 5p); Coral Bay, S of Exmouth Gulf, 23°08.322’S, 113°46.294’E (AM C.595919 p [SK004], C.959956 p [SK001]); N of Point Quobba, 24°26.288’S, 113°24.204’E, WA45-2 (AM C.584727 7p, WAM S74149 5p); Point Quobba, 24°29.124’S, 113°24.501’E, WA45-1 (AM C.584754 5p, WAM S74148 5p); Bottle Bay Cape Peron, 25°32.566’S, 113°29.467’E, WA49-1 (AM C.584755 5p, WAM S74150 5p); Islet off Eagle Bluff, Shark Bay, Peron Peninsula, 26°05.5’S, 113°34.4’E (WAM S72339 6p); Whalebone, 26°07.835’S, 113°38.391’E, WA47-2 (AM C.585657 5p); Kells Rock Shark Bay, 26°10.473’S, 113°12.415’E, WA50-3 (AM C.584734 12p, WAM S74151 6p); Pepper Point (Zuytdorp), 26°23.826’S, 113°18.268’E, WA51-1 (AM C.584725 6p, d, WAM S74152 6p); Chinamans Rock, Kalbarri, 27°42.776’S, 114°09.361’E (AM C.585489 p [M053], C.585490 p [M398], C.585491 p [M399], C.585920 p [SK151]); Red Bluff, 27°44.627’S, 114°08.576’E, WA52-2 (AM C.595908 p [M125], C.585365 p [M126]); Horrocks, 28°21.469’S, 114°24.751’E, WA53-1 (AM C.584680 2p; WAM S74153 2p); Turtle Bay East Wallabi Is, 28°25.804’S, 113°44.538’E, WA55-1 (AM C.584758 5p; WAM S74155 5p); Houtman Abrolhos Islands, 28°25.804’S, 113°44.538’E (AM C.595971 2p), S of Fish Point East Wallabi Is, WA55-2 28°25.816’S, 113°44.633’E (AM C.584720 7p; WAM S74156 2p); Cape Burney Geraldton, 28°52.084’S, 114°38.056’E, WA54-1 (AM C.584749 5p; WAM S74154 5p); Leander Point Port Denison, 29°16.568’S, 114°54.858’E, WA57-1 (AM C.584760 5p, WAM S74157 5p); S end Leander Point Port Denison, 29°16.725’S, 114°54.918’E, WA57-2 (AM C.585517 d); Freshwater Point, 29°36.256’S, 114°58.464’E, WA57-3 (AM C.584693 3p, C.585009 p [SK063], WAM S74158 2p); Illawong Bch rocks, 29°42.198’S, 114°57.551’E, WA57-4 (AM C.584683 2p, WAM S74159 2p); Illawong, 29°42.254’S, 114°57.542’E, WA57-5 (AM C.584694 3p; WAM S74160 2p); Jurien Bay, 30°17.244’S, 115°02.482’E, WA58-1 (AM C.584679 2p; WAM S74161 p); Grey, 30°39.968’S, 115°08.072’E, WA58-2 (AM C.585366 p); Cape Leschenault, 31°17.508’S, 115°27.089’E, WA58-3 (AM C.584712 5p, WAM S74162 5p); Quinns Rock, 31°39.822’S, 115°41.345’E, WA58-4 (AM C.585368 p); Longreach Bay Point, Rottnest Is, 31°59.333’S, 115°32.063’E RI01 (AM C.585600 4p, C.585198 p [M311], C.585199 p [M312], C.585200 p [M313], C.584943 p [SK154], Fig. 71H); Point Brown Swan River, 32°02.344’S, 115°45.471’E, WA59-5 (AM C.585369 p [M128]); Fremantle Hbr, breakwater, 32°03.342’S, 115°43.987’E, WA58-5 (AM C.585519 d); Yallingup, 33°38.358’S, 115°01.481’E, WA60-9 (AM C.584724 6p, WAM S74163 5p); Cowaramup Point, 33°51.934’S, 114°58.904’E, WA60-3 (AM C.585370 p); Sarge Bay Cape Leeuwin, WA60-4 (AM C.585809 p); Yanchep, sheltered limestone cliffs, 34°32.783’S, 115°37.962’E (AM C.595972 p).

External morphology (Fig. 71O). Foot wall usually without irregular black blotches, may be weakly present in some individuals; edge, pneumostomal lobe and cephalic folds all evenly brownish yellow, without any black/darker pigmentation markings, foot sole maybe dark brown/grey, foot edge paler; mantle translucent to transparent, as wide as foot wall, weakly lobed, aligns with undulations of primary shell ribs; the mantle edge thickened with yellowish band, may show dark pigmentation markings aligned with rib interstices; pneumostome wide between right adductor muscles and within mantle; cephalic folds thickened.

Shell (Figs 71D–H, P; Table S9). Medium sized (max sl mean = 17.5 mm SD = 2.7 mm, n = 19); height low to medium; ovate; apex central, apical sides weakly convex;

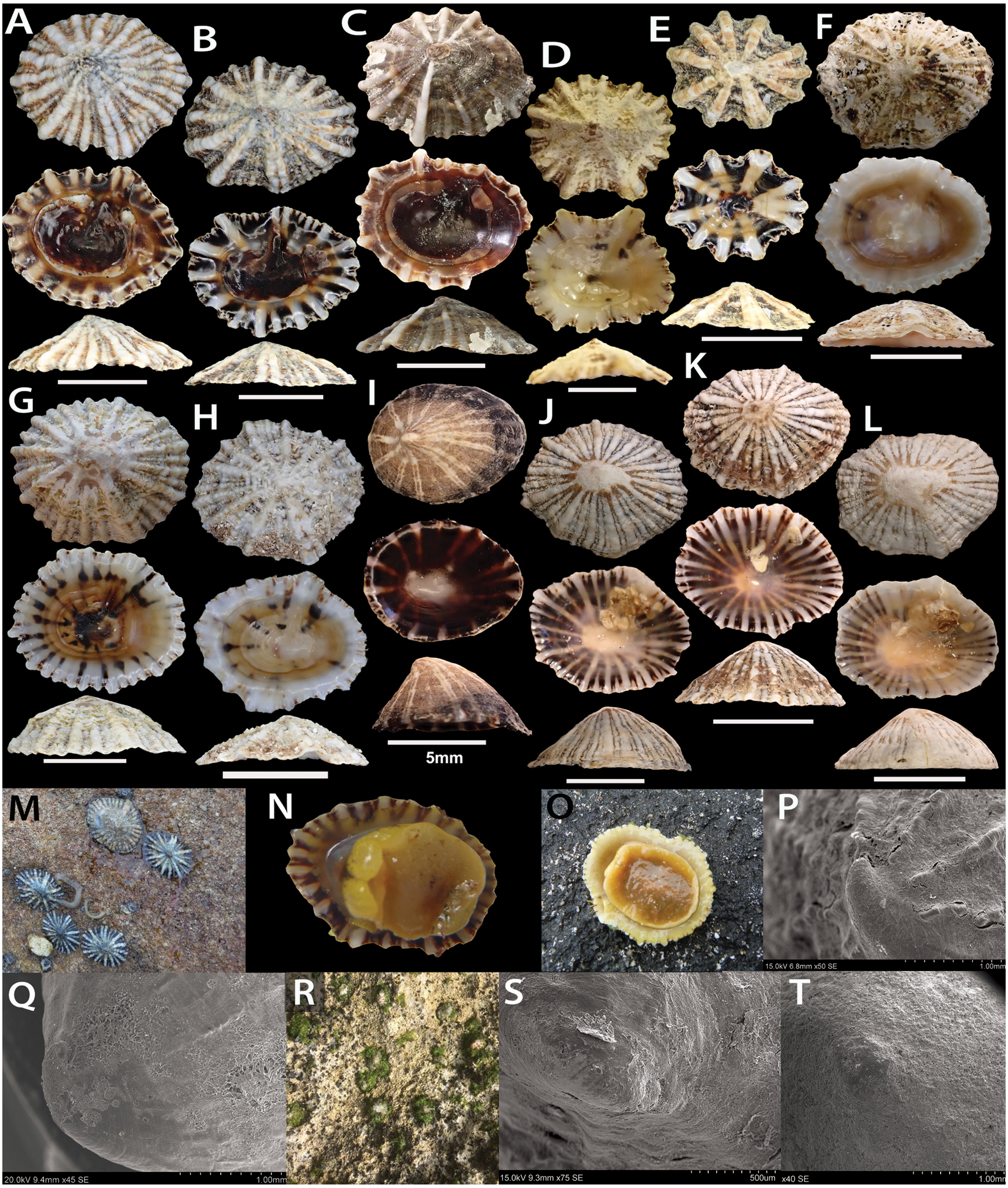

FIGURE 71. Shells of *S. pravitas* **sp. nov.**, *S. recurva* **sp. nov.**, *S. restis* **sp. nov.**, *S. rodriguensis* **sp. nov.** and *S. striata* **sp. nov.** **A–B, M–N, S.** *S. pravitas* **sp. nov. A.** Holotype AM C.585040 [M192, SK118]. **B.** Paratype AM C.585038 [M153]. M. Sydney Harbour, *in situ*. **N.** Sydney Harbour, animal, **S.** Protoconch, AM C.546766 [SK432]. **C.** Holotype of *S. recurva* NMHN IM-2013-55336 [M534]. **D–H, O–P.** *S. restis* **sp. nov.**, WA, Kalbarri. **D.** Holotype WAM S74049 [M400]. E. Paratype WAM S74048 [M100]. **F.** Paratype AM C.585200 [M313]. **G.** Paratype AM C.585919 [SK150]. **H.** Rottnest Is, AM C.584943 [SK154]. **O.** Animal. **P.** Protoconch, AM C.585009 [SK063]. **I, Q–R.** *S. rodriguensis* **sp. nov. I.** Holotype AM C.585197 [SK330]. **Q.** Protoconch, AM C.585196 [M427]. **R.** *In situ*. **J–L, T.** *S. striata* **sp. nov.**, Madagascar, Itampolo. **J.** Holotype AM C.584952 [M264]. **K.** Paratype AM C.584953. **L.** Paratype AM C.584954. **T.** Protoconch, paratype AM C.584953 [M265]. Scale bars = 10 mm.

protoconch direction weakly homostrophic (n = 1, Fig. 71P), shell whorl dextral, protoconch area distinctly darker brown; growth lines distinct; rib count (mean = 42, SD = 8.7, n = 19), weakly raised pale white to cream, weakly extend beyond shell edge, rib interstices dark brown; 10–12 evenly spread primary ribs; siphonal ridge prominent raised rounded, formed by 3 primary ribs; shell lip uneven, scalloped. Interior shell lip cream with brown splashes aligning with rib interstices, paler than shell margin, ADM scar prominent; spatula cream sometimes bluish; shell lip often golden brown with dark brown markings flanking shallow golden brown siphonal groove; CMS weakly concave, similar but darker colouration to spatula and shell margin; thickening of inner shell lip and spatula occurs in larger specimens, whitening covers brown colouration of inner shell lip.

Reproductive system (Figs 72B, D; n = 2). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts positioned between RAM and BM. GA relatively small, with singular GP through foot wall; AO medium sized, broad, bluntly pointed, central bend, joined to upper GA; ED elongated, broad, centrally twisted, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG medium sized, soft whitish tissue, slightly folded, joins at junction of end of ED and extension of single broad long flagellum (F1), end often looped; BD and CD connect closely together into GA between ED join and GP, both ducts long, slightly bent, smooth, narrow, whitish, featureless, pass closely together through outer side of RAM (BD over CD) into soft white folded tissues of MG; MG/AG complex large; CD connecting to ducts, BD without distal loop, often with loop or fold immediately in front of BC; BC embedded in MG folds, close to embedded SV; BC medium, thin whitish translucent test; HD distinct, short, coiled, links ducts in soft white folded tissues of AG to yellowish granulated HG; outer edge of MG lobbed; AG and HG of similar size, sides match curvature of inner foot wall.

Spermatophore (Fig. 72C). Thread-like, test thin, translucent (length = 6.38 ± 3.71, n = 3), flagella incomplete, head section cylindrical, tip bulbous bluntly rounded, containing a white gelatinous core, tapers into the filamentous transparent flagellum, both sections smooth, featureless, head much thicker than flagellum (length = 5.90 ± 3.02, n = 3, ~71% of SPM length, head width = 119 ± 33 µm, n = 3), two SPM embedded in brown gelatinous mass in one bursa (AM C.584943).

Radula (Figs 83I–L). Dentition formula 32:1:32 (n = 1, AM C.320123**)** ; single central rachidian tooth short broad, flanked squarely by 32 half row laterals, 10 are inner, 6 mid and 16 outer laterals; number of transverse rows not counted; central tooth short wide with short unicuspid mesocone; inner laterals (without endo or ectocones) prominent, mesocones of inner and mid laterals bicuspidate (Figs 83I–L), mid laterals with broad pointed ectocone; outer, laterals typically with a 'chisel' shaped mesocone, often weakly bicuspidate, flanked by small, pointed single ecto and endocones, angle of separation of each cone from the mesocone varies and maybe inwardly curved (Fig. 83K).

Comparative remarks. *Siphonaria restis* **sp. nov.** (*atra* group, unit 54) forms a well-differentiated lineage in clade G of the mitochondrial tree (Figs 1, 2). It differs from other species by COI distances of ≥ 21.8% (Table S4). Throughout its range, we found *S. restis* **sp. nov.** in sympatry with seven congeners. Two are species are sympatric in south-western WA: For comparisons with *S. stowae* and *S. jeanae* refer to comparative remarks under these species. Three are sympatric in northern WA: For comparisons with *S. atra*, *S. viridis*, and *S. gemina* **sp. nov.** refer to comparative remarks under these species One species is sympatric in western WA: Refer to comparative remarks under *S. zelandica*. The RS figure of '*S. luzonica'* in Hubendick (1955: 3, fig 3) from Rottnest Is, corresponds well with the RS of *S. restis* **sp. nov.** shown here (i.e., parallel junction of BD and CD into GA, relative size of AO and twist in BD close to BC, Fig. 72B), and not that of *S. sipho*, the senior synonym of *S. luzonica*.

Distribution and habitat. Recorded as endemic to western and northern coasts of WA, Indian Ocean (Fig. 73). In this study, commonly found in sheltered positions on moderately exposed rocky shores, at upper and mid littoral levels.

Etymology. From the Latin 'restis' meaning 'cord'—referring to the cord-like primary ribs on the shell of this species.

Siphonaria rodriguensis sp. nov.

(Figs 71I, Q–R, 72E–F)

Material examined. *Type material.* Holotype, from Rivière Banane 19°11.25'S, 63°22.866'E, N coast Rodrigues; coll. A. Meunier and O. Griffiths, RG01-1, 20 Aug 2018 (AM C.585197 [SK330], Fig. 71I). Paratype same data as holotype (AM C.585196 p [M427, SK133, protoconch D1], Fig. 71Q).

Other, non-type material. Rodrigues: Anse Quiter, SW coast, 19°46.183'S, 63°22.866'E, RG02-1 (AM C.585888 p).

External morphology. Foot wall, mantle, cephalic folds and pneumostome evenly cream, foot sole darker, paler to foot edge; mantle translucent, narrower than foot wall, edge weakly lobed, thickened with broad white edge band; uneven dark/black pigmentation along foot wall and mantle join, concentrated over centre of cephalic folds.

Shell (Figs 71I, Q; Table S9). Small sized (max sl mean = 8.8 mm, SD = 1.3 mm, n = 2), ovate; height medium; centrally broad, thickness thin; exterior even, smooth; protoconch direction weakly homostrophic (n = 2, Fig. 71Q), shell whorl dextral; apex offset to posterior and left of centre, apex offset growth reflected in apical ridge, apical banding fades from tan/brown at shell edge to pale protoconch; anterior and lateral apical sides convex, posterior weakly concave; ribs radiate from apex to shell lip, straight unraised, primary and secondary ribs indistinct, rib count (mean = 39.5, SD = 2.5, n = 2), primary ribs irregularly spaced, whitish, ridges narrow, dual ribs form siphonal ridge, secondary ribs brown/tan;

shell edge un-scalloped, even; growth striae indistinct. Interior spatula glossy, white, inner margin to shell edge dark chocolate brown with narrow white rays aligning under primary ribs, extending from shell lip to inner margin; ADM scar indistinct; CMS straight; siphonal groove very weakly indented. Thickening or whitening of inner shell lip not observed.

Reproductive system (Fig. 72E; n = 4). Positioned within coelom under the respiratory cavity, epiphallic parts positioned between RAM and BM close to MG. ED joins at underside of small GA, AO joins underside of ED, short, blunt, narrower than ED, smaller than GA; ED thick, elongated, centrally twisted, broader at EG, narrower than AO; single broad curled stubby flagellum F1, appears as extension of ED at connection with EG; AO, GA and ED all muscular white tissue; EG broad, relatedly large, soft white tissue; BD and CD connect in parallel to GA at opposite sides of GA, BD without distal loop or MA; BD longer and slightly thinner than CD, both ducts smooth and pass together between RAM and inner foot wall connecting into thick layered folds of MG (BD over CD); BC relatively large, spherical, embedded along with part of BD in AG/MG; SV embedded in AG under BC; HD short narrow, coiled, links large AG to a much smaller yellowish granulated HG, AG and MG folded, soft white tissue, with outer sides curved reflecting the close positioning to curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 72F). Broad head with short flagellum (length = 1.62 ± 0.1 mm, n = 4); test thin, whitish, smooth, featureless; head section broad cylindrical, bulbous, centrally bent, rounded tip; short tapering section merges head to filamentous flagellum; head longer, wider than translucent flagellum (head length = 1.04 ± 0.02 mm, ~ 70% of SPM length, head width = 99 ± 2 µm, flagellum width = 17 ± 0 µm, n = 4); 5 and 14 SPM tightly packed in BC (AM C.585197, C.585196).

Comparative remarks. In our mitochondrial phylogeny, *S. rodriguensis* **sp. nov.** (*laciniosa* group, unit 68) is the sister species of *S. sipho* (unit 24). Both species are closely related to *S. viridis* (Figs 1, 3). *Siphonaria rodriguensis* **sp. nov.** differs from *S. sipho* by COI distances of ≥ 14.9% and from *S. viridis* by ≥ 13.9% (Table S6). We found *S. rodriguensis* **sp. nov.** in sympatry with *S. fuliginata* on Rodrigues, Indian Ocean. For comparative remarks see under *S. fuliginata*. The shell of *S. basseinensis* Melvill, 1893 described from Bombay (Fig. 14M, not reviewed herein) is similar in having a smooth and even exterior, paired flush ribbing, but differs in having a prominent siphonal ridge.

Distribution and habitat. Recorded as endemic to Rodrigues Island, Indian Ocean (Fig. 73). In this study, found on exposed marine rocky shores, at upper and mid littoral levels (Fig. 71R).

Etymology. Named after the type location of Rodrigues Island, Indian Ocean.

Siphonaria striata sp. nov.

(Figs 71J–L, T, 72G–H)

Material examined. *Type material.* Holotype, from Reef in front Sud-Sud Hotel, Itampolo, 24°41.431'S, 43°56.603'E, Madagascar; coll. O. Griffiths, MA03-1, July 2018 (AM C.584952 [M264], Fig. 71J). Paratypes same data as holotype (AM C.585376 10+p, C.584953 p [M265 protoconch H10], Fig. 71K, C.584954 p [M266], Fig. 71L, C.584832 p [SK402]).

