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How many *Siphonaria* species (Gastropoda: Euthyneura) live in southern South America?

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ABSTRACT

This contribution provides the first integrative revision of the *Siphonaria* species described and reported from southern South America, by combining information on shell morphology, distal portion of the genital system, radula, molecular data and living animal. More than 200 lots, from all along the Uruguayan, Argentinean and southern Chilean coasts, including the Malvinas (Falkland) Islands and South Georgia, were studied. Among the nine nominal species listed for this area, only the presence of *Siphonaria lessonii* Blainville, 1827 and *S. lateralis* Gould, 1846 could be confirmed. The intraspecific variability of these two species along their distributional ranges is examined. *Siphonaria magellanica* Philippi, 1855 and *S. antarctica* Gould, 1852 are regarded as probable synonyms of *S. lessonii*. The Magellanic records of *S. tristensis* are reassigned to *S. lessonii* and those of *S. macgillivrayi* to *S. fuegiensis* n. sp. The similarity of *S. redimiculum* Reeve, 1856, *S. laeviuscula* Sowerby, 1835 and *S. lineolata* Sowerby, 1835 to the three species confirmed in the studied area is discussed. The Chilean *S. laevis* Philippi, 1846 is considered a *nomen dubium*. All available types are figured and a lectotype is designated for *S. redimiculum*.

INTRODUCTION

The Siphonariidae are pulmonate limpets, typically living on hard substrates in intertidal habitats. In South America the family appears to be represented by the genera *Siphonaria* and *Williamia*, the former being the more species-rich, with a total of nine nominal species listed for the southernmost part of South America (i.e. the Argentinean and Magellanic biogeographic provinces). The first species of *Siphonaria* described from this area was *S. lessonii* Blainville, 1827 from the Malvinas (Falkland) Islands. Subsequently, Sowerby (1835) described *S. lineolata* and *S. laeviuscula* from Chilean waters; Gould (1848) described *S. lateralis* from Cape Horn and Philippi (1855) a species from the Chilean coast, *S. magellanica*. Four other species, *S. tristensis* Sowerby, 1823, *S. concinna* Sowerby, 1823, *S. antarctica* Gould, 1852 and *S. redimiculum* Reeve, 1856, all with unknown type localities, have been regarded as living in southern South America (Strebel, 1907; Hubendick, 1945, 1946; Olivier & Penchaszadeh, 1968). *Siphonaria macgillivrayi* Reeve, 1856, described from 'Island of St. Paul's' (Indian Ocean) was also listed for this area (Hubendick, 1945, 1946; Olivier & Penchaszadeh, 1968). Most of these species were not reported again after their original description, and a number of misidentifications and confusing synonymies concerning these taxa appear in the literature. In this regard, Rochebrune & Mabille (1889) identified specimens from Cape Horn as *S. redemiculum* (sic), which were subsequently reassigned to *S. lateralis* by Suter (1913). Strebel (1907), Hubendick (1946) and Dell (1964) regarded *S. redimiculum* as a synonym of *S. lateralis*. However, this synonymy is not in agreement with Iredale's (1915) opinion, as he regarded both *S. redimiculum* and *S. lateralis* as distinct species (with *S. redimiculum*, *S. macgillivrayi* and *S. tristensis* as 'geographic races' of a single species). Reeve (1856), Dall (1870) and Strebel (1907) considered *S. lessonii* to be a synonym of *S. tristensis*, and d'Orbigny (1841) regarded *S. laeviuscula* as a synonym of *S. lessonii*. However, Hubendick (1945, 1946) concluded that *S. lessonii*, *S. tristensis* and *S. laeviuscula* are distinct species, the former including as synonyms *S. laevis* Philippi, 1846 and *S. tenuis* Philippi, 1860, both species described from the Chilean coast.

The last comprehensive study of South American siphonariids was by Hubendick (1946), who recognized three valid species for the area: *S. lessonii*, *S. lateralis* and *S. macgillivrayi*. However, a proper description and illustration of these species and their intraspecific variability is still lacking, thus making it difficult (if not impossible) to recognize these species unequivocally. Further uncertainty arises from a recent comprehensive molecular phylogeny of the Indo-West Pacific species of *Siphonaria* (Dayrat, Goulding & White, 2014), which mentioned the existence of two cryptic species within '*S. lateralis*' in southern South America.

The aims of this contribution are to describe the morphological and anatomical variability of *S. lessonii* and *S. lateralis*, to describe a new species from southern South America, and to re-evaluate the similarities of these three taxa with the other siphonariids described or reported from this area.

MATERIAL AND METHODS

The study area comprises the southern part of South America, from 41°43′S (Chile) on the Pacific coast, southwards to Tierra del Fuego, the Beagle Channel, Magellan Strait, the Malvinas (Falkland) and South Georgia Islands, and northwards to 33°56′S (Uruguay) on the Atlantic coast (Fig. 10C).

South American siphonariids have been previously referred to *Siphonaria*, *Pachysiphonaria*, *Kerguelenella* (replacement name for *Kerguelenia* Mabille & Rochebrune, 1889 not Stebbing, 1888) or *Liriola*, variously regarded as genera, subgenera or ‘sections’ (Hubendick, 1945, 1946; Dell, 1964; Olivier & Penchaszadeh, 1968; Aldea & Rosenfeld, 2011). In the present contribution we use *Siphonaria* for all considered species, following White & Dayrat (2012) and Dayrat *et al.* (2014).

The synonymy provided for each species includes the original description and subsequent descriptions (by the same or other authors) for which it was possible to confirm the identity of the species. These lists are restricted to records from the studied area.

Material studied

The material for this study comes mainly from hand-collected specimens obtained during several field trips in the Magellanic and Argentinean provinces (Fig. 10C; localities listed in Supplementary Material). Additional specimens come from the collections of Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires (MACN); Museo de La Plata (MLP); Museo de Zoología de la Universidad de Concepción (MZUC); Natural History Museum of Los Angeles County (LACM); Natural History Museum, London (NHMUK); Zoologisches Museum Hamburg (ZMH) and Museo Nacional de Historia Natural, Montevideo (MNHNM). All available types of the species described or reported from the area, housed at NHMUK; Muséum National d’Histoire Naturelle, Paris (MNHN); Museo Nacional de Historia Natural, Santiago (MNHN-CH); National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and the Museum of Comparative Zoology, Harvard (MCZ), were studied. The number of specimen(s) [sp(s).] and shells (s.) of each lot is indicated in the Material examined sections (see Supplementary Material, S1–3 for locality details). Measurements are shell length (L).

Morphological studies

Small specimens, radulae and jaws were studied and illustrated with scanning electron microscopy (SEM); larger specimens were studied and illustrated under stereoscopic light microscope. The radula was examined in 29 specimens of *S. lessonii*, 12 of *S. fuegiensis* n. sp. and 10 of *S. lateralis*, including specimens from the whole range of distribution, of morphological variation and of size.

Anatomical studies

Gross anatomical information was obtained from 10 specimens of each species decalcified by rinsing in a 10% solution of formalin and 5% acetic acid. Histological studies were performed on the distal portion of the reproductive system of five specimens of each species. Dissected parts were fixed in Bouin’s solution and embedded in Historesin® Leica™. Sections, 5 μm thick, were prepared with a Leica RM2255 motorized microtome and stained with Gill’s haematoxylin and eosin (Gabe, 1968).

Molecular studies

Considering the results of Dayrat *et al.* (2014), the cytochrome *c* oxidase subunit I mitochondrial gene (COI) was selected as an adequate marker to test the discrimination of the studied taxa. DNA was extracted from foot muscle by means of a CTAB-chloroform protocol. Universal primers (Folmer *et al.*, 1994) were used for amplification of COI. Amplified products were sent out individually for forward and reverse sequencing and subsequently assembled. Alignments were obtained using Clustal W in MEGA v. 5.0 (Tamura *et al.*, 2007) and refined manually to increase positional homology. The ends of the sequences were trimmed to yield a 671 bp alignment.

A haplotype network was reconstructed by the median-joining method (Bandelt, Forster & Röhl, 1999) implemented in NETWORK v. 4.612 (available at http://www.fluxus-engineering.com/sharenet.htm). Subsequently, sequences representing every haplotype from each sampled locality were selected to perform the phylogenetic analyses. Information on vouchers, haplotypes per locality and GenBank accession numbers are provided in Supplementary Material (Table S5). Based on the phylogeny of Dayrat *et al.* (2014), sequences of *Trimusculus reticulatus* (Sowerby I, 1835), *S. funiculata* Reeve, 1856, *S. japonica* (Donovan, 1824) and *S. pectinata* (Linnaeus, 1758) were included in the analyses (GenBank acc. nos: HQ660001, JX680959, HQ659999 and HQ386654, respectively). Prior to maximum likelihood (ML) and Bayesian phylogenetic analyses, the best-fitting evolutionary model (TPM2uf + G) was selected using Modeltest v. 3.7 (Posada & Crandall, 1998). ML analysis was performed using PhyML (Guindon *et al.*, 2010) and node support was evaluated using 1,000 bootstrap (BS) replicates. Analysis by Bayesian inference (BI) was performed using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck, 2003) with four simultaneous runs of 100 generations each, a sample frequency of 100 and burn-in of 10%. *Trimusculus reticulatus* was selected as outgroup for BI. Posterior probabilities (PP) were used to evaluate node support.

SYSTEMATIC DESCRIPTIONS

***Siphonaria* Sowerby, 1823**

***Siphonaria lessonii* Blainville, 1827**

(Figs 1, 2A–C, 3A–F, 4)

Siphonaria lessonii Blainville, 1827a: pl. 44, figs 2, 2a (Îles Malouines; 4 syntypes MNHN 5091; Fig. 1A). Blainville, 1827b: 296. d’Orbigny 1839: pl. 56, figs 12–14. d’Orbigny, 1841: 469. Gould, 1852: 91, fig. 463, a, b. Carcelles, 1935: 7, textfig. Carcelles, 1944: 265, pl. 5, fig. 51. Hubendick, 1945: 12; 1946: 21, pl. 1, figs 1–3. Carcelles, 1950: 72, pl. 3, fig. 60. Olivier & Penchaszadeh, 1968. Bastida, Capezzani & Torti, 1971. Figueiras & Sicardi, 1974: 341, pl. 19, fig. 254. Scarabino, 1977: 196, pl. 2, fig. 12. Rios, Noziglia & Guzmán, 1987: 77. Ageitos de Castellanos, Landoni & Dadon, 1993: 23, fig. 35A–C. Rios, 1994: 223, pl. 77, fig. 1101. Tablado, López Gappa & Magaldi, 1994. Pastorino, 1995: 11, pl. 2, fig. 15a–c. Reid & Osorio, 2000: 128, fig. 4G, H. Tablado & López Gappa, 2001. Scarabino & Zaffaroni, 2004: 7. Aldea & Rosenfeld, 2011: 121, fig. 5H, I. Dayrat *et al.*, 2014: 266, fig. 3K.

Pachysiphonaria lessonii—Ageitos de Castellanos, 1967: 159, pl. 1, fig. 9.

Siphonaria antarctica ‘Couthouy’ Gould, 1852: 362 (no locality; 3 syntypes MCZ 216830 and 216745, currently labelled “Orange Bay, Tierra del Fuego”; Fig. 1B). Gould, 1860: pl. 30, fig. 464, a, b.

Siphonaria concinna—Hupé, 1854: 249. Plate, 1894: 222 (both not Sowerby, 1823).

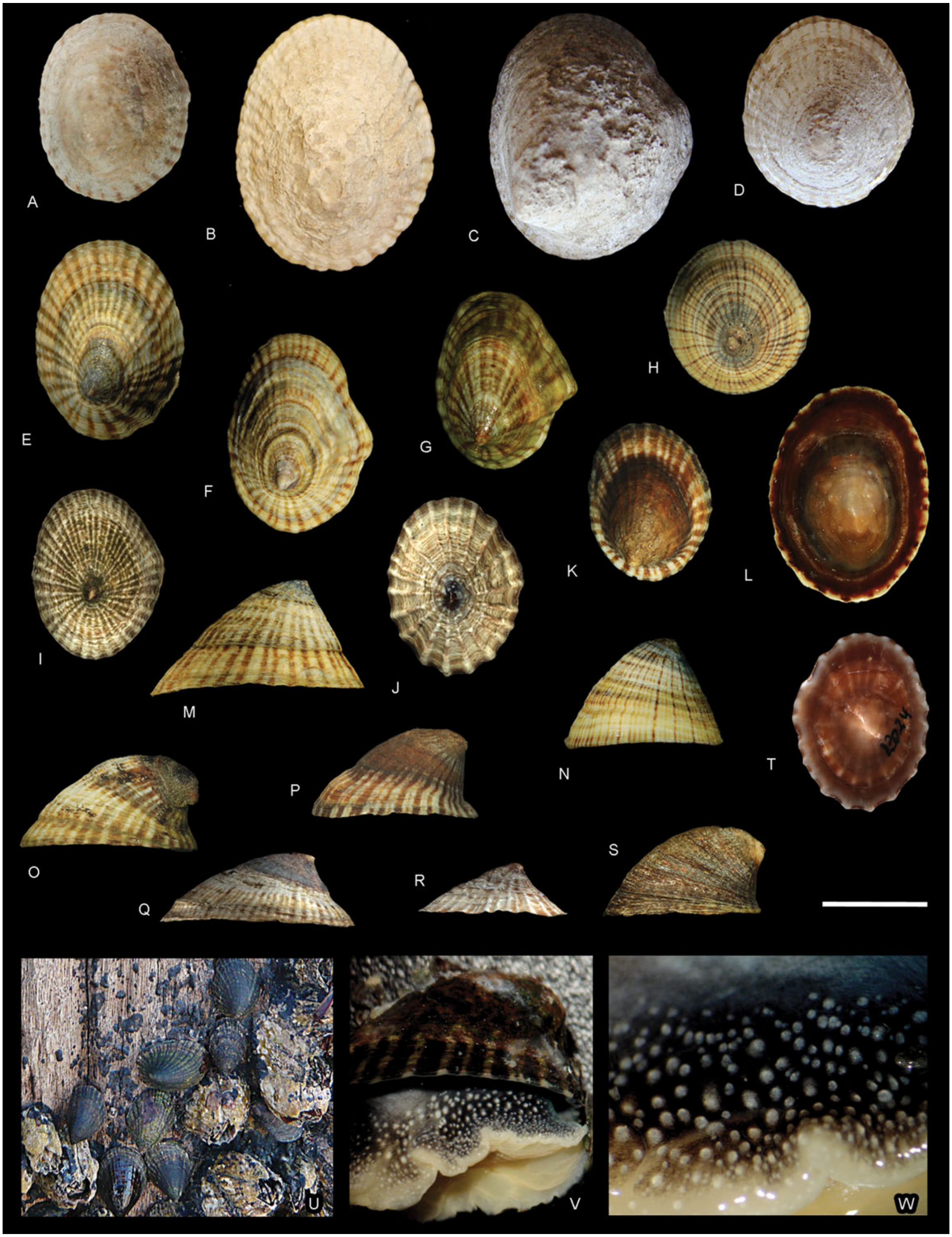

Figure 1. *Siphonaria lessonii*: morphology. **A.** *S. lessonii*, syntype (MNHN 5091). **B.** *S. antarctica*, syntype (MCZ 216830). **C, D.** *S. magellanica*, syntypes (MNHN-CH unnumbered). **E, F, L, M.** Punta Frías (MNHNM 19946). **G, S.** Puerto Lobos (MACN-In 40119). **H, N.** Isla Lilihuapi (MZUC). **I, J.** Puerto Quequén (MACN-In 13024). **K, P**. Isla Navarino (MZUC). **O.** Mar del Plata (MACN-In 40112). **Q, R.** Puerto Harris (MACN-In 12429). **A–K.** Dorsal views. **L, T.** Ventral views. **M–S.** Lateral views. **U–W.** Living animals. **U**. La Lucila del Mar, on dock piling. **V, W**. Details of foot papillae; Puerto Deseado. Scale bar: **A–T** = 1 cm.