Other, non-type material. **Madagascar:** Ilot de Lokaro, 24°56.5'S, 47°07.1'E, TM05 (MNHN IM-2009-13792 p [M579], IM-2009-13769 p [M581]).

External morphology. Foot wall, mantle, cephalic folds and pneumostome evenly cream, foot sole darker, paler to foot edge; mantle translucent, wide, thin, mantle edge weakly lobed with thickened whitish band; no dark/black pigmentation markings.

Shell (Figs 71J–L, T; Table S9). Small sized (max sl mean = 15.6 mm, SD = 1.2 mm, n = 3), circular ovate; medium to tall, apex offset weakly to left and posterior of centre, apical sides strongly convex, posterior side straight to weakly convex; protoconch direction weakly homostrophic (n = 2, Figs 71K), shell whorl dextral; growth lines distinct; ribs (count mean = 45, SD = 2.5, n = 3), raised, whitish, straight, rib ridges rounded, width strongly increases to shell lip; rib interstices narrow, dark brown; majority of ribs primary, extend from apex to slightly protrude beyond shell edge, secondary ribs fill between primary ribs, 3 primary ribs form siphonal ridge; shell lip uneven, scalloped, aligning with primary rib ends. Interior; white rays aligning under primary ribs extend from shell lip to inner shell margin to golden tan spatula, with dark chocolate brown infill between rays; muscle scar impression distinct, same as shell margin colouring, CMS straight; thickening or whitening of shell edge not observed.

Reproductive system (Fig. 72G; n = 1). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts embedded between RAM and BM close to MG, AG and BC. Join of AO and ED distinct together at top of GA, AO smaller than GA, elongated, blunt, centrally bent; ED thick, elongated, narrower than AO; AO, GA and ED all muscular white tissue; EG broad, soft white tissue, single looped narrow flagellum F1 extends from ED; BD and CD connect side by side into GA, BD bulbous entry with short distal loop and MA in front of ED; CD enters inner side of GA; BD much longer with similar thickness to CD, both ducts smooth and pass together just inside outer side of RAM connecting into MG (BD over CD), BC white opaque test, relatively small, bulbous, embedded along with part of BD in folds of MG/AG; HD short narrow, coiled, links broad AG to an elongated wide yellowish granulated HG, AG and MG folded, soft white tissue, AG larger than HG, with outer sides curved reflecting the close positioning to curvature of inner foot wall at right posterior quarter of coelom; SV embedded on left side of AG close to BC.

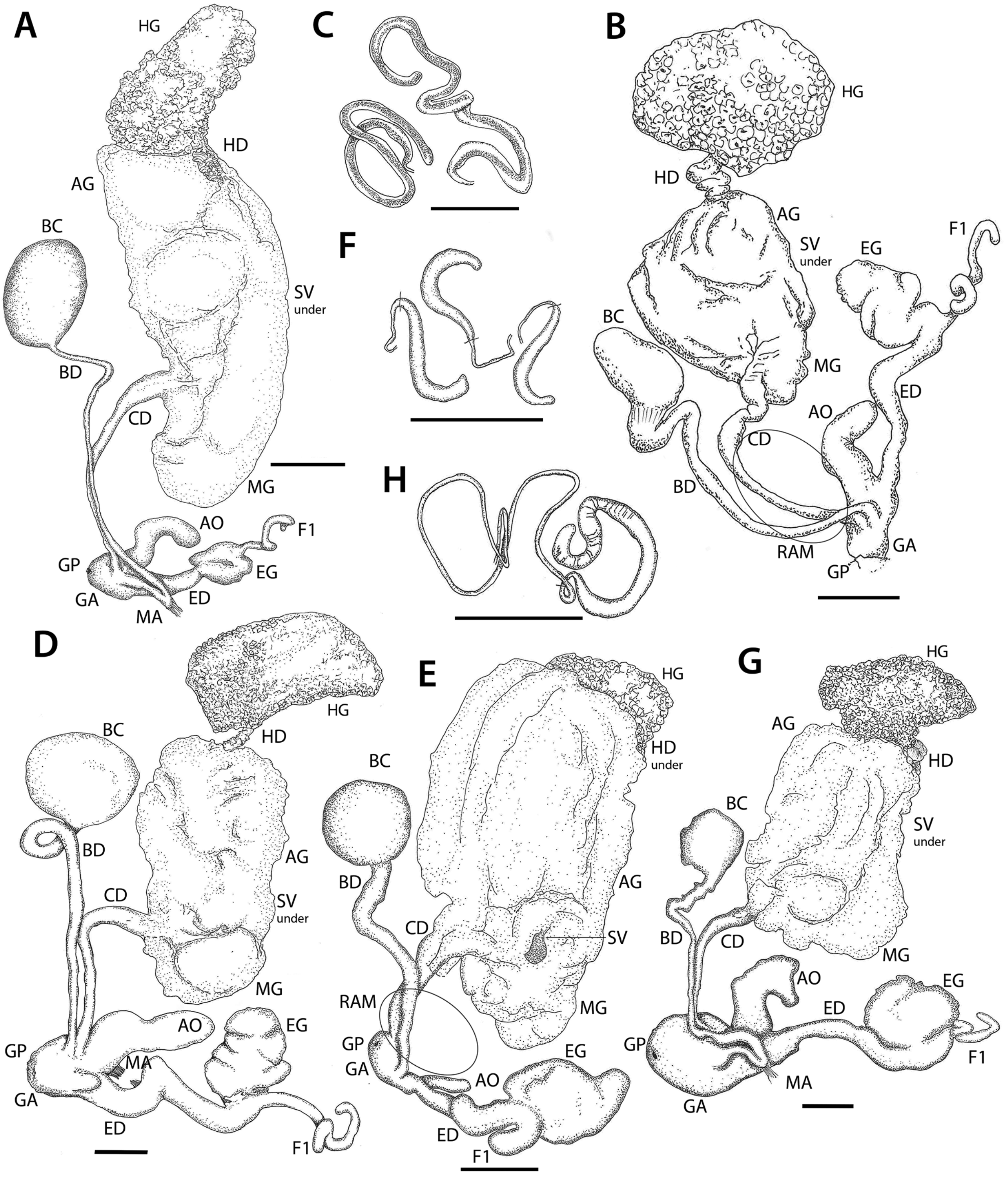

FIGURE 72. Reproductive morphology of *S. recurva* **sp. nov.**, *S. restis* **sp. nov.**, *S. rodriguensis* **sp. nov.** and *S. striata* **sp. nov.** **A.** Holotype of *S. recurva* **sp. nov.** MNHN IM-2013-55336 [M534]. **B–D.** *S. restis* **sp. nov. B.** WA, Kalbarri, holotype WAM S74049 [M400]. **C.** WA, Rottnest Is, AM C.584943 [SK154]. **D.** WA, Point Maud, AM C.585919 [SK150]. **E–F.** Holotype of *S. rodriguensis* **sp. nov.** AM C.585197 [SK330]. **G–H.** Holotype of *S. striata* **sp. nov.** AM C.584952 [M264]. Scale bars = 1 mm.

Spermatophore (Fig. 72H). Body cylindrical, thread-like (length = 8.72 mm, n = 1, AL = 10.2 mm), test thin, translucent, smooth, featureless; head broad, containing a white core, laterally banded in front half, tip tapered bluntly rounded, tapers to a thin flagellum (head width = 121 µm, flagellum width = 17 µm, n = 1); single SPM tightly coiled in orange gelatinous mass in BC of the holotype.

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 2), *S. striata* **sp. nov.** (*atra* group, unit 74) forms a clade with *S. alternata* (unit 29) from the Caribbean and Gulf of Mexico and *S. kurracheensis* (unit 28) from Pakistan. It differs from *S. kurracheensis* by COI distances of ≥ 8.6% and from *S. alternata* by ≥ 5.8% (Table S5). Notably, the genetically most similar species, *S. alternata*, is not known to occur in the Indian Ocean. *Siphonaria kurracheensis* differs in having a lower, paler shell with more prominent darker and broader interior rays extending to the spatula, a shorter F1, shorter twisted ED, and BD without a bursal loop. We found *S. striata* **sp. nov.** in sympatry with two congeners in Madagascar: For comparisons with *S. madagascariensis* and *S. itampoloensis* **sp. nov.** refer to comparative remarks under these species. The epiphallic parts of RS are very similar to those in *S. madagascariensis*. However, the hermaphroditic parts differ markedly (i.e., arrangement of HG and AG, BC and BD smaller, SPM shorter in *S. striata* **sp. nov.**).

Distribution and habitat. Recorded as endemic to Madagascar, Indian Ocean (Fig. 73). In this study, found on moderately exposed inner lagoon rocky reef, at upper and mid littoral levels.

Etymology. Derived from Latin adjective "striatus" meaning 'striated / wrinkled / lined / grooved' referring to the shell's external striated sculpture.

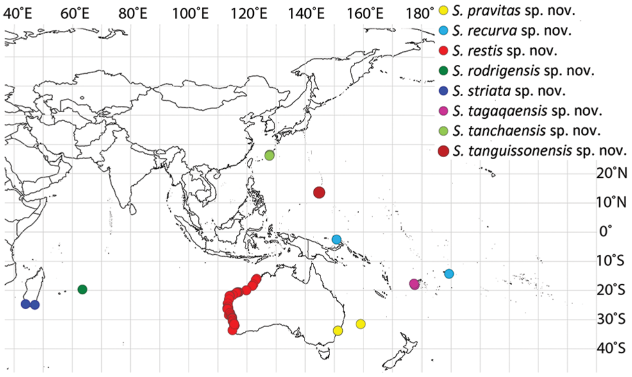

FIGURE 73. Known occurrence records of *S. pravitas* **sp. nov.**, *S. recurva* **sp. nov.**, *S. restis* **sp. nov.**, *S. rodriguensis* **sp. nov.**, *S. striata* **sp. nov.**, *S. tagaqaensis* **sp. nov.**, *S. tanchaensis* **sp. nov.** and *S. tanguissonensis* **sp. nov.**

Siphonaria tagaqaensis **sp. nov.**

(Figs 74A–C, M, 75A–B)

Material examined. *Type material.* Holotype, from nr Tagaqa 18°11.802'S, 177°38.640'E, S. coast of Viti Levu, Fiji; coll. B.W. Jenkins, FI02-1, 22 Aug 2018 (AM C.584852 [M275, SK182], Fig. 74A). Paratypes: Same data as holotype (AM C.586005 3p, C.584854 p [SK287], Fig. 74B, C.584855 p [SK297], Fig. 74C).

Other, non-type material. **Fiji, Viti Levu:** nr Tagaqa, SW coast, 18°11.802'S, 177°38.640'E, FI02-1 (AM C.584851 p [SK298]).

External morphology. Foot sole grey; foot wall, mantle, cephalic folds, pneumostome evenly cream, paler to foot edge; irregular small blotches of black pigmentation on foot wall and centre of cephalic lobes; mantle slightly narrower than foot wall, covers exposed inner shell lip, wider at anterior, mantle edge strongly lobed with bands of black pigmentation aligned with shell rib interstices; genital pore indistinct, located on foot wall to right anterior of right cephalic fold; small black epithelial eye spot centralised on each of centrally touching cephalic folds; pneumostomal lobe under mantle, unpigmented, between the right ADMs.

Shell (Figs 74A–C; Table S9). Small to medium sized (max sl mean = 14.8 mm, SD = 1.7 mm, n = 4), ovate; height medium to tall; exterior very uneven, growth disjointed /discontinuous; apex offset central sightly posterior (usually eroded), apical sides convex, straight to concave at posterior; protoconch direction heterostrophic (n = 1), below apex, shell whorl dextral; growth striae prominent in bands, shell thickness thick; rib count (mean = 46, SD = 11, n = 4), marked size difference between primary and secondary ribs; 12–15 primary ribs white, prominent, fairly straight, increasingly raised rounded ridge, width broadens to and protrudes weakly beyond shell lip to unevenly scallop and corrugate the edge; paired slightly separated primary ribs form strongly raised siphonal ridge; secondary ribs fill spaces between primary ribs, fairly even in width, rib interstices narrow, darker; some irregular radial coloured banding, dark around apex, paler/cream with dark flecks between primary ribs in lower areas. Interior shell edge and margin white under ribs, brown rays/bands align under rib interstices extend from lip to ADM, siphonal groove distinct, whitish; spatula dark chocolate brown under apex, paler to ADM scar, CMS straight; thickening of shell lip apparent, infills and reduces lip scalloping.

Reproductive system (Fig. 75A; n = 1). Proportionally RS very large structure to animal size, positioned within coelom under the respiratory cavity, epiphallic parts positioned over back of BM, F1 draped over left side of BM; very small GA, AO broad, bent, rounded, bluntly pointed, rests against MG, joins top of GA; ED long, narrow, slightly bent, joins side of GA; EG medium with folds, overlaps join of ED flagellum (F1) join, F1 long, narrow, appears as an extension of ED; AO, GA and ED all muscular white tissue; BD and CD (bulbous at join) connect closely together in opposing directions into GA close to ED and AO entries; BD with distal loop and MA, BD longer and slightly narrower than CD, both ducts smooth, narrow, both pass together through outer side of RAM (BD above CD), connecting into folds of MG; BC embedded in MG, size medium, bulbous test soft translucent, SV embedded within AG; HD lobed, links AG to small brownish granulated HG, MG and AG small folded soft white tissue, anterior edge of MG lobed, AG smaller than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 75B). Body cylindrical, elongate (length = 7.05 mm, n = 1); test thin, translucent; head bulbous, tip bluntly rounded, wide, evenly cylindrical, containing a core white gelatinous mass, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless. Head section longer, much wider than flagellum (head length = 4.77 mm, n = 1, ~ 68% of SPM length, head width = 1.33 mm, flagellum width = 13 µm). 2 SPM tightly coiled and embedded in brown gelatinous mass in BC of holotype.

Comparative remarks. *Siphonaria tagaqaensis* **sp. nov.** (*laciniosa* group, unit 66) represents a well-differentiated lineage in the phylogenetic tree (Figs 1, 3). It differs from other species by COI distances of ≥ 27% (Table S6). *Siphonaria yagasaensis* is anatomically similar concerning the shape of AO, ED, F1 and SPM, but differs in having a lower, thicker, paler, whitish shell. We found *S. tagaqaensis* **sp. nov.** in sympatry with two congeners on Viti Levu: For comparison with *S. namukaensis* refer to comparative remarks under that species. *Siphonaria vudaensis* **sp. nov.** has a smaller, taller shell with stronger scalloped edge, flared siphonal ridge, darker interior, a narrower AO, and a larger BC, and BD without a bursal loop.

Distribution and habitat. Recorded as endemic to Viti Levu, Fiji (Fig. 74M). In this study, found in sheltered positions on moderately exposed rocky shores at mid-littoral level.

Etymology. For the type locality of Tagaqa, S coast of Viti Levu, Fiji.

Siphonaria tanchaensis sp. nov.

(Figs 74D–F, O–P, 75C–D)

Siphonaria laciniosa—Hubendick 1946: 46; Oyama *et al.* 1954: 14; Kira 1962: 201, pl. 69, fig. 11a, b; Habe & Kohno 1980: 23 (not *S. laciniosa* (Linnaeus, 1758)).

Siphonaria (*Siphonaria*) *laciniosa*—Higo 1973: 287 (not *S. laciniosa* (Linnaeus, 1758)).

Siphonaria '*laciniosa* group, unit 20'—Dayrat *et al.* 2014: 267, fig. 4B.

Material examined. *Type material.* Holotype: from Okinawa, Tancha Bay, 26°27.897'N, 127°49.131'E; coll. B.W. Jenkins, JP01-5, 20 March 2020 (AM C.585615 [M495, SK314], Fig. 74D). Paratypes: same data as holotype (AM C.585949 15p, C.584912 p [SK386], Fig. 74E); Moon Bay (26°26.653'N, 127°48.230'E), Onna, Okinawa, Japan; coll. B.W. Jenkins, JP01-4, 18 March 2020 (AM C.584913 p [M505, SK326], Fig. 74F).

Other, non-type material. **Japan, Okinawa**: Cape Maeda, 26°26.573'N, 127°46.113'E, JP01-2 (AM C.585624 5p); Moon Bay, Onna 26°26.653'N, 127°48.230'E, JP01-4 (AM C.595956 5p); Sun Marina Beach, Onna, 26°27.842'N, 127°48.755'E, JP01-1 (AM C.585623 5p, C.595921 p [SK537], C.595924 p [SK538], C.595926 p [SK536]); Tancha Bay 26°27.897'N, 127°49.131'E, JP01-5 (AM C.584853 p [SK399]); Tancha Bay 2, rocky point 26°27.941'N, 127°49.194'E, JP01-6 (AM C.585628 4p).

External morphology (Fig. 74O). Foot sole dark grey; foot wall, mantle, cephalic folds, pneumostome lobe evenly grey, paler to foot edge; irregular small blotches of black pigmentation on foot wall and centre of cephalic lobes; mantle translucent, wider than foot wall, covers inner shell lip, wider at anterior, mantle edge strongly lobed with bands of black pigmentation aligned with shell rib interstices; genital pore indistinct, located on foot wall to right anterior of right cephalic fold; small black epithelial eye spot centralised on each of centrally touching cephalic fold; pneumostomal lobe under mantle.

Shell (Figs 74D–F; Table S9): medium sized (max sl mean = 19.8 mm, SD = 2.3 mm, n = 4), circular ovate; tall; apex offset central and sightly left, apical sides convex; protoconch direction homostrophic (n = 2; holotype C.585615 [M495], paratype C.584913 [M505]), shell whorl dextral; shell exterior and edge uneven; growth striae prominent; pale brown radial banding with irregular darker flecks; shell thickness thick; rib count (mean = 43.3, SD = 0.8, n = 4), 10–12 fairly evenly spread primary ribs, pale white, weakly bent and uneven, strongly raised rounded ridges (some > 1mm), widen to shell edge, protrude beyond shell lip to unevenly scallop between primary ribs and corrugate the edge, ends of primary ribs may be flared creating uneven roughness on rib ridges; between primary ribs brown flecks/bands with 0–6 finer whitish secondary ribs (commonly 2), rib interstices narrow darker; siphonal ridge formed by three adjacent ribs, no more raised than other primary ribs. Interior shell margin white to cream, with fine dark brown markings on shell edge under rib interstices, may extend over shell margin, white rays align on shell edge under primary/ secondary ribs, ADM scar distinct, brown to white as spatula; cephalic muscle straight to weakly concave; thickening and vivid whitening of shell lip common (Fig. 74F).