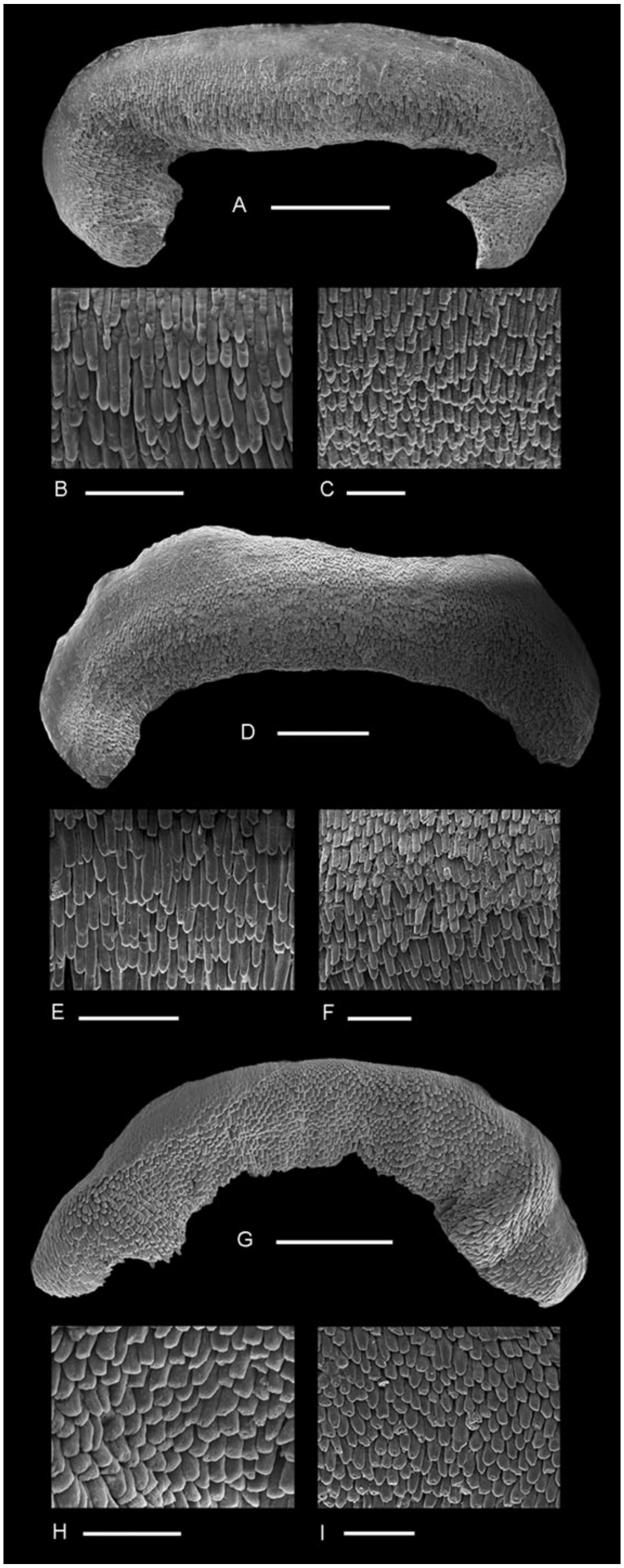

Figure 2. Jaws. **A–C.** *Siphonaria lessonii*. **A.** Jaw. **B, C.** Detail of jaw. **D–F.** *Siphonaria lateralis*. **D.** Jaw. **E, F.** Detail of jaw. **G–I.** *Siphonaria fuegiensis* n. sp. **G.** Jaw. **H, I.** Detail of jaw. **A–C.** Puerto Deseado (MACN-In 40125). **D–F.** Puerto Deseado (MACN-In 40131). **G–I.** Bahía Golondrina (MACN-In 40129). Scale bars: **A, D, G** = 200 μm; **B, C, E, F, H, I** = 50 μm.

Siphonaria magellanica Philippi, 1855: 207, 208 (colonia de Magallanes [Magellan Strait]; 6 syntypes MNHN-CH unnumbered; Fig. 1C, D). Philippi, 1856a: 100. Philippi, 1856b: 163, 165.

Siphonaria tristensis—Reeve, 1856: sp. 23, fig. 23a, b. Dall, 1870: 33. Strebel, 1907: 170, pl. 3, figs 31–34 (all not Sowerby, 1823).

Kerguelenella lateralis—Figueiras & Sicardi, 1974: 342 (in part: Uruguayan records) (not Gould, 1846).

Shell (Fig. 1): Large (max. L = 32.0 mm), tall to low, nearly equilateral (i.e. outline bilaterally symmetrical), solid. Base ovate (longer than wide) to subcircular; anterior and posterior margins evenly curved; left margin widely arcuate; right margin evenly arcuate to variably projected laterally (Fig. 1A–T). Apex acute, usually eroded in larger specimens; located on posterior half of shell, usually at posterior third, not extending beyond shell base; slightly displaced towards left (Fig. 1E–K, M–S). Anterior slope convex to straight; posterior slope shorter, usually straight, sometimes concave (Fig. 1M–S). Shell sculpture: 17–37 primary radial ribs, low, straight, narrow to moderately wide, regularly distributed; crossed by low, irregular growth lines (Fig. 1E–K). Interspaces usually as wide as ribs; sometimes with intercalated (secondary) radial ribs. Siphonal ridge forming prominent to almost imperceptible keel (Fig. 1E–K). Ventral margin nearly smooth to undulating (Fig. 1L, T). Outer shell surface dark brown to pale buff, with pale ribs and dark interspaces; frequently appearing greenish due to algal growth. Usually with darker apex and commarginal bands of colour (Fig. 1E–K, M–V). Inner shell surface shiny, brown to lilac, lighter at margin, which is similar to outer colour pattern (Fig. 1L, T).

Anatomy: Jaw (Fig. 2A–C): large, arcuate, with numerous, juxtaposed, rod-like elements with rounded tips, 6.6 ± 0.8 μm wide ($n = 10$).

Radula (Fig. 3A–F, Supplementary Material, Fig. S4A–C): up to 142 tooth rows, each with rachidian tooth flanked by 13–52 lateral teeth on each side (up to 76 according to Hubendick, 1946), reducing in size outwards (Supplementary Material, Fig. S4A–C). Rachidian tooth with strong, elongate, Y-shaped base, which gradually widens posteriorly (Fig. 3A–C); cusp about one half length of base, arrow-shaped, unicuspid, sharply pointed to rounded. Lateral teeth with wide bases; cusps about one half length of base (Fig. 3A–F). First lateral teeth with mesocone only (Fig. 3A), or meso- and ectocone (Fig. 3B, C); in former case, first 8–17 lateral teeth similar in shape, with bluntly triangular, bicuspid or tricuspid mesocone (Fig. 3A) and following 5–13 lateral teeth also bearing short, pointed ectocone (Fig. 3D); in latter case, first 21–32 lateral teeth similar in shape, with simple, sharply pointed meso- and ectocone, the latter one third size of former (Fig. 3B, C, E, F). Remaining laterals with sharply pointed endocone and ectocone, of similar size (Fig. 3E, F, Supplementary Material, Fig. S4B, C); cusps from elongate to subquadrate, mesocone from bicuspid (sometimes tricuspid) to blunt outwards (Fig. 3D–F, Supplementary Material, Fig. S4B, C). Outermost lateral tooth vestigial (Supplementary Material, Fig. S4C).

Foot (Fig. 1V, W): base whitish; lateral sides light to dark grey, with white papillae in living specimens.

Distal portion of reproductive system (Fig. 4): epiphallus at side of buccal mass, slightly curved or having terminal portion strikingly recurved (Fig. 4A). Central portion of epiphallus robust, short, wide, with constriction at distal third, which separates base and terminal portion ('head'); the latter somewhat swollen (Fig. 4B, C). Epiphallus with narrow central duct, expanded in highly ramified lateral folds (Fig. 4D–G). Duct of bursa and ovispermiduct

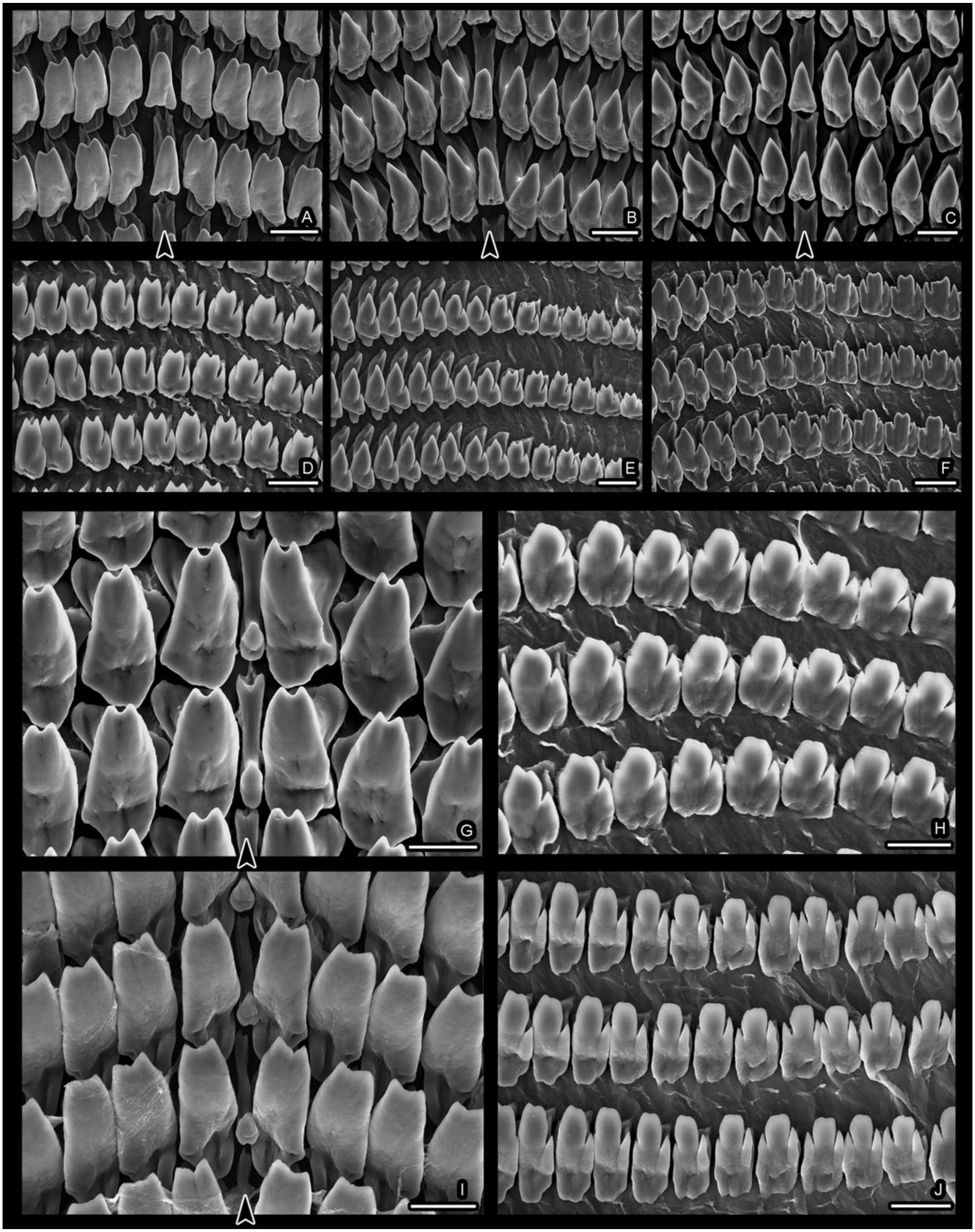

Figure 3. Details of central field of radulae. **A–F.** *Siphonaria lessonii*. **G, H.** *Siphonaria lateralis*. **I, J.** *Siphonaria fuegiensis* n. sp. **A–C, G, I.** Detail of rachidian (arrowheads) and innermost lateral teeth. **D–F, H, J.** Lateral teeth. **A.** José Ignacio (MNHNM 19945). **B, E.** Punta Cuevas (MACN-In 40120). **C, I, J.** Bahía Golondrina (MACN-In 40129). **D.** La Lucila del Mar (MACN-In 40111). **F.** Puerto Deseado (MACN-In 40125). **G, H.** Puerto Deseado (MACN-In 40131). Scale bars: **A–J** = 20 μm.

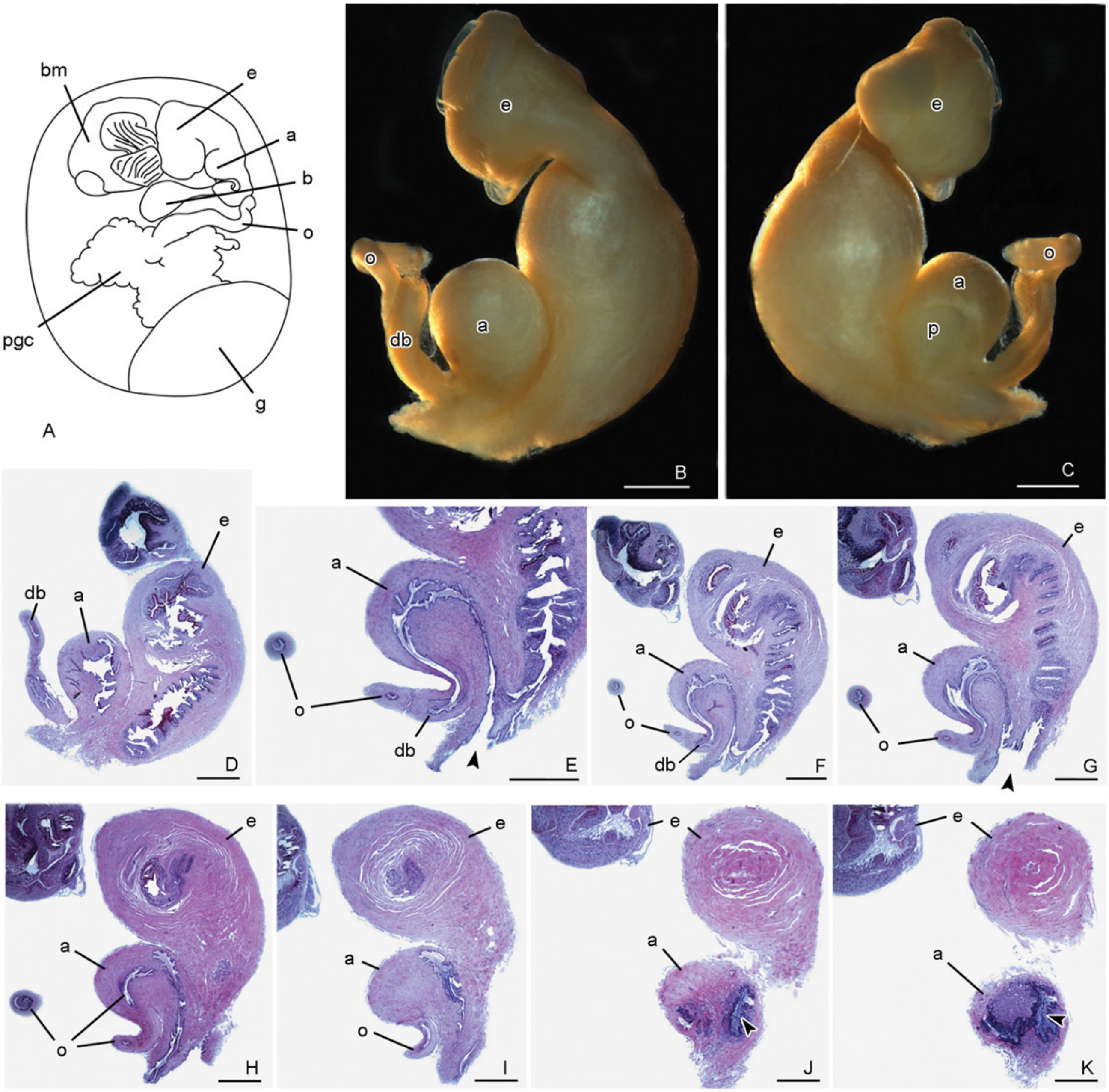

Figure 4. *Siphonaria lessonii*: anatomy. **A.** Schematic drawing showing location of reproductive system. **B, C.** Distal portion of reproductive system. **D–K.** Histological sections of distal portion of reproductive system, from dorsal to ventral side. **D.** Lumen of epiphallus, accessory organ and duct of bursa. **E.** Detail of duct of bursa entering the accessory organ (arrowhead indicates common atrium). **F, G.** Connection of accessory organ with epiphallus (arrowhead indicates common atrium). **H, I.** Ovispermiduct reaching accessory organ. **J, K.** Terminal, glandular portion of ovispermiduct in accessory organ (arrowheads). **B–K.** Specimen from Puerto Deseado. Abbreviations: a, accessory organ; b, bursa; bm, bucal mass; db, duct of bursa; e, epiphallus; g, gonad; o, ovispermiduct; p, protuberance; pgc, pallial glandular complex. Scale bars: **B–K** = 1 mm.

reaching base of epiphallus from posterior end, parallel at final portion where they reach so-called ‘accessory organ’ (*fide* Hubendick, 1945) (Fig. 4D–I); both ducts running across right shell adductor muscle. Bursa globose, variably developed according to physiological state, located behind epiphallus, transversely directed with respect to foot axis (Fig. 4A). Duct of bursa relatively short, wide, curving after entering accessory organ on its outer side (Fig. 4B, E–G), where it opens into branched system of ducts before joining atrium at base of epiphallus (Fig. 4G). Ovispermiduct thinner than duct of bursa, with strong muscular wall, bending upwards immediately after joining accessory organ at inner side (Fig. 4C, H). Within accessory organ, ovispermiduct opens into glandular branched system, appearing macroscopically as whitish ventral protuberance of accessory organ (Fig. 4C, I–K); lumen of branched glandular portion opens into folded system at terminal portion of duct of bursa. Epiphallus opening anterior to opening of duct of bursa, ending in small genital atrium (Fig. 4G). ‘Accessory organ’ varies from well-developed structure at posterior side of epiphallus (Fig. 4B, C) to nearly imperceptible swelling; cuticular stylet absent.

Geographical distribution: Rocha (Uruguay) to Cape Horn and the Malvinas (Falkland) Islands in the Atlantic Ocean, through the Beagle Channel and Magellan Strait, north to Chiloé Island (Chile) in the Pacific Ocean (Supplementary Material S1). Published references extend the distributional range of this species to Santa Catarina, Brazil, in the Atlantic Ocean (Rios, 1994) and to Paita, Perú, in the Pacific (Morrison, 1963), with an additional report from Nicaragua (Dall, 1909); however, these records require confirmation (see Remarks).

Remarks: Siphonaria lessonii shows marked variability in shell morphology, terminal portion of the reproductive system and the radula. Variation in shell morphology has been previously associated with population parameters (e.g. density), environmental characteristics (e.g. substrate, wave exposure and level of organic matter) (Olivier & Penchaszadeh, 1968; Tablado & López Gappa, 2001) and geographic location (d'Orbigny, 1841). In the present study different morphological variants have been found within a single locality. Tablado, López Gappa & Magaldi (1994) reported that shell morphology can be modified by translocation of specimens.

Specimens with a well-developed to almost imperceptible 'accessory organ' were observed among specimens from a single locality, sampled on the same date. Such variability was also reported by Hubendick (1945).

Previous studies have suggested that the radula varies not only in the number of lateral teeth (Olivier & Penchaszadeh, 1968), but also in the presence or absence of ectocones on the innermost laterals. Hubendick (1946) described the absence of ectocones as the 'common' condition for the species, mentioning their presence in only one of the specimens he studied. In contrast, Olivier & Penchaszadeh (1968) described the presence of ectocones in specimens from Mar del Plata (38°S), although these elements were absent in the specimens that we studied from the same locality. We also found individuals with and without ectocones on the innermost laterals in Punta Cuevas (42°S), Bahía Buen Suceso (54°S) and Bahía Golondrina (54°S). In addition, a specimen from El Sótano (40°S) and two from Punta Cuevas (42°S) showed vestigial ectocones. The presence or absence of ectocones and their degree of development was found to be similar all along the radula of each individual, and was not related to the size of the specimens. Another variable radular character is the morphology of the mesocones of the innermost laterals, which may be unicuspid, bicuspid or tricuspid. This variability was found among specimens from the same locality, and sometimes appeared among different rows or even when comparing left and right sides of a single radula.