Reproductive system (Fig. 75C; n = 2). Proportionally RS very large structure to animal size, positioned within coelom under the respiratory cavity, epiphallic parts compacted, positioned over back of BM to side of RAM, F1 draped over left side of BM; very small GA, AO broad, bent, rounded, bluntly pointed, rests against MG, joins top of GA; ED long, narrow, bent, joins side of GA; EG medium with folds, overlaps join of ED flagellum (F1) join, F1 long, narrow, appears as an extension of ED; AO, GA and ED all muscular white tissue; BD and CD (bulbous at join) connect closely together in opposing directions into GA ED and AO junction; BD with distal loop and MA, BD longer and slightly narrower than CD, both ducts smooth, narrow, pass together through outer side of RAM (BD above CD), connecting into folds of MG; BC embedded in MG, smallish, bulbous test soft translucent, SV embedded within AG; HD lobed, links AG to small brownish granulated HG, MG and AG small folded soft white tissue, anterior edge of MG lobed, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Fig. 75D). Broad head with short flagellum (length = 1.67 mm, n = 1); head section cylindrical, bulbous, centrally bent, tip rounded; test thin, smooth, featureless, translucent encasing a white opaque thin central core; short looped tapering section merges head to filamentous flagellum, head longer, wider than flagellum (head length = 1.41 mm, flagellum length = 0.26 mm, n = 1, 85% of SPM length, head width = 172 µm, flagellum width = 21 µm); 2 SPMs tightly coiled in brown gelatinous mass in BC of one specimen [SK538].

Comparative remarks. *Siphonaria tanchaensis* **sp. nov.** (*laciniosa* group, unit 20) represents a well-differentiated lineage in the mitochondrial tree (Figs 1, 3). It differs from its sister species *S. poindimiensis* **sp. nov.** (unit 19) by COI distances of ≥ 21.8% (Table S6). We found *S. tanchaensis* **sp. nov.** in sympatry with four congeners on Okinawa: For comparative remarks see under *S. camura* **sp. nov.**, *S. rucuana*, *S. subatra*, and *S. sipho*, respectively. Generally, shell features of this species closely resemble those of other members of the *laciniosa* group (i.e., few prominent, weakly extending primary ribs, secondary ribs patterning and colouration, internal colouration, irregular weakly scalloped shell edge, thickened white shell margin lip). Figured specimens of '*S. laciniosa*' in Kira (1962: pl. 69, fig. 11) from central Honshu and of '*laciniosa* group, unit 20' (Dayrat *et al.* 2014: fig. 4B) from Okinawa corresponds well with typical features of *S. tanchaensis* **sp. nov.**

Distribution and habitat. Recorded as endemic to Okinawa, Japan (Fig. 73). In this study, found on exposed rocky shores at mid littoral level (Fig. 74P).

Etymology. Named after the type locality of Tancha Bay, Okinawa, Japan.

***Siphonaria tanguissonensis* sp. nov.**

(Figs 74G–J, N, Q–R, 75E–H)

Material examined. *Type material.* Holotype, from S end Tanguisson Beach, 13°32.549'N, 144°48.443'E, Guam; coll. B.W. Jenkins, GM02-1, 27 Dec 2018 (AM C.584877 [M417, SK102 (RS, SPM)], Fig. 74G). Paratypes same data as holotype (AM C.585897 7p, C.584878 p [M438, SK163], Fig. 74I; C.584875 p [M342], Fig. 74H; C.584881 p [SK253], Fig. 74J).

Other, non-type material. **Guam:** Tanguisson Beach, S end 13°32.549'N, 144°48.443'E GM02-1 (AM C.585995 10p, C.584876 d[M349], C.584879 p [M341], C.584880 p [M350], C.584882 p [SK141 protoconch D10]).

External morphology (Fig. 74R). Foot sole and foot wall evenly pale grey, paler at foot/wall edge; foot wall with patches of black pigmentation, mantle edge with vertical bands of black pigmentation aligned with shell rib interstices; mantle weakly lobed to unlobed, non-translucent, narrower than width of foot wall, covers exposed inner shell lip; genital pore noticeable, located on foot wall to right anterior of right cephalic fold; two small black epithelial eye spots centralised on two centrally touching black pigmented cephalic folds; pneumostomal lobe long, under the mantle, unpigmented, between the right ADMs.

Shell (Figs 74G–J; Table S9): small sized (max sl mean = 12.9 mm, SD = 0.6 mm, n = 7), circular ovate; height low; apex offset central and to left; apical sides weakly convex, posteriorly weakly concave, protoconch direction homostrophic (n = 1, Fig. 74Q), shell whorl dextral; growth striae not prominent; radial colour bands, protoconch area dark, paler central band, edge band dark; in some individuals central band is eroded creating concave sides (Fig. 74H); shell thick, pale grey; rib count (mean = 36.3, SD = 3.9, n = 7), primary ribs white, fairly straight, flattened, increasingly broaden (up to double width) and often raised to shell edge, weakly protrude beyond uneven shell lip to corrugate the edge; 1–2 secondary ribs between primary ribs, rib interstices narrow, black to dark brown; paired primary ribs (often fused) form siphonal ridge, end raised at shell edge. Interior shell margin and shell lip off-white under primary/secondary ribs, dark chocolate brown rays align under rib interstices; siphonal groove distinct, white to golden brown; spatula and distinct ADM scar dark brown to mottled tan, CMS convex; thickening of shell lip not noted.

Reproductive system (Figs 75E, G; n = 3). Positioned within coelom under the respiratory cavity, hermaphroditic glands positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between BM and RAM. Join of AO and GA indistinct, AO elongated, bluntly pointed, centrally bent with no prominent MA, larger than GA, much thicker than ED; ED relatively long, coiled, twisted, thickened; EG white, folded, elongated; single flagellum F1 on EG, very long, reasonably straight, unlooped, positioned over BM, thin; AO, GA and ED all muscular white tissue; BD and CD with opposing bulbous connections to GA between ED, AO and GP; BD wrinkled, not twisted, much longer and thinner than short CD with prominent looping on anterior side, both ducts smooth and pass together through RAM connecting into MG (BD above CD), BC translucent, white test, small sized and bulbous; HD short, coiled, links AG to a small elongated yellowish finely granulated HG; MG and AG relatively large, folded, soft white tissue; SV embedded on left side of AG, AG larger than HG, sides match curvature of inner foot wall at right posterior quarter of coelom.

Spermatophore (Figs 75F, H). Relatively long (length 12.7 ± 4.4 mm, AL = 9 mm, n = 2), test thin, translucent, over half-length comprises a translucent cylindrical head section (~ 64% of SPM length), lip bluntly rounded, containing a white gelatinous thread-like core; tapers into a filamentous transparent flagellum; head section longer and much thicker than flagellum (head length = 7.9 ± 0.4 mm, head width = 78 ± 12 μm, flagellum width = 14 ± 4 μm, n = 2), both sections smooth, featureless; SPM tightly coiled, embedded in red-brown gelatinous mass [SK102, SK414].

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 3), *S. tanguissonensis* **sp. nov.** (*plicata* group, unit 59) is the sister species of *S. lirata* (unit 58) also from Guam. Both species differ by COI distances of ≥ 11.6% (Table S7).

We found *S. tanguissonensis* **sp. nov.** in sympatry with three congeners on Guam: For comparative remarks see under *S. guamensis*, *S. lirata*, and *S. normalis*, respectively.

The shell sculpture and ribbing in *S. tanguissonensis* **sp. nov.** is coarser and more raised than in the former species. The rayed colouration of the internal shell lip in *S. tanguissonensis* **sp. nov.** resembles that of *S. normalis, S. guamensis* (darker), and *S. lirata* (paler, finer).

Distribution and habitat. Recorded only from northern Guam (Fig. 73). In this study, found in sheltered positions on moderately exposed rocky shores, at upper littoral level (Fig. 74N).

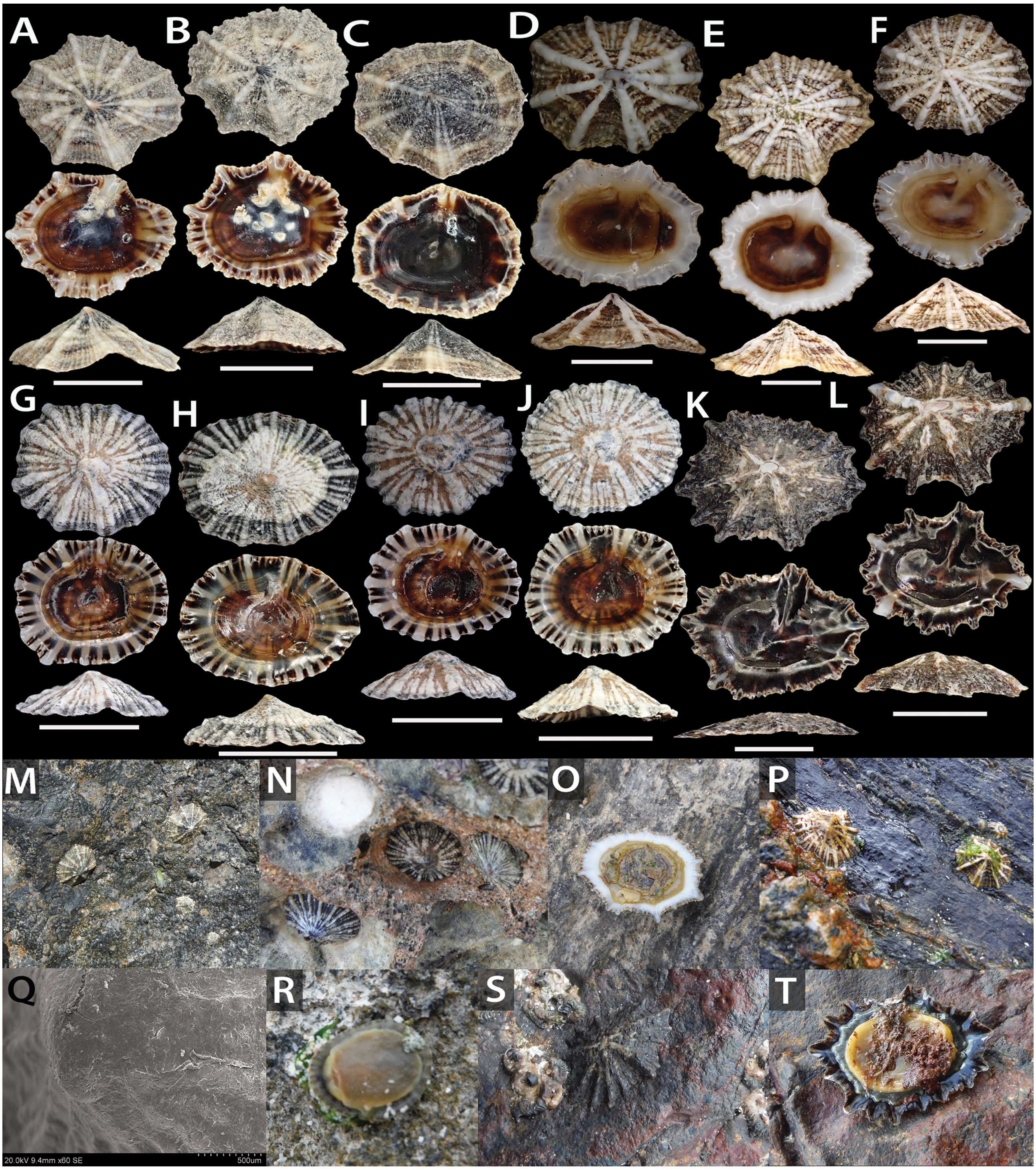

FIGURE 74. Shells of *S. tagaqaensis* **sp. nov.**, *S. tanchaensis* **sp. nov.**, *S. tanguissonensis* **sp. nov.** and *S. tenebrae* **sp. nov. A–C, M.** *S. tagaqaensis* **sp. nov.** , Fiji, Viti Levu. **A.** Holotype AM C.584852 [M275]. **B.** Paratype AM C.584854 [SK287]. **C.** Paratype AM C.584855 [SK297]. **M.** *In situ*. **D–F, O–P.** *S. tanchaensis* **sp. nov. D–E.** Okinawa, Tancha Bay. **D.** Holotype AM C.585615 [M495, SK314]. **E.** Paratype AM C.584912 [SK386]. **F.** Okinawa, Onna, paratype AM C.584913 [M505, SK326]. **O.** Onna, animal. **P.** Tancha Bay, *in situ*. **G–J, N, Q–R.** *S. tanguissonensis* **sp. nov.**, Guam, Tanguisson Beach. **G.** Holotype AM C.584877 [M417]. **H.** Paratype AM C.584875 [M342]. **I.** Paratype AM C.584878 [M438, SK163]. **J.** Paratype AM C.584881 [SK253]. **N.** *In situ*. **Q.** Protoconch, AM C.584882 [SK141]. **R.** Animal. **K–L, S–T.** *S. tenebrae* **sp. nov.**, CI, Point Flying Fish Cove. **K.** Holotype AM C.584664 [M305, SK256]. **L.** Paratype WAM S74050 [SK120]. **S.** *In situ*. **T.** Animal. Unlabelled scale bars 10 mm.

Etymology. For the type, of Tanguisson Beach, Guam.

Siphonaria tenebrae sp. nov.

(Figs 74K–L, S–T, 75I–J)

Siphonaria '*laciniosa* group, unit 38'—Dayrat *et al.* 2014: 264, fig. 5U (in part).

Material examined. *Type material.* Holotype, from Ethel Beach 10°27.827'S, 105°42.497'E, Christmas Is, Australia, Indian Ocean; coll. B.W. Jenkins, CI02-1, 11 Sept 2018 (AM C.584664, [M305, SK256], Figs 74K, T). Paratype: E side Smith Point Flying Fish Cove 10°25.749'S, 105°39.957'E, Christmas Is, Indian Ocean; coll. B.W. Jenkins, CI01-2, 9 Sept 2018 (WAM S74050 [SK120], Fig. 74L).

Other, non-type material. **Christmas Is:** E side Smith Point Flying Fish Cove, 10°25.749'S, 105°39.957'E CI01-2 (AM C.585979 p, C.585980 p [SK413]).

External morphology (Fig. 74T). Foot edge, foot wall, mantle, cephalic folds and pneumostomal lobe all yellow in colour with indistinct darker pigmentation markings; foot sole darker yellow to grey; mantle translucent, wider than foot wall, wider over anterior, strongly lobed with a thickened edge, tips of the major and minor mantle lobes align under primary ribs, wide bands of dark grey pigmentation align under the dark brown colouration of rib interstices; mantle lobes large, mould/extend to cover area of shell lip and align with undulations of primary shell ribs; pneumostome narrow, positioned between right adductor muscles and within mantle.

Shell (Figs 74K, L; Table S9). Small to medium sized (max sl mean = 17.6 mm, SD = 1.9 mm, n = 2), elongate ovate; height very low; apex offset to posterior and left, apical sides concave, protoconch direction undetermined, shell whorl dextral; growth striae indistinct, shell thin; rib count (mean = 28.5, SD = 1.5, n = 2), exterior evenly dark chocolate brown, pale white where rib ridges eroded, ribs straight, ridges rounded, larger broaden to and protrude beyond shell lip to strongly scallop and weakly corrugate the edge, some ends squared off; smaller secondary ribs fill gaps between primary ribs, rib interstices narrow; bent paired primary ribs on siphonal ridge. Interior evenly dark chocolate brown, some off-white rays under outer ends of primary ribs, siphonal groove shallow distinct; ADM scar distinct, CMS straight; thickening of shell lip not observed.

Reproductive system (Fig. 75I; n = 3). Positioned against inside of foot muscle and foot wall on the right side within coelom, under the respiratory cavity. GA, EG and ED positioned between BM and RAM. AO small, bluntly pointed, joins to larger GA with singular GP; ED relatively long, broad, straight, much larger than AO, joins to upper GA; GA, AO, ED all white muscular fibrous tissue; EG small soft whitish with single wide adjacent flagellum (F1) appearing as an extension of ED and of similar length; BD and CD jointly but in opposing positions connect to GA between AO and GP; BD with a prominent distal loop and large MA to inner body wall is longer and slightly thinner than CD; both ducts smooth, relatively long and pass closely together through outer side of RAM (BD over CD); CD connects into MG; BC small, bulbous, with thin translucent test, embeds in lower folds of MG/AG close to SV; HD short, bulbous, orange coloured, coiled, links AG to a smaller, yellow/orange,granulated HD; MG and AG large, folded, soft white tissue; AL = 11.78 mm.

Spermatophore (Fig. 75J). Body cylindrical, elongate (length = 11.8 mm, AL = 13 mm, n = 1); test thin, translucent; head tip bluntly rounded, wide, evenly cylindrical, containing a core white gelatinous mass, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless. Head section longer, much wider than flagellum (head length = 6.7 mm, n = 1; ~ 56% of SPM length, head width = 103 µm, flagellum width = 17 µm); SPM tightly coiled, embedded in whitish gelatinous mass [SK413].

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 2), *S. tenebrae* **sp. nov.** (*atra* group, unit 92) is the sister species of *S. subatra* (unit 38). Both species differ by COI distances of ≥ 15.1% (Table S3). Both species also differ in shell characteristics, RS structure, and external morphology. *Siphonaria tenebrae* has been found in sympatry with five congeners on CI: *Siphonaria umbra* **sp. nov.** has a less scalloped shell edge, more raised and prominent ribs, a paler interior with a darker spatula, and a larger AO and BC. For comparisons with *S. alba*, *S. incerta*, *S. christmasensis* **sp. nov.**, and *S. delicata* **sp. nov.** refer to comparative remarks under these species.

Distribution and habitat. Known distribution endemic to CI, Australia, Indian Ocean (Fig. 78). In this study, found in sheltered positions on moderately exposed and exposed limestone rocky platforms, at mid littoral levels (Fig. 74S).

Etymology. Derived from Latin noun 'tenebrae' meaning 'dark', referring to the evenly dark interior of the shell for this species.

Siphonaria poindimiensis sp. nov.

(Figs 76A–C, J–K, 77A–B)

Siphonaria laciniosa (in part)—Hubendick 1946: 47 (not *S. laciniosa* (Linnaeus, 1758)).

Siphonaria '*laciniosa* group, unit 19'—Dayrat *et al.* 2014: 261, fig. 4A (in part).

Material examined. *Type material.* Holotype, from Poindimie, 21°55.901'S, 165°19.672'E, NC; coll. B.W. Jenkins, NC03-2, 23 Oct 2018 (AM C.584999 [M352, SK128], Fig. 76A). Paratypes, same data as holotype (AM C.585837 p [SK129], Fig. 76B); Tiari, 21°05.644'S, 165°26.646'E, NC; coll. B.W. Jenkins, NC04-3, 27 Oct 2018 (AM C.585002 p [SK261], Fig. 76C).

Other, non-type material. **NC:** Tiari, 21°05.644'S, 165°26.646'E, NC04-3 (AM C.585010 p [SK262]); Poum 2, 20°13.754'S, 164°01.699'E, NC05-3 (AM C.585998 6p).