Siphonaria antarctica (Fig. 1B) was originally distinguished from *S. lessonii* by having a more oblong foot, the head somewhat shorter and broader, and more widely separated eyes (Gould, 1852). These supposed differences are subtle, varying according to the shape and degree of retraction of the specimens. In fact, although the position of the eyes appears as a difference in Gould's (1860) dorsal views in his figures 463b (*S. lessonii*) *vs.* 464b (*S. antarctica*), they are not evident in his lateral views (figs 463 and 464, respectively). Beyond these characters, *S. antarctica* does not differ morphologically from *S. lessonii*, of which it is therefore regarded as a probable synonym.

Philippi (1855: 208) described *S. magellanica* as "clearly distinct" from *S. lessonii* by having a thinner shell, a more prominent siphonal ridge and more excentric apex. The species was never figured. Six specimens in MNHN-CH (unnumbered) from 'Magallanes', collected by 'Schythe' and identified as '*Siphonaria magellanica*' (in Philippi's handwriting) are here considered to be syntypes (Fig. 1C, D). Out of these specimens, the three largest agree with the above-mentioned set of characters described by Philippi (Fig. 1C); the three other (smaller) specimens have a more evenly rounded outline, with the siphonal ridge ill-defined and a subcentral apex (Fig. 1D). We consider that all these specimens fit within the morphological variability of *S. lessonii*, although their anatomy is unknown.

The shell morphology of the syntypes of *S. laeviuscula* Sowerby, 1835 (Fig. 5A–F), described from Valparaíso, also fits within the range of variability here recognized for *S. lessonii*. Hubendick (1946: 20) identified specimens from central and northern Chile (Valparaíso and Taltal) and Perú as *S. laeviuscula*. He pointed out as distinctive shell characters of these specimens "the thickness [of shell] and a sharp and extremely finely notched edge, as well as the colour of the interior, which almost always gradually becomes paler towards the edge", and particularly emphasized the lack of a scalloped edge of the shell in *S. lessonii*. According to this author, these specimens can also be "most reliably distinguished from other species [including *S. lessonii*] by the occurrence of an organ with a cuticular stiletto" at the distal portion of the reproductive system (Hubendick, 1945: fig. 13) and by having "the bases of the innermost lateral teeth ... weakly and roundly crenelated in front". Thus far the 'scalloped' edge, which appears in some heavily sculptured specimens of *S. lessonii* (e.g. Fig. 1T), is the only character mentioned by Hubendick (1945, 1946) to have been found in the specimens considered in the present study. Furthermore, none of the sectioned specimens showed a 'stiletto'. Consequently, we consider that *S. laeviuscula* may be a distinct species.

From the same area from which Hubendick (1946) reported *S. laeviuscula*, two other species have been described, based exclusively on shell characters: *S. tenuis* Philippi, 1860 (Fig. 5J, M, N) from Isla Blanca (23°30′S) to the mouth of Río Bueno (40°15′S) and *S. lineolata* Sowerby, 1935 (Fig. 5G–I, Q, R) from Payta, Perú and Chiloé, Chile. The relationship of these species with *S. lessonii* and *S. laeviuscula* remains unclear. Consequently, the records of '*S. lessonii*' from northern Chile and Perú (e.g. Dall, 1909; Morrison, 1963; Marincovich, 1973; Ashton, 2007) require further study.

Siphonaria laevis Philippi, 1846, was regarded as a synonym of *S. lessonii* by Hubendick (1946). The original description is rather poor and lacking details necessary for recognizing the species; it refers to weak radial ribs, a laterally displaced apex and black colour of inner and outer shell surfaces. The species was never figured and the types could not be traced at MNHN-CH or at Zoologisches Museum Berlin (ZMB). The type locality was given only as 'Chile' in the original description. Due to these uncertainties, *S. laevis* is here regarded as a *nomen dubium*.

Siphonaria tristensis 'Leach' Sowerby, 1823 was considered a senior synonym of *S. lessonii* by Reeve (1856). This synonymy was accepted by Dall (1870, 1876) and Strebel (1907), who used the name to refer to the specimens they studied from the Malvinas (Falkland) Islands, and Tierra del Fuego and Chubut provinces (Argentina). Although the type locality of *S. tristensis* was not specified in the original description, the specimens currently labelled as syntypes (Fig. 5K, L, O, P), which agree with the original illustration, come from Tristan da Cunha (Atlantic Ocean). In shell morphology, these specimens resemble *S. lessonii*. However, Hubendick (1945, 1946), after studying other specimens from Tristan da Cunha, confirmed that *S. lessonii* and *S. tristensis* are anatomically and morphologically distinct: *S. tristensis* has a single genital opening and the ovispermiduct "not convoluted, but with lobes in pairs" (Hubendick, 1946: 22), whereas *S. lessonii* has two genital openings and a convoluted, not lobed ovispermiduct. The radula of *S. tristensis* was described by Hubendick (1946: 22) as "thicker" than in *S. lessonii*, but with "the edge and base of the central tooth… very small". Hubendick (1946) also distinguished *S. tristensis* from *S. lessonii* by having remarkably thin shells, with indistinct radial lines. Based on the above-mentioned differences, Hubendick (1946) suggested that Magellanic records of *S. tristensis* might

Figure 5. A–F. *Siphonaria laeviuscula*, syntypes (NHMUK 19817). **G–I, Q, R.** *S. lineolata*, syntypes (NHMUK 198120). **J, M, N.** *S. tenuis*? (original figure by Philippi, 1860, referable to this species although not referred to in the text, when describing the species). **K, L, O, P.** *S. tristensis*, syntypes (NHMUK 20120080). Scale bar: **A–R** = 1 cm.

correspond to misidentifications of *S. lessonii*. Our study of the specimens referred by Strebel (1907) to *S. tristensis* (housed in ZMH) confirms this misidentification. Moreover, Reeve's (1856: fig. 23a, b) illustrations of *S. tristensis* also correspond to *S. lessonii*. Consequently, there is no reason to retain the name *S. tristensis* in the Magellanic fauna.

Hupé (1854) and Plate (1894) identified specimens from the Chilean coast as *S. concinna* Sowerby, 1823, but these records were reassigned to *S. lessonii* by Hubendick (1946). Figueiras & Sicardi (1974) reported *S. lateralis* from Uruguay, although this record was subsequently reassigned to *S. lessonii* by Scarabino & Zaffaroni (2004).

Siphonaria lateralis Gould, 1846

(Figs 2D–F, 3G–H, 6, 7)

Siphonaria lateralis Gould, 1846: 153 (Burnt Island, Orange Harbor [Tierra del Fuego] [*fide* Gould, 1852]; holotype USNM 5853; Fig. 6A, E, I). Gould, 1852: 363. Gould, 1860: pl. 30, fig. 462, 462a, 462b. Strebel, 1907: 172, figs 28, 29 (in part). Hubendick, 1945: 17 (in part). Hubendick, 1946: 26, pl. 1, figs 22–25 (in part). Dayrat *et al.*, 2014: 259, fig. 3F, G (as '*S. lateralis*' group, unit 6).

Kerguelenella lateralis—Figueiras & Sicardi, 1974: 342 (in part). Ageitos de Castellanos *et al.*, 1993: 24, fig. 32.

Shell (Fig. 6): Medium-sized (max. L = 20.5 mm), relatively low in profile, inequilateral, solid. Base ovate, longer than wide; anterior and posterior margins evenly curved; left margin nearly straight; right margin slight to markedly projecting (Fig. 6A–H, N). Anterior slope straight to convex; posterior slope shorter, straight to slightly concave (Fig. 6I–M). Apex markedly acute, perpendicular to adult apertural plane, frequently eroded in larger specimens, located at posterior third of shell, markedly displaced towards left, not extending beyond shell base (Fig. 6A–D, G–M). Shell surface rough, sculptured with up to 49 weak to well marked, sinuous and nodulose radial ribs. Interspaces wider than or as wide as ribs, sometimes with intercalated (secondary) radial ribs. Siphonal ridge usually imperceptible, sometimes forming prominent keel (Fig. 6A–D, G, H).

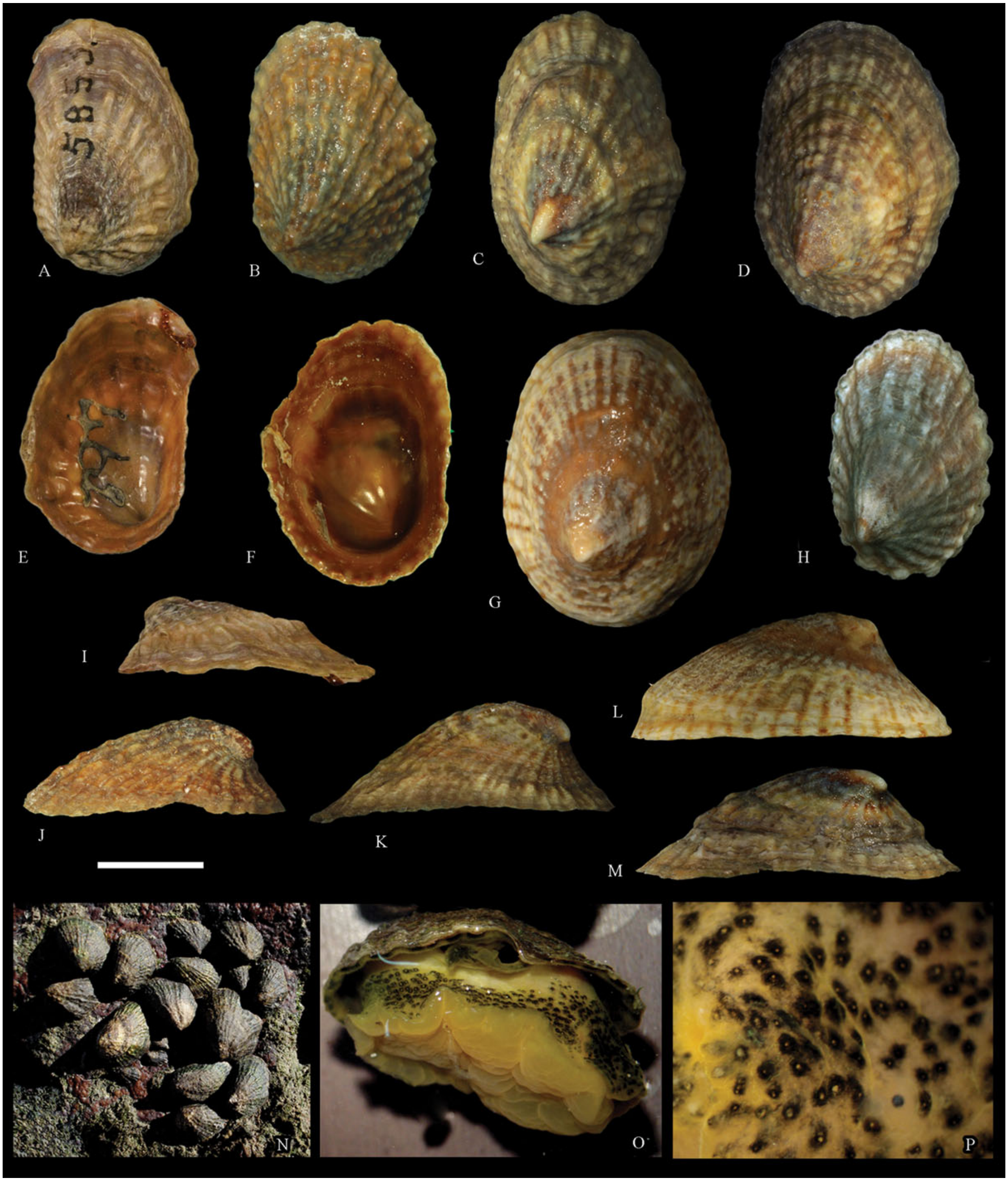

Figure 6. *Siphonaria lateralis*: morphology. **A, E, I.** Holotype (USNM 5853). **B–D, F, G, J–M.** Puerto Deseado (MACN-In 40131). **H.** Bahía Golondrina (MACN-In 40133). **A–E, G, H.** Dorsal views. **F.** Ventral view. **I–M.** Lateral views. **N–P.** Living animals. **N.** Animals on intertidal rocks. **O, P.** Details of foot papillae. Scale bar: **A–M** = 5 mm.

Growth lines well marked. Shell margin somewhat undulating (Fig. 6E, F).

Outer shell surface greenish brown, with light apex (Fig. 6A–D, G–N). Inner shell surface ochraceous, usually lighter at margin (Fig. 6E, F).

Anatomy: Jaw (Fig. 2D–F): large, arcuate, with numerous, juxtaposed, rod-like elements with rounded tips, 5.0 ± 0.4 µm wide ($n = 10$).

Radula (Fig. 3G, H, Supplementary Material, Fig. S4E, F): Of up to 141 tooth rows, each with small rachidian tooth flanked

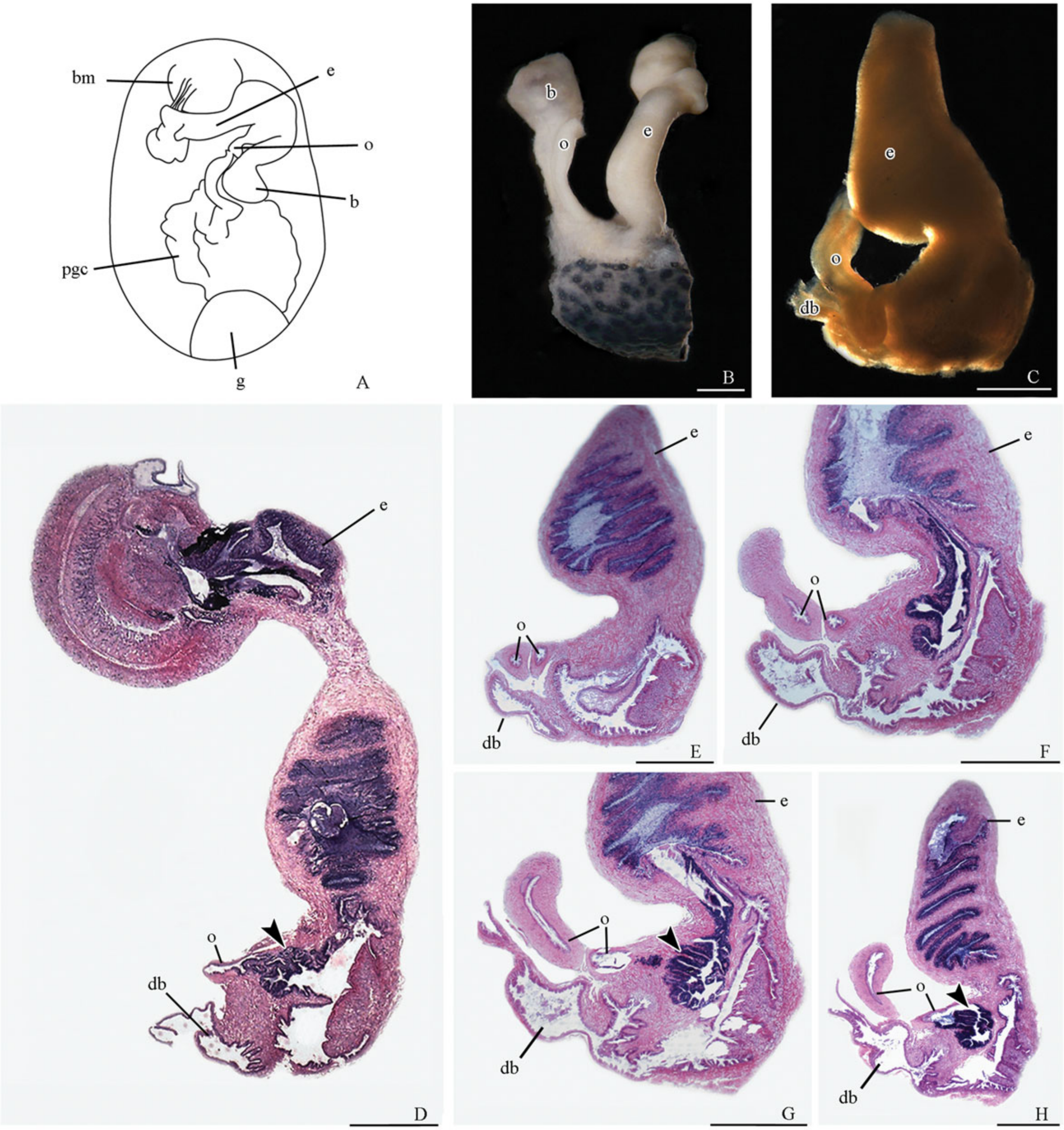

Figure 7. *Siphonaria lateralis*: anatomy. **A.** Schematic drawing showing location of reproductive system. **B, C.** Distal portion of reproductive system. **B.** Dorsal view. **C.** Ventral view. **D.** Histological section of epiphallus. **E–H.** Histological sections of distal portion of reproductive system, from dorsal to ventral side. **E.** Lumen of epiphallus, ovispermiduct and duct of bursa. **F.** Detail of duct of bursa joining epiphallus. **G, H.** Connection of ovispermiduct with epiphallus. **B–H.** Specimen from Puerto Deseado. Abbreviations: b, bursa; bm, bucal mass; db, duct of bursa; e, epiphallus; g, gonad; o, ovispermiduct; pgc, pallial glandular complex. Arrowhead indicates terminal, glandular portion of ovispermiduct. Scale bars: **B–H** = 1 mm.

by 36–40 lateral teeth on each side, reducing in size outwards (Supplementary Material, Fig. S4D). Rachidian tooth small, delicate, with slender, elongate, Y-shaped base, which widens posteriorly (Fig. 3G); cusp slightly pointed, about one quarter length of base. First 8–11 lateral teeth similar in shape, wide at the base, with mesocone triangular, bicuspid, as large as base (Fig. 3G). Following 8–13 lateral teeth with bicuspid mesocone which becomes unicuspid, pointed to blunt towards the outside, and a narrow, pointed ectocone, about one half length of mesocone (Fig. 3H). Remaining laterals with sharply pointed endocone and ectocone, of similar size, and larger mesocone with rounded to straight tip; cusp of laterals ranging from elongate to subquadrate outwards (Fig. 3H, Supplementary Material, Fig. S4E, F). Outermost lateral vestigial (Supplementary Material, Fig. S4F).

Foot (Fig. 6O, P): base yellowish or orange; lateral sides olive green to lead; papillae dark green, with a lighter central dot in living specimens.