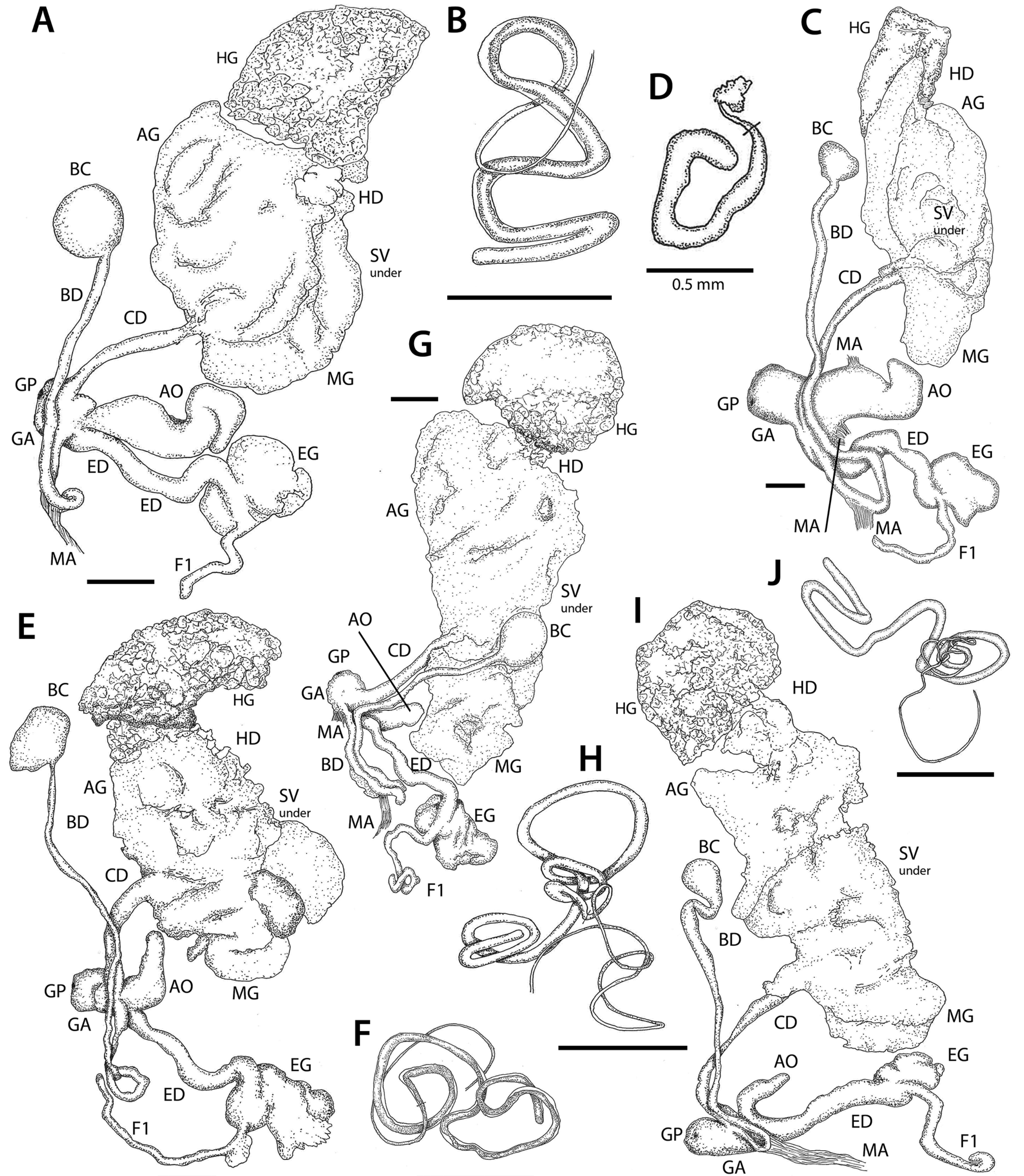

FIGURE 75. Reproductive morphology of *S. tagaqaensis* **sp. nov.**, *S. tanchaensis* **sp. nov.**, *S. tanguissonensis* **sp. nov.** and *S. tenebrae* **sp. nov. A–B.** Holotype of *S. tagaqaensis* **sp. nov.** AM C.584852 [M275, SK182]. **C–D.** *S. tanchaensis* **sp. nov.**, Okinawa. **C.** Paratype AM C.584913 [M505, SK326], Tancha Bay. **D.** Onna, AM C.595924 [SK538]. **E–H.** *S. tanguissonensis* **sp. nov.**, Guam, Tanguisson Beach. **E–F.** Holotype AM C.584877 [M417, SK102]. **G–H.** Paratype AM C.584878 [M438]. **I–J.** *S. tenebrae* **sp. nov.**, CI, Ethel Beach. **I.** Holotype AM C.584912 [M305, SK256]. **J.** Paratype WAM S74050 [SK413]. Unlabelled scale bars = 1 mm.

Taxonomic remarks. The record of *S. laciniosa* from NC (Hubendick 1946: 47) possibly refers to this species.

External morphology. Foot sole grey; foot wall evenly dark cream, paler to foot edge; irregular black pigmented blotches on foot wall; cephalic folds thick narrow; black pigmentation darker over centre of cephalic folds, paler to foot; mantle wide thin with heavy broad lobes, wider extended at anterior, edge thickened with black pigmentation aligning with rib interstices; pneumostome small, under mantle.

Shell (Figs 76A–C, J; Table S9). Medium to large sized (max sl mean = 12.9 mm, SD = 1.6 mm, n = 3), elongate ovate; medium to tall; apex strongly offset to left posterior, apex hooked, curved to posterior; apical sides strongly convex, weakly concave to straight on posterior side; shell growth often irregular; protoconch direction central to homostrophic (n = 2, Fig. 76J) shell whorl dextral; growth striae prominent, shell thick, exterior uneven; rib count (mean = 45, SD = 6.2, n = 3), marked difference between primary and secondary ribs, 9–11 primary ribs solidly raised, rounded ridge, weakly crooked, pale white, strongly protrude beyond shell lip to unevenly scallop and corrugate the shell edge; paired ribs form siphonal ridge; areas of finer secondary ribs dark brown/black between primary ribs, often with narrow white flecks/bands. Interior shell lip and lower margin white, changing to dark brown in spatula; dark brown bands extending from shell edge to spatula under secondary ribs and rib interstices; siphonal groove distinct, same colour as shell edge; spatula evenly dark chocolate; ADM scar distinct, CMS straight; thickening of shell lip not apparent, the number of primary ribs may be reduced to 7 in one specimen (Fig. 76C).

Reproductive system (Fig. 77A; n = 2). Positioned within coelom under the respiratory cavity, hermaphroditic complex (HG, AG and MG) to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior between RAM and over BM; AO very large, elongated, centrally bent, bluntly bulbous to pointed, merges to upper part of indistinct GA, singular very small GP; ED relatively long, broad, twisted, longer than AO, joins to lower side of GA; GA, AO, ED all white muscular fibrous tissue; EG soft whitish, slightly folded, smaller than AO; single long blunt twisted flagellum (F1); BD and CD jointly but opposing connections to GA between AO and GP; BD long narrow with prominent distal loops (may loop behind ED) and MAs to inner body wall; CD broad short, wider than BD; both ducts smooth and pass closely together through outer side of RAM (BD over CD); CD connects into MG; BD connects to small bulbous BC with thin translucent test, embedded in folds of MG close to embedded SV; HD short, thick, white, coiled, links AG to smaller yellowish granulated HD; MG and AG folded, soft white tissue.

Spermatophore (Fig. 77B). Test thin, translucent (length 4.11 mm, n = 1), head bulbous, tip bluntly rounded, containing a white gelatinous mass; taper region into the filamentous transparent flagellum is extended; both sections smooth, featureless; head longer and much thicker than flagellum (head length = 3.29 ± 0.49 mm, ~72% of SPM length, head width = 74 ± 8 µm, flagellum width = 1 µm, n = 2); SPM tightly coiled in a brown gelatinous mass.

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 3), *S. poindimiensis* **sp. nov.** (*laciniosa* group, unit 19) is the sister species of *S. tanchaensis* **sp. nov.** (unit 20). Both species differ by COI distances of ≥ 21.8% (Table S6). We found *S. poindimiensis* **sp. nov.** in sympatry with seven congeners in NC. For comparisons with *S. atra*, *S. namukaensis* **sp. nov.**, *S. normalis*, *S. bourailensis*, *S. hienghenensis* **sp. nov.**, *S. caledonica* **sp. nov.**, and *S. viridis* refer to comparative remarks under these species. The external morphology of *S. poindimiensis* closely resembles that of *S. vudaensis* **sp. nov.** (unit 37) from Fiji. The specimen figured as '*laciniosa* group, unit 19' by Dayrat *et al.* (2014: fig. 4A) exhibits morphological characters typical for *S. poindimiensis* **sp. nov.**

Distribution and habitat. Recorded as endemic to eastern coast of NC, Pacific Ocean (Fig. 78). In this study, found on moderately exposed rocky shores, at upper and mid littoral levels (Fig. 76K).

Etymology. For the type locality, Poindimie, NC.

Siphonaria umbra sp. nov.

(Figs 76D–E, L–M, 77C–D)

Material examined. *Type material.* Holotype, from Ethel Beach 10°27.827'S, 105°42.497'E Christmas Is, Indian Ocean; coll. B.W. Jenkins, CI02-1, 11 Sept 2018 (AM C.584672 [M306], Fig. 76D). Paratypes, same data as holotype, WAM S74051 p [M409, SK084], Fig. 76E).

Other, non-type material. **Australia. Christmas Is:** CI01-1 E side Smith Point Flying Fish Cove (AM C.585320 p [SK022], C.585321 p [SK070]).

External morphology. Foot wall, foot edge and cephalic folds evenly yellow, foot sole darker yellow to grey; thick narrow; cephalic folds thin. large; mantle translucent, thin, mantle edge thickened lobed, white edge band; pneumostome long, under mantle.

Shell (Figs 76D–E, L; Table S9). Small to medium sized (max sl mean = 12.14 mm SD = 0.16 mm, n = 3); height low to medium; elongate ovate; apex offset weakly posterior and left, often eroded; apical sides weakly convex anterior, weakly concave posterior, straight to concave lateral; protoconch direction weakly homostrophic (n = 2, Fig. 76L), shell whorl dextral; growth lines uneven wavy distorted; radial banding prominent; shell lip uneven, anterior slightly protruded; rib count (mean = 38, SD = 1.6, n = 3), primary and secondary ribs white, raised, extend slightly beyond corrugated shell lip, flare upwardly; often only one small or no secondary rib between primary ribs, rib interstices grey to brown; prominent primary rib gaps either side of and 3–4 times as wide as siphonal ridge, filled with 3–5 very small secondary ribs; siphonal ridge prominent raised rounded with 3 siphonal ribs; interior shell lip and margin dark brown with white rays of varying lengths aligning under primary ribs, extend to white to brown spatula; dark brown/black bands line either side of spatula, siphonal groove and ADM scar prominent; CMS straight to convex, similar but darker colouration to

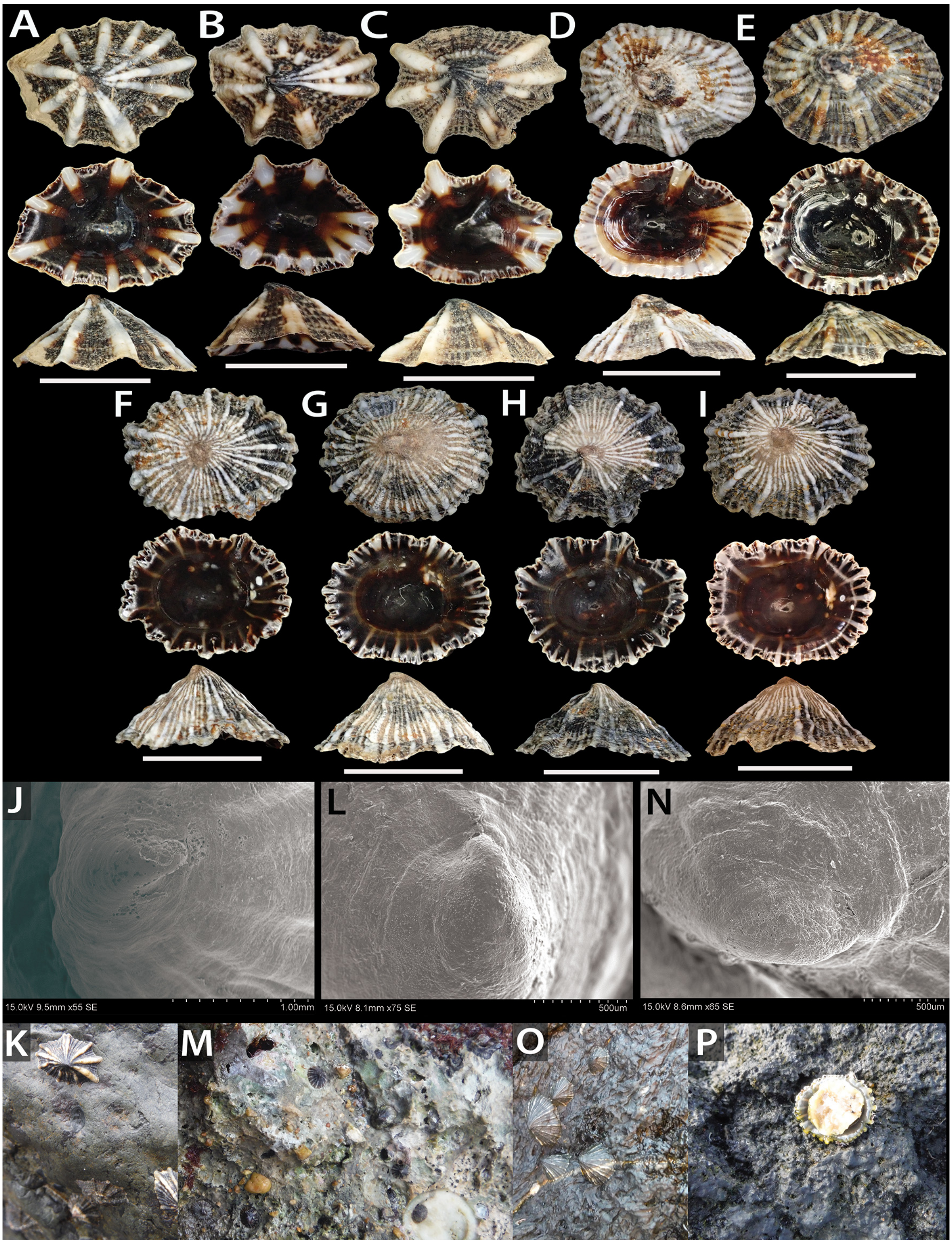

FIGURE 76. Shells of *S. poindimiensis* **sp. nov.**, *S. umbra* **sp. nov.** and *S. undans* **sp. nov. A–C, J–K.** *S. poindimiensis* **sp. nov. A.** Holotype AM C.584999 [M352], NC, Poindimie. **B.** Paratype AM C.585837 [SK129]. **C.** Paratype AM C.585002 [SK261], NC, Tiari. **J.** Protoconch, AM C.585010 [SK262]. **K.** *In situ*. **D–E, L–M.** *S. umbra* **sp. nov.**, CI, Ethel Beach. **D.** Holotype AM C.584672 [M409, SK084]. **E.** Paratype WAM S74051 [M306]. **L.** Protoconch, AM C.585320 [SK022]. **M.** *In situ*. **F–I, O–N.** *S. undans* **sp. nov.**. Hawaii, Big Island. **F.** Holotype AM C.584901 [M294, SK213]. **G.** Paratype AM C.584903 [SK257]. **H.** AM C.584904 [SK258]. **I.** Paratype AM C.585913 [SK388]. **N.** Protoconch, AM C.584905 [SK205]. **O.** *In situ*. **P.** Animal. Scale bars 10 mm.

spatula and shell margin, shell margin noticeably wider at anterior; thickening of inner shell lip and spatula occurs in larger specimens, white layering coats and covers brown/black colouration of inner shell lip.

Reproductive system (Fig. 77C; n = 1). Relatively large to animal size; positioned against inside of foot muscle and foot wall on the right side within coelom, under the respiratory cavity. GA, EG and ED positioned between

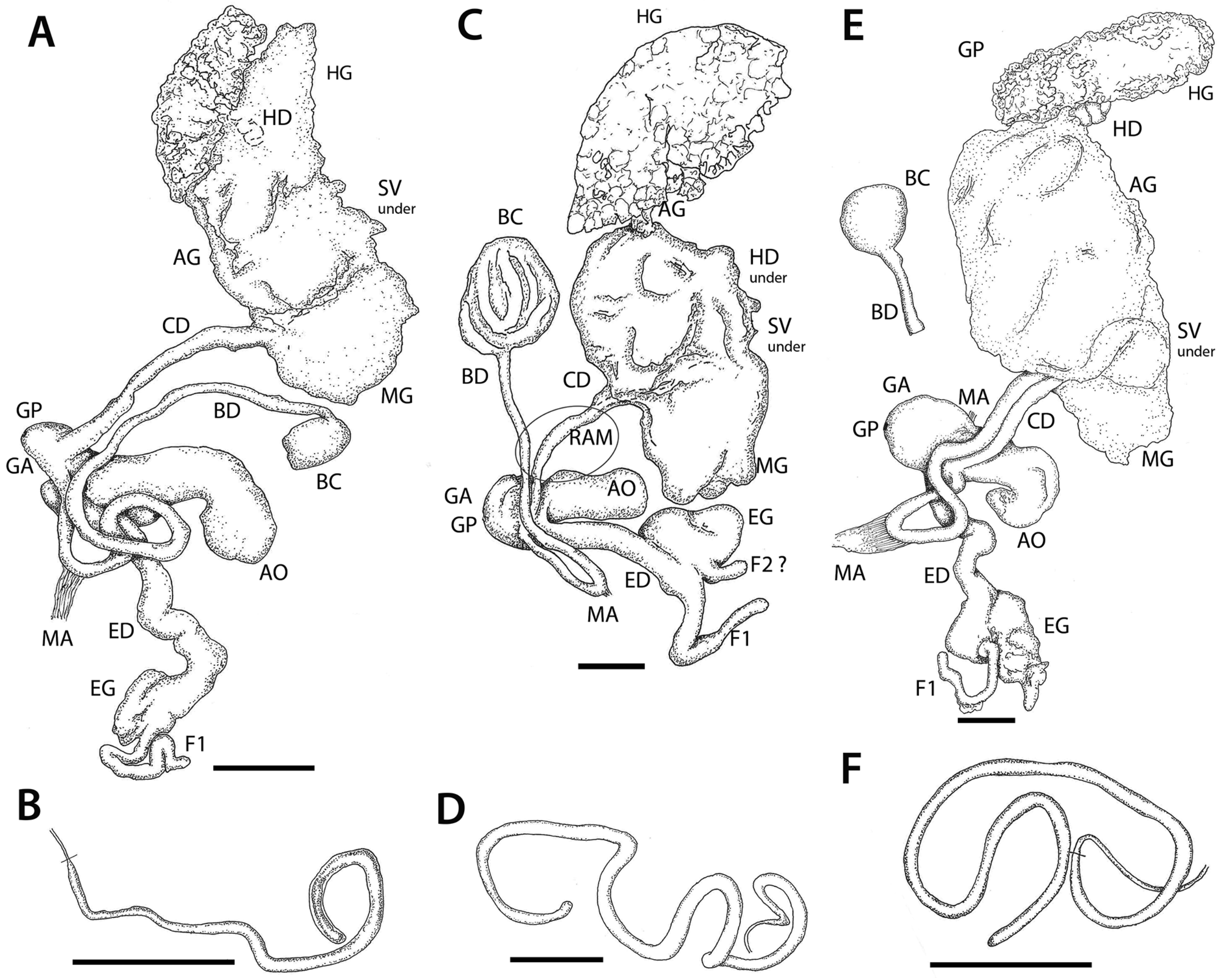

FIGURE 77. Reproductive morphology of *S. poindimiensis* **sp. nov.**, *S. umbra* **sp. nov.** and *S. undans* **sp. nov.** **A–B.** *S. poindimiensis* **sp. nov.**, NC, Poindimie. **A.** Holotype AM C.584999 [M352, SK128]. **B.** Paratype AM C.585837 [SK129]. **C–D.** Holotype of *S. umbra* **sp. nov.** AM C.584672 [M409, SK084], CI, Ethel Beach. **E–F.** Holotype of *S. undans* **sp. nov.**, AM C.584901 [M294, SK213], Hawaii, Big Island. Scale bars = 1 mm.

BM and RAM. AO large, elongated, bluntly bulbous, joins to small white muscular fibrous GA with singular GP; ED relatively short, straight, narrow, smaller than AO, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG soft whitish, slightly folded, similar size to AO, with two flagellum, F1 long (similar length to ED), bent, appears as an extension of ED, internally lays on top of the BM; F2 short, straight, close to EG. BD and CD jointly connect to GA between ED, AO and GP; BD slightly longer and thinner than CD, with a prominent loop over and with MA to mid ED; both ducts smooth and pass closely together through RAM connecting into MG (BD over CD), BC large, spherical, thin translucent test, (2 SPM in one BC), embedded in lower folds of MG/AG close to SV; HD short, narrow, coiled, links smallish AG to a large yellowish granulated HD; MG and AG small, folded, soft white tissue; AG larger than HG, sides match curvature of inner foot wall [M409].

Spermatophore (Fig. 77D). Thread-like (length = 10.4 ± 2.1 mm, n = 6), test thin, translucent, comprises a translucent cylindrical body section containing a white gelatinous thread-like core, tapers rapidly into a filamentous transparent flagellum (head length = 10.3 ± 0.61 mm, ~78% of SPM length, head width = 140 ± 30 µm, flagellum width = 20 ± 0 µm, n = 2), head section thicker than flagellum, head tip bluntly rounded, both sections smooth, featureless; 4 SPM coiled, embedded in red-brown gelatinous mass [M409].

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 2), *S. umbra* **sp. nov.** (*atra* group, unit 46) is the sister species of *S. radians* (unit 95). Both species are genetically well-differentiated differing by COI distances of ≥ 21.8% (Table S4). We found *S. umbra* **sp. nov.** in sympatry with five congeners on CI: For comparisons with *S. alba*, *S. incerta*, *S. tenebrae* **sp. nov.**, *S. christmasensis* **sp. nov.**, and *S. delicata* **sp. nov.** refer to comparative remarks under these species. Shell colour patterns resemble that of *S. gemina* **sp. nov.**

Distribution and habitat. Recorded as endemic to CI, Australia, Indian Ocean (Fig. 78). In this study, found in sheltered positions on moderately exposed rocky shores, at mid to upper littoral levels (Fig. 76M).

Etymology. From ‘umbra’ (Latin = shadow) for the two prominent axial dark areas both externally and internally at either side of the siphonal ridge and spatula groove in the shell of this species; noun in apposition.

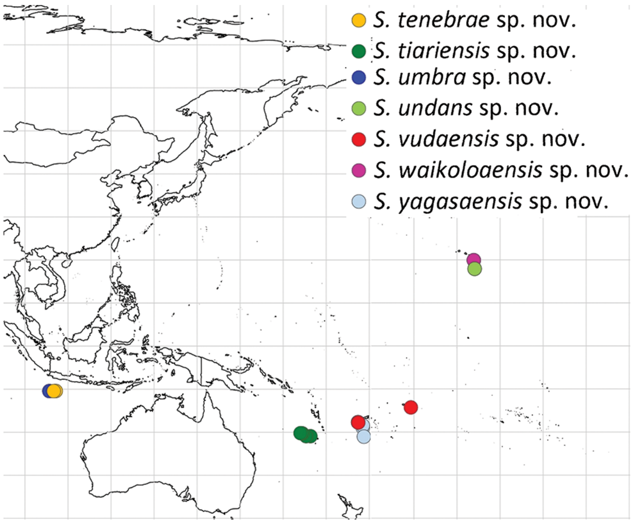

FIGURE 78. Known occurrences of *S. tenebrae* **sp. nov.**, *S. poindimiensis* **sp. nov.**, *S. umbra* **sp. nov.**, *S. undans* **sp. nov.**, *S. vudaensis* **sp. nov.**, *S. waikoloaensis* **sp. nov.** and *S. yagasaensis* **sp. nov.**

Siphonaria undans sp. nov.

(Figs 76F–I, N–O, 77E–F)

Material examined. *Type material.* Holotype, from Waikoloa Beach, 19°55.456’N, 155°53.491’W, Big Island, Hawaii; coll. B.W. Jenkins, HA04-2, 25 June 2018 (AM C.584901 [M294, SK213], Fig. 76F). Paratypes same data as holotype (AM C.585587 4p, C.584903 p [SK257], Fig. 76G, C.584904 [SK258], Fig. 76H, C.585913 p [SK388], Fig. 76I).

Other, non-type material. **Hawaii, Big Island:** Waikoloa Beach, 19°55.026’N, 155°53.282’W, HA04-1 (AM C.585375 10p, 19°55.456’N, 155°53.491’W, HA04-2 (AM C.584905 p [SK205]).

External morphology (Fig. 76P). Foot edge, foot wall, cephalic folds and pneumostomal lobe all evenly yellowish/green, foot sole cream; irregular black pigmentation markings around foot wall, concentrated over central cephalic lobes; mantle translucent narrow thickened edge strongly lobed/folded, mould/extend to cover area of shell lip and align with undulations of primary shell ribs; genital pore indistinct, located on foot wall to right anterior of right cephalic fold; small black epithelial eye spot centralised on each of centrally touching cephalic folds; pneumostome narrow, positioned between right adductor muscles and within mantle.

Shell (Fig. 76I–L, N; Table S9). Small sized (max sl mean = 13.2 mm SD = 0.8 mm, n = 3); height medium; circular ovate, exterior uneven with discontinuities in growth; apex offset posterior and left; apex slightly hooked, curled to posterior; apical sides weakly convex, weakly concave at posterior; protoconch direction weakly homostrophic (n = 2, Fig. 76N), shell whorl dextral; growth lines indistinct, rib growth uneven; radial banding prominent; shell lip uneven, anterior slightly protruded; primary and secondary ribs similar, white, width narrow, very crooked, slightly raised, ridges rounded, not extending greatly beyond scalloped/corrugated shell lip, rib count (mean = 45, SD = 3.3, n = 4); siphonal ridge not prominent, formed by dual primary ribs; often only one small or no secondary rib between primary ribs, rib interstices narrow, brown/black; interior shell lip and margin white under primary ribs, dark chocolate brown rays aligning under rib interstices extend from shell lip to evenly dark chocolate brown spatula; siphonal groove prominent, often with calcification; CMS straight, ADM scar distinct, paler than spatula and shell margin, golden colour; thickening of inner shell lip not apparent in larger specimens.

Reproductive system (Fig. 77E; n = 1). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; epiphallic parts (GA, EG and ED) positioned between BM and RAM, GA medium, with singular GP through foot wall; AO medium, bluntly rounded, joined at base to upper GA, rests against MG; ED long broad twisted centrally bent, joins to side of GA and base EG; GA, AO, ED all white muscular fibrous tissue; EG small, soft folded whitish tissue; single long narrow flagellum (F1) centrally bent and looped, appears as an extension of much wider ED; BD and CD connect closely into GA between ED-join and GP, both ducts tightly aligned, broad whitish curved smooth featureless, pass closely together through outside of RAM (BD over CD) into soft white folded tissues of MG/AG complex; CD short and curves to connect with AG duct, BD with distal loop and flat MA to inner foot wall, embeds in folds of AG; BC medium bulbous thin whitish translucent test, 2 SPM in BC (n = 1); HD broad short coiled whitish, links ducts in soft white folded tissues of AG to granulated yellowish small HG; AG much larger than HG.

Spermatophore (Fig. 77F). Thread-like, test thin, translucent, comprises a translucent cylindrical body section containing a white gelatinous thread-like core, tapers rapidly into a filamentous transparent flagellum (head length = 17.33 mm, n = 1), flagellum incomplete, head section much thicker than flagellum (head width = 222 µm, flagellum width = 74.1 µm, n = 1); head tip narrow bluntly rounded; both sections smooth, featureless; 2 SPM tightly coiled, embedded in dark-brown gelatinous mass [M294].

Comparative remarks. *Siphonaria undans* **sp. nov.** (*plicata* group, unit 61) is a well differentiated lineage in the mitochondrial tree (Figs 1, 3). It differs from its sister species *S. mauiensis* **sp. nov.** (unit 60) by COI distances of ≥ 29.6% (Table S7). We found *S. undans* **sp. nov.** in sympatry with *S. waikoloaensis* on Big Island, Hawaii. Both species are similar, but *S. waikoloaensis* differs by having a less scalloped shell edge, darker shell lip with paler interior, a slightly larger BC, and shorter SPM.

Distribution and habitat. Recorded from Big Island, Hawaii only (Fig. 78). In this study, found in sheltered positions (mainly rock crevices) on moderately exposed fine-algal covered volcanic-rock shores, at upper littoral level.

Etymology. Derived from Latin adjective 'undans' meaning 'wavy', referring to the prominent waviness and unevenness of the primary ribs in the shell of this species.

Siphonaria vudaensis sp. nov.

(Figs 79A–C, K–L, M, 80A–B)

Siphonaria atra—Cernohorsky 1972: 210, pl. 60, fig. 1 (not *Siphonaria atra* Quoy & Gaimard, 1833).

Siphonaria '*atra* group, unit 37'—Dayrat *et al.* 2014: 264, fig. 5S.

Material examined. *Type material.* Holotype, from Heal of foot, First Landing, near Vuda Point 17°40.753'S, 177°23.006'E, Viti Levu, Fiji; coll. B.W. Jenkins, FI03-1, 25 Aug 2018 (AM C.584785 [SK119 (RS and SPM], Fig. 79A). Paratypes, same data as holotype (AM C.585523 21p, C.584859 p [M288], C.584860 p [M289], Fig. 79B, C.584861 p [M291]; C.584862 p [M292], Fig. 79C).

Other, non-type material. **Fiji, Viti Vevu:** Heal of foot First Landing, 17°40.753'S, 177°23.006'E FI03-1 (AM C.584863 p [SK122], C.584995 p [SK121]); Vuda Point Marina seawall, 17°40.878'S, 177°23.009'E, FI03-2 (AM C.585324 p).

External morphology (Fig. 79K). Foot sole and foot wall evenly cream, paler to foot edge; uneven black pigmented blotches on foot wall; cephalic folds thick narrow; black pigmentation darker over centre of cephalic folds, paler to foot; mantle wide thin with heavy broad lobes, edge thickened with black pigmentation aligning with rib interstices; pneumostome small, under mantle.

Shell (Figs 79A–C, J, L; Table S9). Medium to large sized (max sl mean = 22.5 mm, SD = 3.3 mm, n = 5), ovate; low, profile very flat; apex offset slightly posterior and left, apical sides convex; shell whorl dextral, protoconch direction homostrophic (n = 1, Fig. 79L); growth striae apparent, shell thin; rib count (mean = 44.6, SD = 10.4, n = 5), fairly even number of primary and secondary ribs, 14–15 primary ribs pale white, fairly straight often bent, slightly raised, protrude 1–2 mm beyond shell lip to unevenly scallop a flat edge; siphonal ridge formed by 3 close primary ribs shows greatest extension beyond lip; 1–2 secondary ribs between primary, rib interstices white at apex to dark brown black at shell edge. Interior shell margin dark brown with pearly lustre, fine white rays extend over shell margin to spatula aligning under primary/secondary ribs, siphonal groove distinct, slightly curved to lateral; spatula dark chocolate brown to mottled white; ADM scar distinct, darker than margin, same colour as spatula; CMS concave, paler than shell lip; thickening of shell lip occurs, translucent pearly thickening rather than over covering pigmentation or whitening; juvenile specimens thin often translucent; small specimens evenly dark chocolate brown.

Reproductive system (Fig. 80A; n = 1). Positioned within coelom under the respiratory cavity, hermaphroditic complex (HG, AG and MG) positioned to posterior against right foot wall and over foot sole, epiphallic parts positioned to anterior firmly between BM and RAM. AO very large, elongated, centrally bent, bluntly bulbous, joins to upper part of prominent GA, singular GP; ED relatively short, broad, shorter than AO, joins to side of GA; GA, AO, ED all white muscular fibrous tissue; EG soft whitish, slightly folded, smaller than AO; single short blunt twisted flagellum (F1); BD and CD jointly but opposing connections to GA between ED, AO and GP; BD long narrow, with distinct folds prior to GA connection and prominent distal loop with MA to inner body wall; CD broad short, wider than BD; both ducts smooth and pass closely together through RAM (BD over CD); CD connects into MG; BD loops prior to connection to small bulbous BC with thin translucent test, embedded in folds of MG/AG close to embedded SV; HD short, thick, coiled, links AG to smaller yellowish granulated HD; MG and AG folded, soft white tissue.

Spermatophore (Fig. 80B). Thread-like, relatively long (length = 11.4 mm) and thin, translucent, over half-length comprises a translucent cylindrical body section (head length = 7.2 mm, ~63% of SPM length) containing a white gelatinous thread-like core, tapers rapidly into a filamentous transparent flagellum; head section much thicker than flagellum (head width = 133 µm, flagellum width = 13.1 µm); head tip tapered bluntly rounded, both sections smooth, featureless; 2 SPM coiled, embedded in red-brown gelatinous mass [SK119].

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 2), *S. vudaensis* **sp. nov.** (*atra* group, unit 37) is the sister species of a clade containing two species, *S. tenebrae* **sp. nov.** (unit 92) and *S. subatra* (unit 38). *Siphonaria vudaensis* differs from these two species by COI distances of ≥ 10.9% (*S. tenebrae*) and ≥ 13.3% (*S. subatra*) (Table S3).

We found this species in sympatry with three congeners on Viti Levu: For comparisons with *S. namukaensis* **sp. nov.**, *S. normalis*, and *S. tagaqaensis* **sp. nov.** refer to comparative remarks under these species. Specimens from Tuituila, Samoa and Viti Levu figured as 'unit 37, *atra* group' in Dayrat *et al.* (2014: figs 5P, Q) belong to this species. The specimen figured as '*S. atra*' in Cernohorsky (1972: 210, pl. 60, fig. 1) is a specimen of *S. vudaensis* **sp. nov.**

Distribution and habitat. Recorded from Viti Levu, Fiji and Tutuila, American Samoa (Fig. 78). In this study, found in sheltered positions on moderately exposed rocky boulder shores, at mid littoral level.

Etymology. For the type locality, Vuda Point, Viti Levu, Fiji.

Siphonaria waikoloaensis sp. nov.

(Figs 79D–F, N–O, 80C–D)

Material examined. *Type material.* Holotype, from Waikoloa Beach, 19°55.456'N, 155°53.491'W, Big Island, Hawaii; coll. B.W. Jenkins, HA04-2, 25 June 2018 (AM C.584907 [M295, SK214], Fig. 79D). Paratypes:

same data as holotype (AM C.585327 10+p; Waikoloa Beach 19°55.026'N, 155°53.282'W. HA04-1, 25 June 2018 (AM C.585327 p [SK254], Fig. 79E; C.584673 p [SK391], Fig. 79F).

Other, non-type material. **Hawaii. Big Island:** Waikoloa Beach, 19°55.456'N, 155°53.491'W, HA04-2 (AM C.584906 p [SK206]); 19°55.026'N, 155°53.282'W, HA04-1 (AM C.595958 2d).

External morphology. Foot edge, foot wall, cephalic folds and pneumostomal lobe all evenly yellowish/green, foot sole cream; irregular small blotches of black pigmentation on foot wall and centre of cephalic lobes; mantle translucent narrow thickened edge strongly lobed with bands of black pigmentation aligned with shell rib interstices; genital pore indistinct, located on foot wall to right anterior of right cephalic fold; small black epithelial eye spot centralised on each of centrally touching cephalic folds; pneumostomal lobe under mantle, unpigmented, between the right ADMs.

Shell (Figs 79D–F, N; Table S9). Small sized (max sl mean = 10.6 mm, SD = 1.4 mm, n = 3), ovate; height tall, shell thin; apex offset weakly posterior and left, apex often hooked/curled to posterior, apical sides strongly convex, protoconch direction homostrophic to central (n = 2, Fig. 79O), shell whorl dextral; 3 radial colour bands, protoconch brownish, central pale brown and outer showing black interstices; rib count (mean = 45, SD = 7.8, n = 3), ~ 12–14 prominent primary ribs, white, crooked, raised, rounded ridges, width broads to shell lip, protrude beyond shell lip with a raised roll to unevenly scallop and corrugate the edge; interstices between primary ribs with 3–4 smaller secondary ribs; paired primary ribs form siphonal ridge, no more prominent than other primary ribs. Interior shell evenly dark chocolate brown, narrow irregular white rays extend from shell lip to margin aligning under primary/secondary ribs, siphonal groove distinct; ADM scar distinct, CMS straight; thickening of shell lip not observed.

Reproductive system (Fig. 80C; n = 1). Positioned within right side of coelom, against foot wall on foot muscle, under the respiratory cavity; RS proportionally large to animal size compared to other species; epiphallic parts (GA, EG and ED) positioned in between BM and RAM, GA medium, with singular GP through foot wall; AO medium, bluntly rounded, joined at base to upper GA, rests against MG; ED long broad twisted centrally bent, joins to side of GA and base EG; GA, AO, ED all white muscular fibrous tissue; EG large, soft folded whitish tissue; single long broad flagellum (F1) centrally bent, appears as an extension of much wider ED; BD and CD connect closely in opposite directions into GA between ED join and GP, both ducts narrow whitish curved smooth featureless, pass closely together through outside of RAM (BD over CD) into soft white folded tissues of MG/AG complex; CD curves and broadens to connect with AG duct, BC long with distal loop and flat MA to inner foot wall, embeds in folds of AG; BC small bulbous thin whitish translucent test, 2 SPM in BC (n=1); HD very small short coiled whitish, links ducts in soft white folded tissues of AG to granulated small HG; AG much larger than HG.

Spermatophore (Fig. 80D). Relatively short, test thin, translucent, comprises a translucent cylindrical body section containing a white gelatinous thread-like core, tapers into a filamentous transparent flagellum (head length = 8.111 mm n = 1, flagellum incomplete), head section much thicker than flagellum (head width = 185 µm, flagellum width = 74.1 µm n = 1), head tip bluntly rounded; both sections smooth, featureless; 2 SPM tightly coiled, embedded in dark-brown gelatinous mass in holotype.

Comparative remarks. *Siphonaria waikoloaensis* **sp. nov.** (*plicata* group, unit 55) forms a well-differentiated lineage in the mitochondrial tree (Figs 1, 3). It differs from other species by COI distances of ≥ 28% (Table S7). We found *S. waikoloaensis* **sp. nov.** in sympatry with *S. undans* on Big Island, Hawaii. For a comparison see under this species.

Distribution and habitat. Recorded from Big Island, Hawaii, USA, Pacific Ocean (Fig. 78). In this study, found in sheltered positions (mainly rock crevices) on moderately exposed fine-algal covered volcanic-rock shores, at upper littoral level (Fig. 79N).