Distal portion of reproductive system (Fig. 7): located mostly on right side, except for distal portion of epiphallus, which extends to left side of animal, passing behind buccal mass (Fig. 7A). Epiphallus long, almost straight, tubular, somewhat slender, with two constrictions demarcating basal, central and distal portions (Fig. 7B). Distal (glandular) portion of epiphallus well differentiated as a globose 'head' (sometimes forming an angle with central portion), with dark-pigmented small cap on apex and distinct protuberance at base. Lumen of central portion narrow, expanded in lateral folds (Fig. 7D–H). Duct of bursa and ovispermiduct reaching basal portion of epiphallus from posterior end (Fig. 7C, D); both ducts running around right shell adductor muscle. Bursa pyriform, relatively small, directed backwards (Fig. 7B). Duct of bursa moderately long, entering straightly the basal portion of epiphallus (Fig. 7F). Ovispermiduct slightly thinner than duct of bursa, with strong muscular wall, reaching epiphallus above duct of bursa (Fig. 7D–F). After entering epiphallus, ovispermiduct opens into highly folded glandular portion, which opens widely into lumen of basal portion of epiphallus (Fig. 7F–H). Sometimes, terminal portion of ovispermiduct recurving deeply before entering epiphallus, forming small protuberance (Fig. 7C).

Geographical distribution: Puerto Deseado (Argentina) to Beagle Channel and South Georgia (Supplementary Material S2). The species was also reported from the Australia-New Zealand-Kerguelen region (Hubendick, 1946; Dell, 1964; Powell, 1979). Some of these records were subsequently reassigned to *S. innominata* (Iredale, 1915), *S. stewartiana* (Powell, 1939) and *S. macquariensis* (Powell, 1939); the latter regarded either as a subspecies (Powell, 1955, 1960) or a synonym of *S. lateralis* (Dell, 1964; Powell, 1979). The occurrence of *S. lateralis* outside South America requires confirmation.

Remarks: Siphonaria lateralis is distinguished from *S. lessonii* by having a lower shell profile, a truncated left margin of the aperture, a more laterally displaced apex and a shell surface with nodulose ribs. Living specimens can also be easily differentiated by the colour of the foot, which is laterally olive green to leaden, with a yellowish or orange base in *S. lateralis*, but laterally pale to grey with a pale base in *S. lessonii*. Regarding the morphology of the distal portion of the reproductive system, both species are also distinct: in *S. lateralis* the ovispermiduct and duct of the bursa enter the epiphallus, resulting in a single genital aperture, whereas in *S. lessonii* both ducts join each other and open into the common atrium independently from the epiphallus. In addition, the rachidian tooth of *S. lateralis* has a consistently much smaller cusp than that of *S. lessonii*.

Hubendick (1945, 1946) described the presence of a distinctive 'glandular pouch' in the epiphallus of the 'section *Kerguelenia*'. Our histological study revealed that such a 'pouch' actually corresponds to the terminal (glandular) portion of the ovispermiduct and is also present in *S. lessonii*. Hubendick (1945: fig. 18) failed to interpret this glandular portion as part of the ovispermiduct and considered it as part of the epiphallus.

Some of the specimens figured by Strebel (1907: figs 28, 29) as *S. lateralis* do indeed correspond to this species; however, some others (figs 27, 29a) show an overhanging apex, located at the midline, a condition typical of the new species described below.

***Siphonaria fuegiensis* new species**

(Figs 2G–I, 3I–J, 8A–N, 9)

Siphonaria macgillivrayi—Hubendick, 1945: 17 (in part). Hubendick, 1946: 28 (in part), pl. 6, fig. 7 (both not Reeve, 1856).

Siphonaria lateralis—Strebel, 1907: 172 (in part), figs 27, 29a. Dayrat *et al.*, 2014: 259, fig. 3E (as '*S. lateralis*' group, unit 5) (both not Gould, 1846).

Kerguelenella lateralis—Aldea & Rosenfeld, 2011: 121, fig. 5F, G (not Gould, 1846).

Type locality: [54°49′58″S 68°20′07″W], Bahía Golondrina, Tierra del Fuego Province, Argentina.

Type material: Holotype (MACN-In 40134) and 10 paratypes (MACN-In 40135), all from the type locality.

Other material examined: Nine lots from Malvinas (Falkland) Islands [51°37′S] to Isla de los Estados [54°47′S], Argentina, including the Magellan Strait and Beagle Channel (Supplementary Material S3).

Etymology: The name of the species refers to Tierra del Fuego, the island from where most of the studied material originates.

ZooBank registration: urn:lsid:zoobank.org:act:A5455B99-646A-4B3C-B8C7-B02E25218142.

Diagnosis: small *Siphonaria* with prominent, inflated apex, somewhat displaced to left and usually extending beyond posterior margin of aperture; shell surface with smooth, regularly distributed radial ribs; outer shell surface dark leaden to reddish brown.

Shell (Fig. 8A–N): Small (max. L = 15.9 mm), low, moderately inequilateral, delicate. Base ovate (longer than wide), widening anteriorly; anterior and posterior margins rounded; left margin straight to slightly curved; right margin slightly to markedly projecting (Fig. 8A–F, I). Anterior slope long, convex; posterior slope extremely short, concave, straight or convex (Fig. 8G, H, J–L, N). Apex inflated, prominent, acute, frequently eroded in larger specimens; located at posterior end of shell, overhanging, extending beyond posterior margin of aperture; slightly displaced towards left (Fig. 8A–N). Shell sculpture of low, wide, smooth, regularly distributed radial ribs, well developed to almost imperceptible. Interspaces about half width of ribs; intercalated (secondary) ribs generally absent. Siphonal ridge low, almost imperceptible (Fig. 8A–F, G, I).

Outer shell surface dark leaden to reddish brown; sometimes with lighter ribs (Fig. 8A–L, N). Inner shell surface shiny, brown (Fig. 8M).

Anatomy: Jaw (Fig. 2G–I): large, arcuate, with numerous, juxtaposed, rod-like elements with rounded tips, 10 ± 1 μm wide ($n = 10$).

Radula (Fig. 3I, J, Supplementary Material, Fig. S4G–I): up to 117 tooth rows, each with small rachidian tooth flanked by 36–40 lateral teeth on either side, reducing in size outwards (Supplementary Material, Fig. S4G). Base of rachidian tooth elongate, uniformly wide, distally bifid (Fig. 3I). First 16–18 lateral teeth similar in shape, wide at base, with mesocone as large as base. Distal end of mesocone usually bicuspid, sometimes with 3–4 cusps, or even blunt, particularly outwards (Fig. 3I). Following 3–6 teeth with mesocone with rounded to straight tip and narrow, pointed ectocone, about half length of mesocone (Fig. 3J). Remaining laterals usually with sharply pointed endocone and ectocone, similar in size, exceptionally multicuspid, and larger mesocone with rounded to straight tip;

Figure 8. **A–N.** *Siphonaria fuegiensis* n. sp. **A, G, H.** Holotype (MACN-In 40134). **B.** Puerto Navarino (MZUC). **C.** Bahía Golondrina (MACN-In 40137). **D–F, J, M, N.** Paratypes (MACN-In 40135). **I, L.** Bahía Ushuaia (MLP 13170). **K.** Bahía Golondrina (MACN-In 40136). **A–F, I.** Dorsal views. **G, H, J–L, N.** Lateral views. **M.** Ventral view. **O–T.** *S. redimiculum*. **O, T.** Lectotype (NHMUK 19814/1). **P–S.** Paralectotypes (NHMUK 19814/2-5). **U–X.** *S. macgillivrayi*, syntypes (NHMUK 19813). Scale bars: **A–X** = 1 cm.

cusps from elongate to subquadrate outwards (Supplementary Material, Fig. S4H). Outermost lateral vestigial (Supplementary Material, Fig. S4I).

Distal portion of the reproductive system (Fig. 9): mostly on right side of animal, except for distal portion of epiphallus which extends to left side, passing behind buccal mass (Fig. 9A). Epiphallus relatively small, elongate, somewhat distorted, with one distal constriction and an almost imperceptible basal one, demarcating centrobasal and distal portions (Fig. 9B, C). Lumen narrow, expanded in well-defined lateral folds along centrobasal portion (Fig. 9D). Distal portion of epiphallus well differentiated as ovate glandular 'head', with distinct protuberance at base (Fig. 9B, C). Duct of bursa and ovispermiduct reaching epiphallus from posterior end; both ducts running around right shell adductor muscle. Bursa pyriform, posteriorly directed (Fig. 9B, C). Duct of bursa moderately long, entering