Etymology. For the type locality, Waikoloa Beach, Big Island, Hawaii.

***Siphonaria yagasaensis* sp. nov.**

(Figs 79H–J, 80E–F)

Material examined. *Type material.* Holotype, from Oneata Is, 18°26.5166'S, 178°29.583'E, Fiji. SWP 17-116 (AM C.584827 [M437, SK226], Fig. 79H). Paratypes, same data as holotype (AM C.584710 5p); Yagasa, small island to the SW, 18°57.783'S, 178°29.333'E, Tuvana-i-Ra Island, Fiji. SWP 17-103 (AM C.584828 p [M436], Fig. 79J); Tuvana-i-Ra Island 21°02.24'S, 178°45.01'E, Fiji. SWP17-77 (AM C.608181 p [M435], Fig. 79I).

Other, non-type material. **Fiji:** Tuvana-i-Ra Island, SWP17-77, 21°02.24'S, 178°45.01'E (AM C.585937 3p); Yagasa, small island, SW of Tuvana-i-Ra Island, SWP 17-103, 18°57.783'S, 178°29.333'E (AM C.585936 2p).

External morphology (preserved). Foot sole and foot edge without dark pigmentation; foot wall, cephalic folds and pneumostomal lobe evenly cream with irregular blotches of black pigmentation, concentrated over centre of cephalic lobes; mantle translucent, wider than foot wall, edge weakly lobed, without pigmentation.

Shell (Fig. 79H–J; Table S9). Medium sized (max sl mean = 16.7 mm, SD = 4.6 mm, n = 3), elongate ovate; low to medium; apex offset central slightly posterior and left, mostly externally coated with algae similar to *Lithothamnion*; apical sides weakly concave, protoconch direction undetermined, shell whorl dextral, shell thick; rib count (mean = 33, SD = 4.9, n = 3), continuum of forms from primary to secondary ribs; primary ribs pale white, straight, slightly protrude beyond shell lip to unevenly scallop and corrugate the edge; 1–2 interspersed pale white finer secondary ribs, rib interstices narrow; paired primary ribs form siphonal ridge, no more prominent than other primary ribs. Interior shell lip/margin white of irregular widths and lengths, aligning under primary/

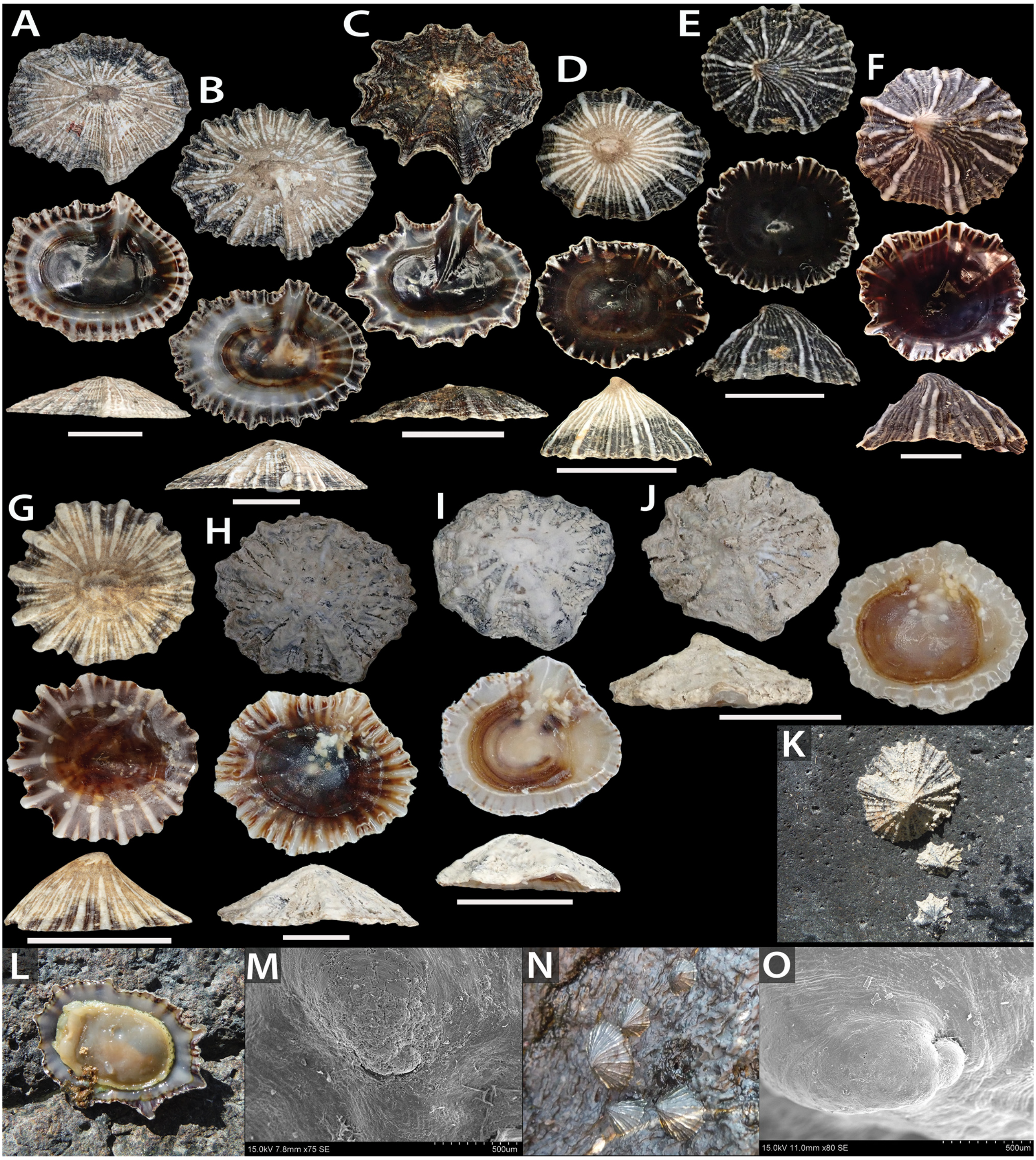

FIGURE 79. Shells of *S. vudaensis* **sp. nov.**, *S. waikoloaensis* **sp. nov.**, *S. amara* and *S. yagasaensis* **sp. nov. A–C, K–L, M.** *S. vudaensis* **sp. nov.**, Fiji, Viti Vevu. **A**. Holotype AM C.584785 [SK119]. **B.** Paratype AM C.608181 [M289]. **C.** Paratype AM C.584862 [M292]. **K.** *In situ*. **L.** Animal. **M.** Protoconch, AM C.584863 [SK122]. **D–F, N–O.** *S. waikoloaensis* **sp. nov.**, Hawaii, Big Island. **D.** Holotype AM C.584907 [M295, SK214]. **E.** Paratype AM C.585327 [SK254]. **F.** Paratype AM C.584673 [SK391]. **N.** *In situ*. **O.** Protoconch, AM C.584906 [SK206]. **G.** Holotype of *S. amara* NHMUK 1981016. **H–J.** *S. yagasaensis* **sp. nov. H**. Holotype AM C.584827 [M437]. **I.** Paratype AM C.584860 [M435]. **J.** Paratype AM C.584828 [M436]. Scale bars = 10 mm.

secondary ribs; spatula dark chocolate brown to ADM, siphonal groove deep and distinct, paler than shell margin and spatula; ADM scar distinct, CMS straight, same colour as spatula; thickening of shell lip common, often in smaller specimens (Figs 79H, I), infills and reduces lip scalloping, becomes pale brown to dark cream.

Reproductive system (Fig. 80E; n = 1). Positioned within coelom under the respiratory cavity, hermaphroditic complex (HG, AG and MG) to posterior against right foot wall and over foot sole, epiphallic parts between BM and RAM, F1 lays over posterior of BM; AO large, elongated, centrally bent, blunt, merges to upper part of indistinct

GA, singular GP; ED short, wide, twisted, short than AO, joins to lower side of GA and AO; GA, AO, ED all white muscular fibrous tissue; EG soft whitish, folded, smaller than AO; single short broad flagellum (F1), possible F2; BD and CD closely but in opposing directions connect to side of GA between AO and GP; both ducts smooth and pass through outside of RAM (BD over broader CD); BD long narrow with prominent distal loop and MA attached to inner body wall in front of BM, joins to BC with thin transparent test; CD shorter wider than BD; CD connects into MG; BC and CD embed in folds of AG and MG; HD broad, lobed, brown markings, under AG, links AG to much smaller yellowish granulated HG; MG and AG folded, soft white tissue.

Spermatophore (Fig. 80F). Thread-like (length = 3.04 mm, n =1), translucent, test thin; head section bluntly rounded, evenly cylindrical, containing a white gelatinous core, tapers along the transparent flagellum to a thin tip; both sections smooth, featureless; head section longer wider than flagellum (head length = 2.48 mm, flagellum length = 0.55 mm, head width = 56 µm, flagellum width = 11 µm, n = 1); SPM tightly coiled in bursa, embedded in brown gelatinous mass.

Comparative remarks. In our mitochondrial phylogeny (Figs 1, 3), *S. yagasaensis* **sp. nov.** (*laciniosa* group, unit 67) is the sister species of *S. namukaensis* **sp. nov.** (unit 22). *Siphonaria yagasaensis* **sp. nov.** differs from other species by COI distances of ≥ 13.9% (Table S6). For a comparison with *S. namukaensis* refer to comparative remarks under this species. *Siphonaria yagasaensis* **sp. nov.** exhibits a similar shell morphology with other species in the *plicata* group.

Distribution and habitat. Recorded exclusively to Oneata, small island SW of Yagasa and Tuvana-i-Ra Islands, southern Fiji (Fig. 78). In this study, found on exposed and moderately exposed rocky shores, at upper littoral level.

Etymology. For the type locality, Yagasa Island, Fiji.

Williamia Monterosato, 1884

Allerya Mörch, 1877 (invalid: Suppressed and placed on the Official Index by Opinion 1410).

Brondelia Bourguignat, 1862 (invalid: Suppressed and placed on the Official Index by Opinion 1410)—Rehder 1984a: 83.

Scutulum Monterosato 1877: 427 (invalid: junior homonym of *Scutulum* Tournouer, 1869 [Echinodermata]). Type species *Ancylus gussoni* Costa, 1829, by monotypy.

Williamia Monterosato 1884: 150 (nom. nov. pro *Scutulum* Monterosato, 1877 non Tournouer, 1869). Type species *Ancylus gussoni* Costa, 1829, by typification of the replacement name—Rehder 1984b: 159; White *et al.* 2011: 295.

Parascutum Cossmann 1890: 883 (invalid: unnecessary nom. nov. pro *Scutulum* Monterosato, 1877 non Tournouer, 1869)

Roya Iredale 1912: 218. Type species *Roya kermadecensis* Iredale, 1912, by monotypy.—Powell 1934: 155.

Taxonomic remarks. Our morphological and molecular studies confirm that *Siphonaria* and *Williamia* are closely related. Indeed, their sister group relationship has recently been confirmed by a phylogenomic study of the Panpulmonata (Krug *et al.* 2022). Morphologically, the patelliform shell of *Williamia* is distinct from that of *Siphonaria*. *Williamia* is distinguished by the combination of the following characteristics: Fragile, externally no ribs or pale axial bands, interior ADM complete circular. By contrast, *Siphonaria* exhibiting a much greater specific diversity, is quite variable in many shell characteristics, such as geometry, colour, position of apex and ribbing, variable thickness, strongly to unraised external ribs. Most significantly, *Siphonaria* differs from *Williamia* by having an internal, horseshoe-shaped ADM. Several *Siphonaria* exhibit shells that somewhat resemble that of *Williamia* (e.g., *S. oblia*, *S. lateralis*, *S. thersites*, *S. compressa* Allanson, 1958 [not examined]). However, these species clearly differ in anatomical characters. The external morphology is similar in both *Siphonaria* and *Williamia*. Both groups have a head anterior to posterior shell apex, dual cephalic lobes with central eye spots, mantle, right lateral position of siphon and rectum, pneumostomal lobe (although it is longer in *Williamia*), and similar sizes of ducts and spermatophore (e.g., *S. obliquata*, *S. sipho* to *S. radiata*.). The radula dentition differs between *Siphonaria* and *Williamia.* In *Williamia*, the central tooth is small and unicuspid, and demarcation of inner and outer lateral teeth is more prominent, inner laterals strongly bicuspid and outer laterals single plates. Hubendick (1946: 8, 18) recognized *Williamia* as a distinct genus within Siphonariidae distinguished from *Siphonaria* by a combination of anatomical and shell characters. However, not all differences are confirmed herein for all species. For example, the BC is in front of the adductor muscle [ADM] in *Williamia* but also in *S. camura* **sp. nov.** The shape of the adductor muscle impression in *Siphonaria* differs from *Williamia* having an unbroken circular scar, but this is also seen in *S. radiata*. The BD in *Siphonaria* runs through or outside this the RAM is correct for most species, but not for *S. camura* **sp. nov.** However, it never runs through the RAM in *Williamia*.

Williamia radiata (Pease, 1861)

(Figs 81A–H, J, 80G)

Tectura radiata Pease 1861: 437 (type locality: 'Sandwich Islands' [Hawaii]).—Dall 1872: 193; Tryon & Pilsbry 1891: 154; Kay 1965: 29, pl. 11, figs 6–7; Marshall 1981: 488.

Williamia radiata—Melville & Standen 1897: 414; Habe & Kikuchi 1960: 64; Habe 1961: 96, pl. 44, fig. 14; Kay 1979: 493, figs 157 k, l; Marshall 1981: 488; Ruthensteiner *et al.* 2007: 17, figs 1A–H, 2A–C, 3A–F.

Capulus nutatus Hedley 1908: pl. 9, figs 15–16 (type locality: around Sydney [NSW, Australia]).—Iredale 1912: 218; Marshall 1981: 488.

Roya kermadecensis Iredale 1912: 218, pl. 9, fig. 10 (type locality: Sunday Island, Kermadec Group, [NZ]).—Marshall 1981: 488.

Williamia radiata Kuroda & Habe in Habe 1961: 96, pl. 44, fig. 14 (type locality Japan).—Marshall, 1981: 488 (invalid; secondary junior homonym of *Tectura radiata* Pease, 1860).

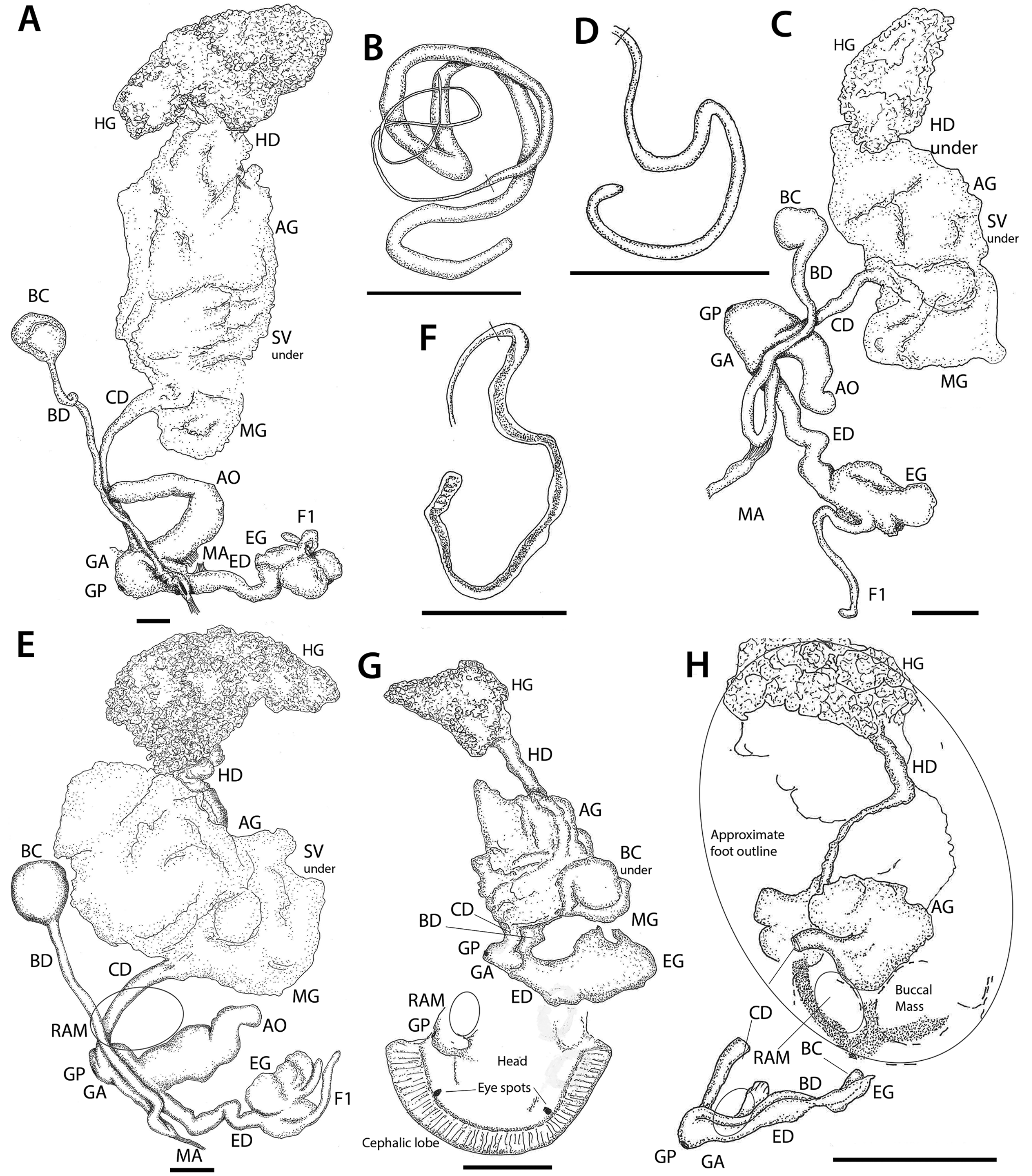

FIGURE 80. Reproductive morphology of *S. vudaensis* **sp. nov.**, *S. waikoloaensis* **sp. nov.**, *S. yagasaensis* **sp. nov.**, *Williamia radiata* and *Williamia* sp. 'Walters Shoal'. **A–B.** Holotype of *S. vudaensis* **sp. nov.** AM C.584785 [SK119]. **C–D.** Holotype of *S. waikoloaensis* **sp. nov.** AM C.584907 [M295, SK214]. **E–F.** Holotype of *S. yagasaensis* **sp. nov.** AM C.584827 [M437 SK226]. **G–H.** *Williamia radiata*. **G.** NZ, Poor Knights Is, NMNZ M.100391/1 [M601, SK555], reproductive organs and animal anterior. **H.** Walters Shoal, MNHN IM 2013-67370 [M567, SK556], reproductive organs, animal anterior, detail of epiphalic parts. Unlabelled scale bars = 1 mm.

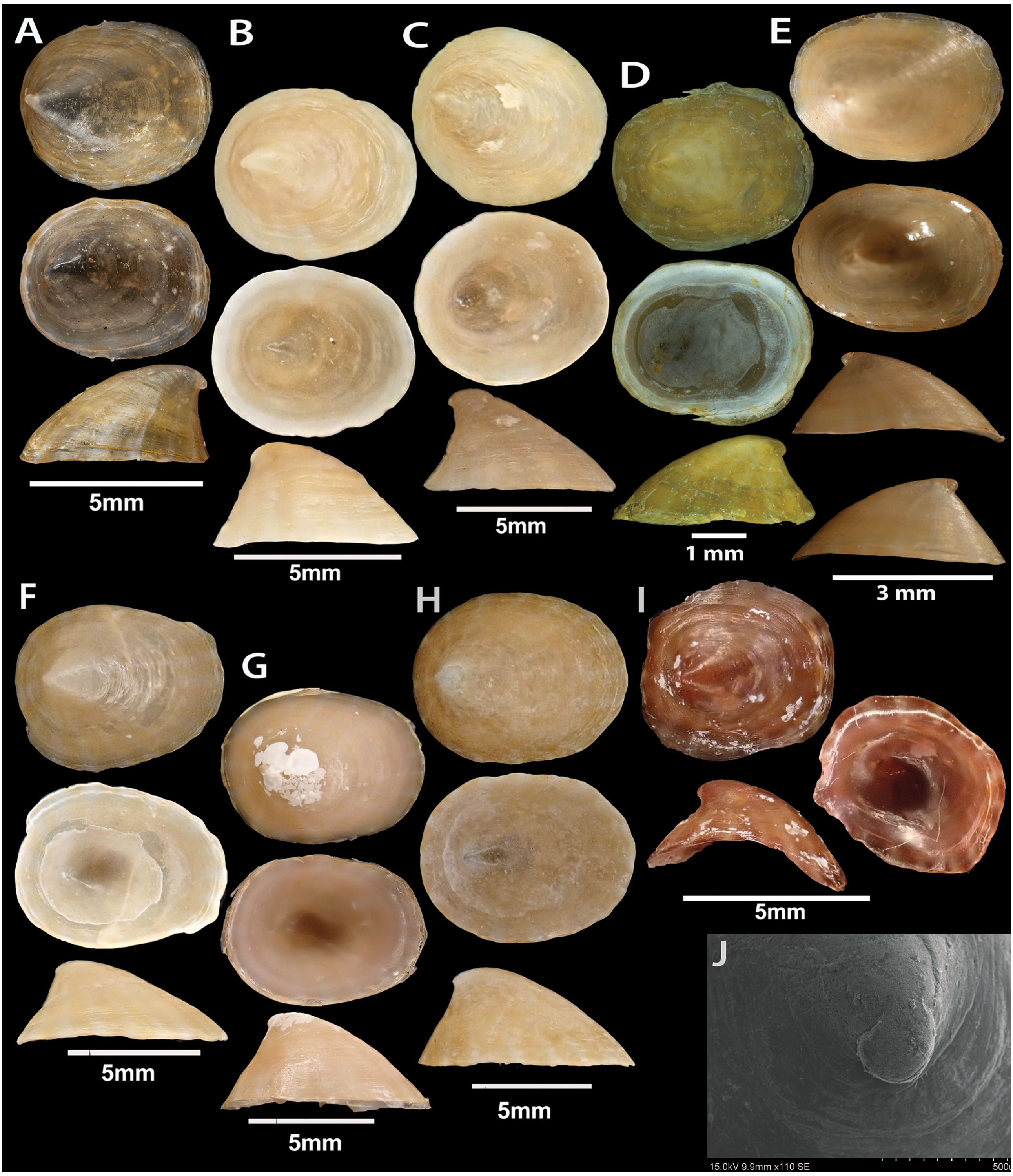

FIGURE 81. Shells if *Williamia radiata*. **A–H, J.** *W. radiata*, **A.** Lectotype of *Tectura radiata* NHMUK 1962837. **B**. Holotype of *Capulus nutatus* AM C.029106. **C**. Paratype of *C. nutatus* AM C.143080. **D.** Holotype of *Roya kermadecensis* CM M.5464. **E**. Holotype of *W. polynesica* USNM 757897. **F.** NSW, Botany Bay, AM C.112575. **G.** NZ, Poor Knights Is, NMNZ M.100391/1 [M601, SK555]. **H.** NZ, Kermadec Is, AM C.110819. **J.** NSW, Port Stephens, AM C.595937 [SK562], protoconch. **I.** Walters Shoal, MNHN IM-2013-67370 [M567, SK556]. Unlabelled scale bars = 10 mm.

Williamia japonica Habe, 1962: 96 (replacement name for *Williamia radiata* Kuroda & Habe, 1961 not Pease, 1861).—Marshall 1981: 488.

Allerya radiata—Habe, 1964: 144, pl. 44, fig. 14. Marshall, 1981: 488.

Williamia radiata nutata—Marshall 1981: 488, figs 1, 2C, D, F, H, I, K; Brook 1998: 199; Raven & Bracegirdle 2010: 46; Duffy & Ahyong 2015: 67.

Williamia polynesica Rehder 1980: 98 (type locality: off Waikiki, Oahu, Hawaii [USA]).—Marshall 1981: 488.

Williamia radiata radiata—Marshall 1981: 488, figs 2A, B, L.
Williamia radiata japonica—Habe *et al.* 1986: 23.

Material examined. *Type material.* Lectotype of *Tectura radiata* Pease, 1860 from 'Sandwich Islands' [Hawaii], Cuming Collection, date? (NHMUK 1962837; Fig. 81A). One paralectotype, same data as lectotype (NHMUK 1962838).

Holotype of *Capulus nutatus* Hedley, 1908 from Balmoral Beach [Sydney, NSW, Australia]; coll. C.T. Starkey, pre. 1907 (AM C.029106; Fig. 81B). Twelve paratypes, same data as holotype (AM C.143080; Fig. 81C largest paratype).

Holotype of *Roya kermadecensis* Iredale, 1912 from Sunday Island, Kermadec Group (CM M.5464; Fig. 81D).

Holotype of *Williamia polynesica* Rehder, 1980 from off Waikiki, Oahu, Hawaii (USNM 757897; Fig. 81E).

Other, non-type material. **NZ:** Kermadec Ids, Raoul (Sunday) Is 29°15'S, 177°52'W (AM C.30230 8d); 4kms N of Cape Rodney, 36°15'S, 174°49'E (AM C.110823 4d); Off Poor Knights Islands 35°28.3'S, 174°44.13'E (NMNZ M.100391/1 p [M601, SK555]). **NC:** Loyalty Is, Lifou Is (AM C.25728 2d; AM C.335728 d). **PNG:** Ella Beach, Port Moresby, 9°29'S, 147°9'E (AM C.335729). **Australia:** Coral Sea, Northeast Herald Cay, 16°56'S, 149°11'E (AM C.335727). Elizabeth Reef, 29°57.2'S, 159°1.18'E (AM C.336005 d), 29°54.78'S, 159°2.78'E (AM C.336013 d), 29°54.78'S, 159°2.78'E (AM C.336015 d); Middleton Reef, 29°23.93'S, 159°6.7'E (AM C.461846 d), 29°24.02'S, 159°6.2'E (AM C.461845 p), 29°24'S, 159°5.16'E (AM C.461844 d), 29°24.03'S, 159°4.37'E (AM C.461843 d). **NI:** 29°2'S, 167°57'E (AM C.59405 p [SK006]). **Qld:** Michaelmas Cay, 16°36'S, 145°59'E (AM C.110822 2d); SW side Euston Reef, 16°40'S, 146°13'E (AM C.335730 9d); Bunker Group, Lady Musgrave Is, 23°54'S, 152°25'E (AM C.398297 d). Caloundra, 26°49'S, 153°10'E (AM C.335994 d). **LHI:** 31°46.55'S, 159°13.4'E (AM C.461858 d), 31°32.5'S, 159°3.75'E (AM C.59697 d). **NSW:** Angourie Point, 29°29'S, 153°22'E (AM C.112574 2d); Clarence River (mouth), 29°25.5'S, 153°21'E (AM C.110824 5d); Woolgoolga, 30°6.7'S, 153°12.3'E (AM C.110818 2d); Point Halliday, 32°4.5'S, 152°33'E (AM C.117308 2d, AM C.336021 4d); North Fingal Bay, 32°44.75'S, 152°10.5'E (AM C.110814 11d, AM C.117310 d); Port Stephens, 32°42'S, 152°5'E (AM C.110812 5d, C.595937 p [SK562]); Sydney, Balmoral Beach, Middle Harbour, 33°49.7'S, 151°15.02'E (AM C.143080 12d, AM C.29106 d); Coogee Bay, 33°55.5'S, 151°15.4'E (AM C.110813 2d); Kurnell, Botany Bay, 33°57'S, 151°12.37'E (AM C.107325 8d, AM C.110817 d, AM C.117309 d, AM C.112575 19d); Bate Bay, Cronulla Beach, 34°2.5'S, 151°10'E (AM C.110815 2d). Shell Harbour, 34°35'S, 150°52'E (AM C.398294 d); Gerringong, 34°44.28'S, 150°50'E (AM C.110816 d); Ulladulla, 35°21.5'S, 150°28.5'E (AM C.398293 d); Twofold Bay, 37°5.11'S, 149°55.35'E (AM C.50019 d). **Tas:** Flinders Island, Fotheringate Beach, 40°12.948'S, 148°2.106'E (TMAG E36516 d, TMAG E36516 p). **WA:** Turtle Beach, W side of North West Cape, 21°48'S, 114°10'E (AM C.110825 d); North West Cape, 21°49'S, 114°11'E (AM C.110821 2d); Point Quobba, N of Carnarvon, 24°29'S, 113°25'E (AM C.398298 d); Off Chinaman's Bluff, Kalbarri, 27°42'S, 114°9'E (AM C.336007 d); South of Cowaramup, 33°53'S, 114°59'E (AM C.110820 d).

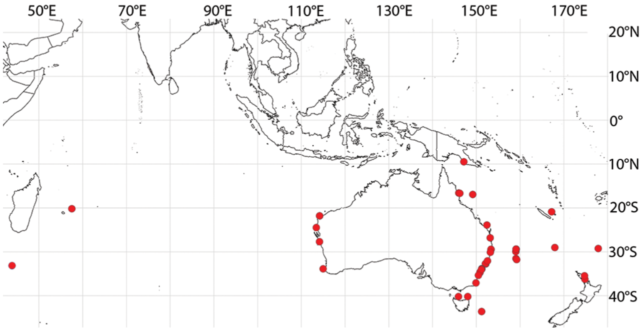

FIGURE 82. Known occurrence records of *Williamia radiata*.

Taxonomic remarks. The lectotype of *Tectura radiata* has been designated by Kay (1965). The name *W. radiata* Kuroda & Habe, 1961 (in Habe 1961) is a junior secondary homonym of *W. radiata* (Pease, 1861). Habe (1962: 96, pl. 44, fig. 14) introduced *W. japonica* as a replacement name (Art. 12.2 of the Code). Subsequently, Habe (1964: 144) treated *Williamia japonica* as a junior synonym of *W. radiata*, which was confirmed by Marshall (1981: 488). Marshall (1981) recognised two geographic subspecies; *W. radiata radiata* (Pease, 1861) and *W. radiata nutata* (Hedley, 1908), but suspected that both taxa would 'ultimately prove to be synonyms'.

External morphology (preserved). Animal evenly dark yellowish, black pigmentation absent; foot wall and mantle narrow, mantle edge thickened unlobed, singular cephalic fold, wide, front wide, striated, 2 black eye spots separately located within cephalic fold (Fig. 80G).

Shell (Figs 81A–H, J; Table S9). Circular ovate, small sized (max sl mean = 6.7 mm, SD = 0.8 mm, n = 8), tall, shell thickness thin; exterior smooth, evenly yellowish brown, growth striae indistinct; apex offset weakly posterior and central, lateral and anterior apical sides strongly convex, posterior side concave, protoconch below shell apex, direction weakly heterostrophic (n = 1, Fig. 81J), shell whorl dextral; ribs pale axial bands, fairly straight, increasingly broaden to shell lip, periostracum extends beyond uncorrugated shell edge. ribs unraised, rib count (mean = 24, SD = 1.9, n = 8), Interior paler than exterior. ADM circular and complete (Figs 81D, F), thinner over siphonal opening and CMS.

Reproductive system (Fig. 80G; n = 1). Positioned within coelom under the respiratory cavity, epiphallic parts (AO, EG, ED, F1) positioned over and behind BM, hermaphroditic complex (HG, AG and MG) to posterior against right foot wall under intestine and over foot sole; singular GP positioned immediately behind right side of cephalic fold; ED long wide, joins to lower side of small GA, AO indistinct; EG large, soft, folded, flagellum (F1) indistinct; BD and CD jointly connect to side of GA, CD passes between foot wall and outside RAM, CD short wide flat, passes on inner side of RAM, both BD and CD connect into folds of AG and MG; BC medium spherical embedded under MG; HD long, broad, unfolded, links AG to smaller HG; MG and AG folded, soft white tissue.

Comparative remarks. Throughout the known range of *W. radiata* no sympatric congener has been recorded. The shells figured in Kay (1979: figs 157K–L), Marshall (1981: fig. 2B, D, F) correspond well with shells figured herein (Figs 81B–H) as well as the lectotype figured in Kay (1965: pl. 11, figs 6, 7; Fig. 81A herein). The circular and complete ADM scar (Fig. 81F) corresponds well with the scar figured in Iredale (1915: pl. 9, fig. 10) as '*Roya kermadecensis*' from Sunday Is, Kermadecs. The figured horseshoe shaped ADM scar of *Williamia* in Hubendick (1946: fig. 9) is incorrect. The RS of 'W. *radiata'* described and figured in Ruthensteiner *et al.* (2007: figs 1A–C) corresponds well with that figured herein (Fig. 80G). The record of *Roya* sp. in Powell (1934: 155) likely refers to *W. radiata*.

Distribution and habitat. Recorded from Kermadec Islands, NZ, NC, PNG, Indian Ocean, E and SW Australia (Fig. 83) in subtidal depths.

Nomina inquirenda

Siphonaria amara Reeve, 1856

Siphonaria amara Reeve 1856: pl. 7, species 33 (type locality: California [probably in error]).—Hanley 1858b: 151; Carpenter 1864b: 676; Paetel 1873: 117, 1875: 92, 1883: 178, 1889: 428; Pilsbry 1920b: 379; Hubendick 1946: 66; Cernohorsky 1972: 210; Galindo 1977: 416; Kay 1979: 493; Trew 1983: 7; White & Dayrat 2012; Dayrat *et al.* 2014: 267.

Siphonaria normalis var. *amara*—Pilsbry 1920b: 380.

Siphonaria normalis omara Edmondson 1946: 188; Ostergaard 1950: 77, 111 (invalid; incorrect subsequent spelling of *amara*).

Taxonomic remarks. The species description was attributed by Reeve to Nuttall, but Reeve is the author of the name. Initially, the name was first mentioned by Jay (1839: 39) as a *nomen nudum* without a description (Art. 12.1 of the Code) for a specimen from the 'Sandwich Isles' (Hawaii). The name has not been made available subsequently by Catlow & Reeve (1845: 100) or Jay (1850: 104) (no description, Art. 12.1). Carpenter (1864a: 646) correctly recognised Reeve as the author of the name and stated that the species was from Hawaii. Similarly, White & Dayrat (2012: 61) indicated the distribution to be 'very likely Hawaii'. Suter's (1913: 599) reference to 'Hutt.' as author of the name is likely in error for 'Nutt[all]'. Suter (1909b: 258, 1913: 599) reported *S. amara* from 'New Guinea', which is considered incorrect and stated that it 'is also a near relation of *S. cookiana'* (= *S. propria* Jenkins, 1983) from NZ, which is also not accepted herein. Hubendick's (1946: 66–67) included *S. amara* in the list of *nomina nuda* due to uncertainty of type locality (California or Hawaii ?), but it is not a *nomen nudum*. Examination of the holotype of *S. amara* (NHMUK 1981016 revealed some similarly with *S. waikoloaensis* **sp. nov.** from Hawaii. However, the external surface is more uneven, and the ribbing appears significantly broader, projecting at edge. The siphonal ridge is less prominent in *S. amara*.

Siphonaria coreensis A. Adams & Reeve, 1850

Siphonaria coreensis A. Adams & Reeve 1850: 69, pl. 13, fig. 1a, b (type locality: 'Corean Archipelago' [Korean Archipelago]).—H. Adams & A. Adams 1855 (in 1853–58): 271; Hanley 1858b: 151, A. Adams 1863: 271; Paetel 1873: 117, 1883: 178, 1889: 428; Pilsbry 1895: 5, 161; Kuroda & Habe 1952: 86; Cernohorsky 1972: 210; Galindo 1977: 416; White & Dayrat 2012: 62.

Taxonomic remarks. The original description, original figures and type locality provide the only indication to the identity of *S. coreensis*. No types of *S. coreensis* could be located at the UKNHM (J. Ablett, pers. comm.). The identity of the species cannot be clarified based on the original description and figures alone and remains indeterminable. The identity of this species may be resolved in the future when suitable topographic material should become available. The original figures are not of *S. sirius* (Figs 36E, F), which differs in shell morphology (i.e., multiple ribs on siphonal ridge) nor of *S. japonica* (Figs 7A–E), which differs in shell geometry. Subsequently, Reeve (1856) listed *S. coreensis* as a synonym of *S. atra*. However, Reeve's description and figure are based on a misidentification and herein attributed to *S. sirius* (Figs 36E0F). Lischke (1871: 105) and Cernohorsky (1972: 210) followed Reeve's treatment as a synonym of *S. atra*.

Nomina dubia

Siphonaria alternicosta Potiez & Michaud, 1838

Siphonaria alternicosta Potiez & Michaud 1838 [in 1838–1844]: 55, pl. 10, figs 18–20 (no type locality).—Menke 1844: 54; Catlow & Reeve 1845: 100; Jay 1850: 104; White & Dayrat 2012: 60.

Siphonaria alternicostata Hanley 1858b: 151.—Paetel 1889: 427 (invalid; incorrect subsequent spelling of *alternicosta*).

Taxonomic remarks. The original description and original figure as the only indication to the identity of *S. alternicosta* provide insufficient information to identify this species. No type specimen(s) are known to exist (Philippe Bouchet; pers. comm.). Menke (1844: 54) considered *S. alternicosta* (incorrectly attributed to Quoy & Gaimard) as an accepted species occurring on the W coast of Australia. The original figure resembles *S. restis* **sp. nov.** from WA somewhat, but this similarity is not considered taxonomically significant. We consider *S. alternicosta* as a *nomen dubium*.

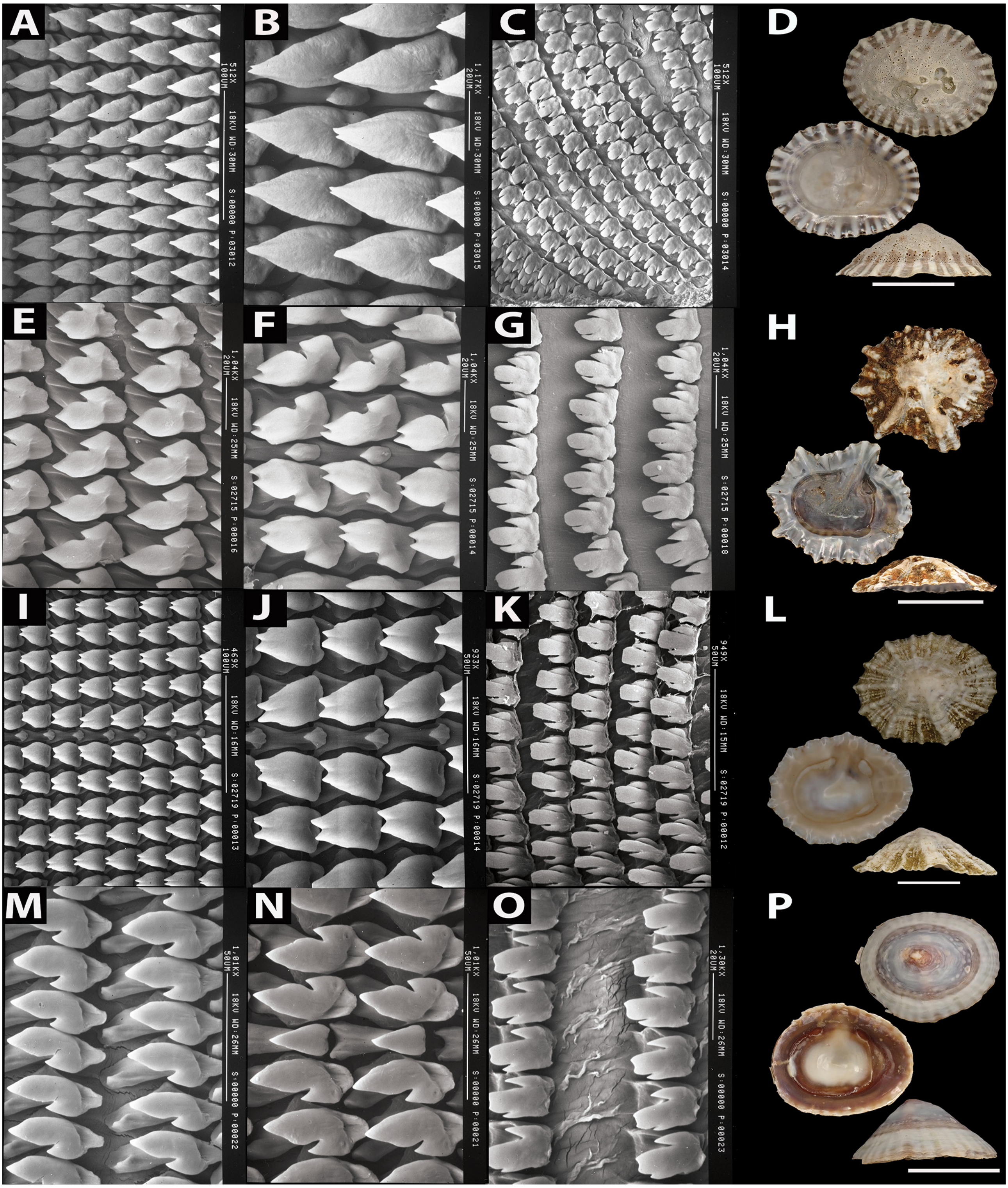

FIGURE 83. Radula morphology of *S. diemenensis*, *S. denticulata*, *S. restis* **sp. nov.** and *S. tasmanica*. **A–D.** *S. diemenensis*, Tas, Recherche Bay, AM C.201772. **A**. Inner central area x256. **B.** central area x585. **C.** Outer laterals x256. **D.** Shell. **E–H.** *S. denticulata*, NSW, Sydney, AM C.315783 x520. **E.** Inner central area. **F.** Central area. **G.** Outer laterals. **H.** Shell. **I–L.** *S. restis* **sp. nov.** WA, Rottnest Is, AM C.320123. **I**. Inner central area x234. **J.** Central area x466. **K.** Outer laterals x466. **L.** Shell. **M–P.** *S. tasmanica*, Tas, Eaglehawk Neck, AM C.311615. **M**. Inner central area x505. **N.** Central area x505. **O.** Outer laterals x650. **P.** Shell. Unlabelled scale bars 1 mm.

Siphonaria laciniosa **(Linnaeus, 1758)**

(Fig. 84A)

Patella laciniosa Linnaeus 1758: 781 (type locality: 'Habitat in India').—Linneaus 1767: 1258.

Taxonomic remarks. Utter confusion exists regarding the existence of a possible type specimen, the type locality, and the identity of *S. laciniosa*. Linnaeus (1758: 781) provided a brief description ('ribs raised unequal, the darker outwardly blunted') and a type locality ('India') referring to figures in pre-Linnean works, such as Rumphius (1705: 121, pl. 40, fig. C, 1711: 8, 1741: 121; pl. 40, fig. C) and D'Argenville (1757: 184, pl. 2, fig. O). The shells depicted in both works are of the '*atra* group'. Linnaeus (1767: 1258) and Gmelin (1791: 3695) expanded the original description and stated that *P. laciniosa* 'lives in Indian seas' (translation), re-citing the engravings of Rumphius and D'Argenville but adding references to Knorr (1789: 11, pl. 30, figs 2–4, 7–8), showing patellids but not siphonariids, and Martini & Chemnitz (1769 [in 1769–1829]: pl. 10, fig. 81), showing a modified copy of Rumphius' (1705: 121) engravings. We conclude that Linneaus was uncertain of the identity of *P. laciniosa* and how it related to shells described by pre-Linnean authors as these represented different species.

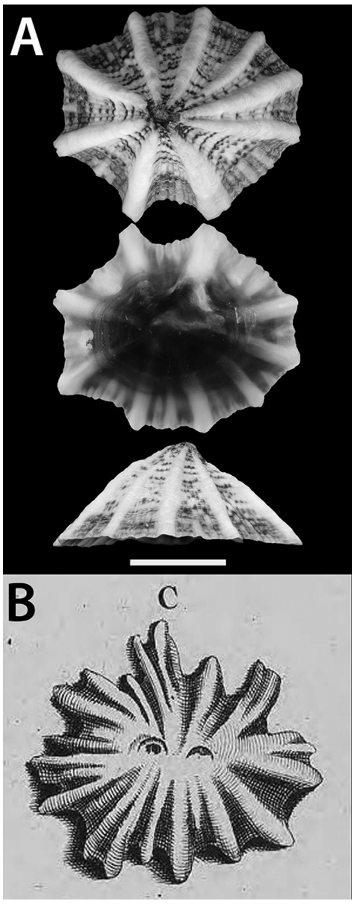

FIGURE 84. *Siphonaria laciniosa.* **A.** Alleged holotype of *Patella laciniosa* UUZM # 912. **B.** Reproduction of 'the two-eyed spotted species' in Rumphius (1705: pl. 40, fig. C).

The alleged type specimen of *Patella laciniosa* Linneaus, 1758: 781 UUZM # 912 (specimen label without locality and provenance; Fig. 84A) has been accessioned by the UUZM with the following information: "Protologue: 1758: 781. Donation: Gustav IV Adolf. Preparation: dry. Swartz label: *laciniosa*". It is a shell of the '*laciniosa* group' and clearly a distinct from the species figured by Rumphius' as 'two-eyed spotted species', which is of the '*atra* group' (Fig. 6N).

Dillwyn (1817: 1021) and Hanley (1855: 417) opined that the name *P. laciniosa* was essentially based on the figure of Rumphius (1705–1741). This would mean that the UMMZ specimen cannot be a type. Hanley (1855) was uncertain of the identity of the shell figured in Rumphius (1741). According to Sherborn (1940), Benthem Jutting (1959) and Dance (1967), most of Rumphius' specimens have been lost. We could not trace any information on a specimen of '*Patella tertia*' or 'two-eyed spotted' figured by Rumphius (1741). It is possible, perhaps even likely, that Rumphius' depicted a shell from Indonesia. Dillwyn (1817: 1021) stated that the species 'inhabits the coasts of Amboyna' [Ambon, Indonesia]. This might be the type locality of *P. laciniosa* if Linneaus's statement on the origin of this species was a reference to Rumphius. Morrison (1972: 58) suggested that the 'Eye spots' are likely due to erosion of the shell apex, a feature confirmed herein to be commonly observed in species of the '*atra* group'. Hubendick's (1946) was the first to attribute type status to the UUMZ specimen mentioned above. Hubendick (1946: 48) stated that 'the type of *S. laciniosa* is in the keeping of the Zool. Mus., Uppsala', but confusingly identified it as a specimen of *S. laciniosa* forma *exigua* referring to a name introduced by Sowerby I, 1823. Subsequently, Dance (1967: 80) stated that no type specimen of *P. laciniosa* was found in the Linnaean collection and considered it to be lost. However, according to Odhner (1954: 26) and Wallin (2001: 89) there is a type of *P. laciniosa* in the UUZM catalogue of Linnaean type specimens.

The identity of this alleged type of *P. laciniosa* cannot be ascertained. It is likely a siphonariid of the '*laciniosa* group', but its features are insufficient to identify this species. Moreover, the generic type locality 'India' may refer to any place in the Tropical parts of the Indian Ocean, including the Indonesian archipelago and is too vague to allow to narrow the selection down to a single species.

Morrison (1972) considered Hubendick's claim of a type specimen as an invalid type designation stating that 'Linne didn't indicate that he had ever seen a specimen up to 1767'. Alternatively, Morrison (1972: 58) designated the non-binomial 'the two-eyed spotted species' figure in Rumphius (1705: 125, pl. 40, fig. C; Fig. 84B) as 'the type of *laciniosa*'. This type designation has subsequently been accepted by Christiaens (1980a: 78). However, Hubendick's and Morrison's type concepts are irreconcilable with each other contributing to the confusion around this name. If we accept Hubendick's claim that the UMMZ specimen is the type, then *S. laciniosa* is an unidentifiable species in the '*laciniosa* group' and distinct from the species depicted by Rumphius. However, if we accept Morrison's view, then *S. laciniosa* is an unidentifiable species of the '*atra* group' possibly from Indonesia.

We are of the view that the ambiguity surrounding this name cannot be resolved without a ruling of the commission and therefore we treat the name *P. laciniosa* herein as a *nomen dubium*. This name has been used throughout the body of taxonomic literature, but because of the ambiguity surrounding its identity, subsequent uses invariably were hypothetical and often contradictory. The earliest taxonomists effectively reiterated the name referring to the original description of Linnaeus (1758: 380) without contributing any clarification of the original concept (e.g., Schröter 1784: 403; Röding 1798: 5; Roissy 1805: 214; Dillwyn 1817: 1021; Lamarck 1819: 325; Sowerby I 1825: 29; Hanley 1855: 417). Pilsbry (1892 [in 1891–1892]: 160) listed *P. laciniosa* as 'unidentified Patellidae ...possibly = *P. stellaeformis*'. Eventually, Hubendick (1946: 47) transferred the species to *Siphonaria* based on examination of the probable type. However, his delimitation of the species is speculative and not accepted herein. Specimens identified as '*S. laciniosa'* by Hubendick (1946: 47) are not from the type locality and many examples comprise mixed lots.

Siphonaria sowerbyi Michelin, 1832

Siphonaria sowerbyi Michelin 1832: unpaginated, pl. 17 (without type locality).—Anton 1838: 26; Hanley 1858b: 152; Paetel 1889: 429; Hubendick 1946: 69; White & Dayrat 2012: 68.

Taxonomic remarks. The original description and original figure of Michelin (1832) do not provide enough detail to resolve the identity of this species. No type specimen(s) are known to exist (Philippe Bouchet; pers. comm.). While the original figure in Michelin (1832: pl. 17) matches the features of the *atra* group, particularly that of *S. atra* and *S. alba,* this species remains indeterminable. Hubendick (1946: 69) incorrectly rejected *S. sowerbyi* as a *nomen nudum* (followed by White & Dayrat, 2012: 68). Morrison (1972: 56–58) treated *S. sowerbyi* Michelin, 1832, *S. sowerbyi* Guerin, 1832 and *S. sowerbyi* Michelin,1868 as synonyms of *S. laciniosa* based on similarity in shell form and 'common reproductive development'. These synonymies are not accepted here. This nominal species remains a *nomen dubium*.

Siphonaria stellata (Helbling, 1779)

Patella stellata Helbling 1779: 109, pl. 1, fig. 11 (without type locality).—Satyamurti 1952: 252, pl. 34, fig. 2a, b.
Siphonaria stellata—Martens 1868: 235; Nagabhushanam & Krishnan 1993: 480; White & Dayrat 2012: 68.

Taxonomic remarks. The original description and original figure provide the only indication for the identity of *S. stellata* (Helbling, 1779). No type specimen(s) are known to exist. Martens (1868: 235) transferred *Patella stellata* Helbling, 1779 to *Siphonaria,* indicating that *S. exigua* Sowerby was the 'best' name reversing the priority. This transfer to *Siphonaria* rendered *S. stellata* Blainville, 1827 as a junior secondary homonym (Art. 57.3; White & Dayrat, 2010: 68). Examination of Helbling's figure (1779) reveals a shell that resembles specimens from Hawaii (e.g., *S. waikoloaensis* **sp. nov.**, Figs 72D–F; *S. mauiensis* **sp. nov.**, Figs 56G–I) or Mauritius (e.g., *S. incerta*; Figs 35H–L) and is unlike the shell of *S. exigua* (Fig. 3J). The identity of *S. stellata* is currently unknown and there is no prospect of clarifying its identity based on the original description alone. The use of the name *S. stellata* (Helbling) for material from the Bay of Bengal in Nagabhushanam & Krishnan (1993: 480) is therefore questionable. We consider this taxon as a *nomen dubium*.

Invalid or unavailable species names

Siphonaria stellata Blainville, 1827

This species was described by Blainville (1827: 297) and attributed to 'de Roissy' from an unknown origin. It is a secondary junior homonym of *Patella stellata* Helbling, 1779 and therefore invalid (Art. 57.3 of the Code). The name has subsequently been referred to by Hanley (1858b: 153) and Paetel (1889: 429). Hubendick (1946: 48) and Morrison (1972: 56) treated it as a junior synonym. The listing of *S. stellata* in Adcock (1893: 11) as a synonym of *S. luzonica* (from SA, Australia; misidentified *S. zelandica*) is incorrect and a reversal of priority. Figures of '*S. stellata*' RS in Hubendick (1945: figs 42, 53) are here attributed to *S. javanica* Figs 6H, I. Shells of '*S. stellata'* figured in Hubendick (1946: 91, pl. 3, fig. 20–23) are of various accepted species, such as *S. viridis* (fig. 20 from Thursday Island, fig. 22 from WA) and *S. javanica* (fig. 21 from Mindanao, fig. 23 from Java). A shell figured in Satyamurti (1952: 252, pl. 34, fig. 2a, b) resembles Helbling's figure of *P. stellata*. Morrison (1972: 56–58) treated *S. stellata* Blainville 1827 along with 29 other nominal species as a synonym of *S. laciniosa*. The identity of *S. stellata* listed in Ravenish & Biju Kumar (2015: 38) is unknown (unfigured, no reference specimens).

Siphonaria crebricostata Jay, 1839

Introduced by Jay (1839: 39) as a *nomen nudum* and attributed to Nuttall without description this is an unavailable name (Art. 12.1 of the Code; see also White & Dayrat, 2012: 62). It was listed as a synonym and therefore not made available subsequently by Catlow & Reeve (1845: 100), Jay (1850: 104), Reeve (1856: pl. 2, species 9), Paetel (1873: 117, 1875: 92, 1883: 178, 1889: 428), Pilsbry (1920b: 379), Schrenck (1867: 306), Hutton (1880: 36), and Hubendick (1946: 47). Galindo (1977: 416) misspelled the name as '*crebicostata*'. *Siphonaria crebidentata* Smith in Galindo (1977: 416) is a separate emendation referring to this *nomen nudum*. Because *S. crebricosta* is not an available name, the lectotype designation by Baker (1964: 159) is also invalid (Art. 74.2 and 5 of the Code).

Siphonaria stella Jay, 1839
Introduced by Jay (1839: 39) as a *nomen nudum* and attributed to Petit without description and unfigured this is an unavailable name (Art. 12.1 of the Code). It was not made available subsequently by Catlow & Reeve (1845: 100), Paetel (1889: 429), Hubendick (1946: 69) nor White & Dayrat (2012: 62).

Siphonaria costata Hombron & Jacquinot, 1841
Described from Otago (Tavaï-Pounamou, Nouvelle-Zélande) [New Zealand] without figure by Hombron & Jacquinot (1841: 192), this name is a primary junior homonym of *S. costata* Sowerby, 1835 and permanently invalid (Art. 52.2 of the Code).

Siphonaria sowerbyi H. Adams & A. Adams, 1855
Introduced by H. Adams & A. Adams (1855 [in 1853–1858]: 271) as a replacement name for *S. radiata* Sowerby I, 1835, this name is permanently invalid as it is an objective junior homonym of *S. sowerbyi* Michelin, 1832 (Art. 52.2 of the Code).

Siphonaria laciniata Paetel, 1873
Introduced by Paetel (1873: 117) as a *nomen nudum* without description and attributed to Dunker this is an unavailable name (Art. 12.1 of the Code). Not made available subsequently by Paetel (1883: 178, 1889: 428). It remains an unavailable name. Hubendick (1946: 68) suggested it may be a misspelling of *S. laciniosa*.

Siphonaria godeffroyi Paetel, 1873
Introduced by Paetel (1873: 117) as a *nomen nudum* without description and incorrectly attributed to Crosse this is an unavailable name (Art. 12.1 of the Code). It has not been made available subsequently by Paetel (1883: 178, 1889: 428).

Siphonaria punctulata Paetel, 1889
Introduced by Paetel (1889: 429) as a *nomen nudum* without description and incorrectly attributed to 'Quoy' (= Quoy and Gaimard, 1833), this is likely an incorrect subsequent spelling of *S. punctata.* However, Paetel (1889: 429) separately listed *S. punctata*.

Siphonaria alternata var. _intermedia_ Davis, 1904
Introduced by Davis (1904: 127) as a variety of *S. alternata* (Say, 1827), the name is an objective junior homonym of *S. sipho intermedia* Schrenck, 1867 and permanently invalid (Art. 57.2 of the Code).

Parellsiphon commixtus Iredale, 1940
Parellsiphon commixtus was introduced by Iredale (1940: 437 as a *nomen nudum* without description (Art. 13.1 of the Code). The name was not made available subsequently by Morrison (1972: 57; no description) nor White & Dayrat (2012: 61; not intentionally declared as new, Art. 86.2 of the Code). It remains an unavailable name.

Legosiphon mulinus Iredale, 1940
Legosiphon mulinus was introduced by Iredale (1940: 437) as a *nomen nudum* without description (Art. 13.1 of the Code). The features mentioned refer to *Legosiphon*. We have not found any subsequent usage of this name. It remains an unavailable name.

Mestosiphon parmelas Iredale, 1940
Mestosiphon parmelas was introduced by Iredale (1940: 437) as a *nomen nudum* without description (Art. 13.1 of the Code). It was not made available subsequently by Cernohorsky (1972: 210; synonym of *S. atra*), Morrison (1972: 57; no description) nor Short & Potter (1987: 122). It remains an unavailable name.

Siphonaria crebidentata Galindo, 1977
Siphonaria crebridentata was introduced by Galindo (1977: 437) and attributed to Smith as a *nomen nudum* without description (Art. 13.1 of the Code). The name was not used again subsequently and remains an unavailable name.

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Disclosure statement

The authors declare no potential conflicts of interest.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper: Supplemental Tables S1–S9.