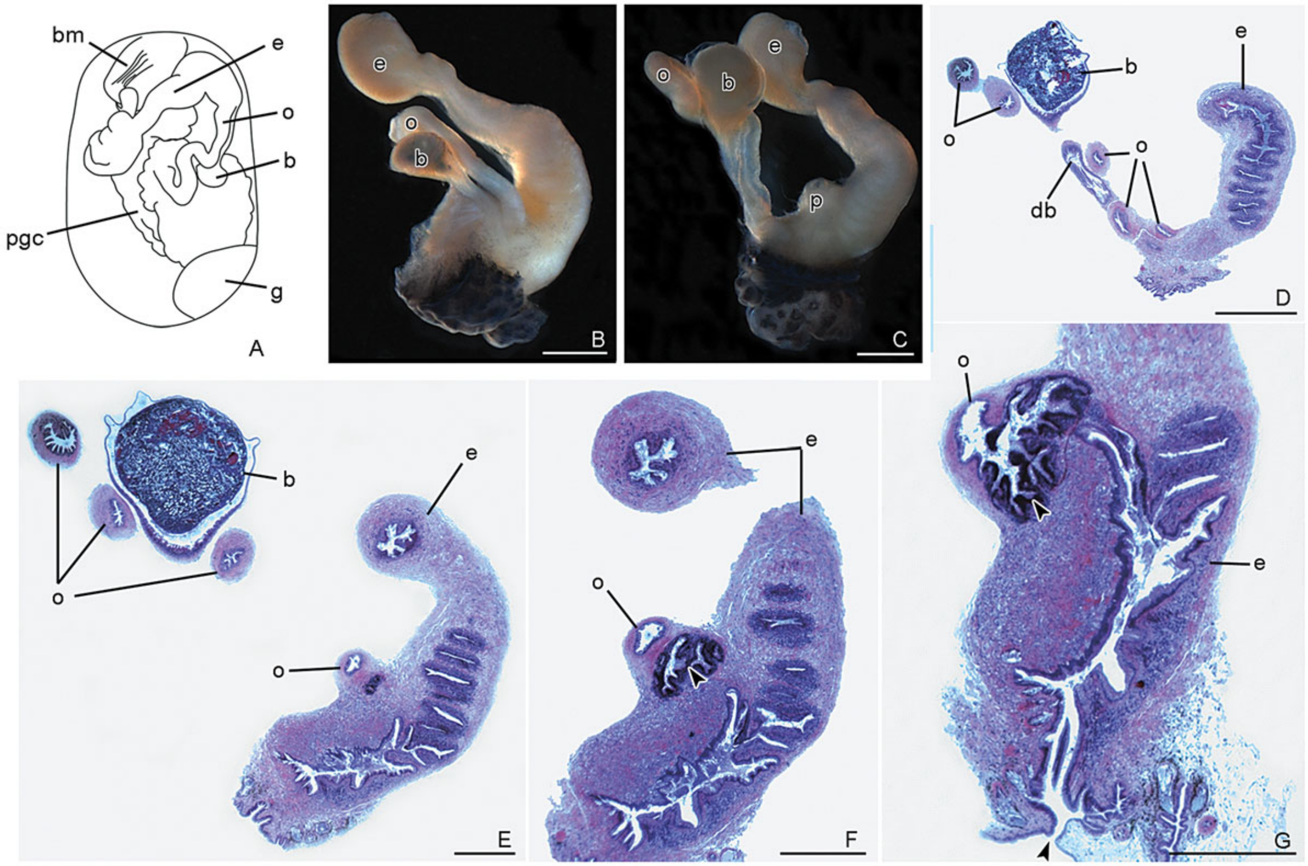

Figure 9. *Siphonaria fuegiensis* n. sp.: anatomy. **A.** Schematic drawing showing location of reproductive system. **B, C.** Distal portion of reproductive system, dorsal view. **D–G.** Histological sections of reproductive system figured in **C**, from dorsal to ventral side (arrowhead indicates terminal, glandular portion of ovispermiduct). **G.** Detail of ovispermiduct reaching epiphallus duct (arrowheads indicate terminal glandular portion of ovispermiduct and genital pore). **B–G.** Specimens from Bahía Golondrina. Abbreviations: b, bursa; db, duct of bursa; e, epiphallus; g, gonad; o, ovispermiduct; p, protuberance; pgc, pallial glandular complex. Scale bars: **B–D** = 1 mm; **E–G** = 500 µm.

straightly the basal portion of epiphallus (Fig. 9C, D). Ovispermiduct frequently wider than duct of bursa, with strong muscular wall, reaching epiphallus above duct of bursa, at about one-third length of centrobasal portion (Fig. 9E, F). After entering epiphallus, ovispermiduct opens into highly folded glandular portion, which widely opens into lumen of epiphallus (Fig. 9F, G). Usually, terminal portion of ovispermiduct recurving deeply when entering epiphallus, forming small protuberance (Fig. 9C: 'p', E–G).

Geographical distribution: Currently known from Magellan Strait, Beagle Channel, Cape Horn and Malvinas (Falkland) Islands.

Remarks: Siphonaria fuegiensis resembles the sympatric *S. lateralis*, with which it was previously confused (see below). Both species, however, differ strikingly in the shape and position of the apex. It is inflated, terminal, somewhat displaced to the left and usually extends beyond the posterior margin of the aperture in *S. fuegiensis*, whereas in *S. lateralis* it is low, pointed, markedly displaced to the left and does not reach the shell margin. *Siphonaria fuegiensis* has low, smooth, regularly distributed ribs, separated by narrow interspaces, while *S. lateralis* shows sinuous, nodulose ribs, separated by wide interspaces. Furthermore, *S. fuegiensis* has a consistently darker shell. The above-mentioned set of characters appears to be constant and consequently is useful for distinguishing both species externally, despite Dayrat, Goulding & White (2014: 259) having reported these taxa as two units within the '*S. lateralis*' group that were "not distinguishable externally". The radula also shows some differences between these species: in *S. fuegiensis* the rachidian tooth has a weaker base and the innermost laterals wider cusps than those of *S. lateralis*. The reproductive system only shows slight differences from *S. lateralis*: (1) the more elongate, generally distorted epiphallus (straight in *S. lateralis*), with an almost imperceptible basal constriction and (2) the ovispermiduct reaching the epiphallus at approximately one third of its length (at the base in *S. lateralis*).

The specimens figured by Strebel (1907: figs 27, 29a) and Aldea & Rosenfeld (2011: figs 5F, G) as *S. lateralis* and *Kerguelenella lateralis*, respectively, correspond to *S. fuegiensis*.

Siphonaria fuegiensis resembles *S. redimiculum* and *S. macgillivrayi*. The lot currently labelled as type material of *S. redimiculum* (NHMUK 19814/1-5), from an unknown locality, contains five specimens, apparently belonging to more than one species (Fig. 8O–T); only one of them (NHMUK 19814/1) agrees with the original description and figure by Reeve (1856: sp. 23) by having a "tumidly conical, *Capulus*-shaped" shell, with a "conspicuously obliquely twisted" apex (Fig. 8O, T). This specimen is here designated as lectotype, with the explicit purpose of fixing the concept of the species. The morphological characters present in the lectotype clearly differ from those in *S. fuegiensis*, namely by being considerably higher, with a markedly twisted apex, with fewer irregular ridges separated by wider interspaces, and a strongly crenulated margin. Furthermore, the name *S. redimiculum* has been applied to specimens from the Australia-New Zealand-Kerguelen region (Hubendick, 1946). Due to the uncertainties concerning the provenance of the type material, the usage of this name in other biogeographic regions, and the fact that none of the specimens studied from southern South America agree with the diagnostic characters of the species, we find no reason to retain this name in the area considered herein.

The syntypes of *S. macgillivrayi* (Fig. 8U–X) differ from *S. fuegiensis* by having a higher shell profile with more recurved apex and a more evenly ovate aperture, not flattened on the left side. Hubendick (1945, 1946) identified as *S. macgillivrayi* specimens from St Paul Island, Indian Ocean (the type locality) and the Magellan Strait, pointing out some anatomical differences between the specimens from these two localities. According to the author the studied St Paul Island specimen has the hermaphrodite duct "provided with a number of vesicles on all sides" (Hubendick, 1946: 29; 1945: fig. 17, 'z.g.'), while those folds are only present laterally in the specimens from the Magellan Strait (Hubendick, 1945: fig. 16, 'z.g.'). The latter condition was also observed in the Magellanic specimens studied herein. We therefore reassign Hubendick's (1945, 1946) Magellanic records of *S. macgillivrayi* to *S. fuegiensis*.

MOLECULAR RESULTS

Sequences of COI showed 241 variable sites out of 671 bp. The topologies obtained by ML and BI were coincident, with each node for the three studied species well supported by high BS (>79%) and PP (>0.96) values, showing reciprocal monophyly (Fig. 10B). Our results showed that *S. lessonii*, *S. lateralis* and *S. fuegiensis* have clear genetic differences. Pairwise genetic (K2P) distances between groups were 27.2% between *S. lessonii* and *S. lateralis*, 26.3% between *S. lessonii* and *S. fuegiensis*, and 7.3% between *S. lateralis* and *S. fuegiensis*. Interestingly, there was almost no intraspecific variation, even in the case of the widely distributed species *S. lessonii*. Within-group distances were 0.17% for *S. lessonii*, 0.04% for *S. lateralis* and 0.12% for *S. fuegiensis*. A clear gap exists between the highest within-group distance and the lowest between-group mean distances.

The haplotype network obtained for *S. lessonii* showed a star-shaped topology, with the most frequent haplotype present in 68% of the specimens, coming from all sampled localities (Fig. 10A). About one third of these specimens showed unique haplotypes, most differing in one or two nucleotide positions. Four haplotypes were found among the studied specimens of *S. fuegiensis*, three of them present in specimens from Bahía Ushuaia, and the remaining one represented by one specimen from Bahía Golondrina (Fig. 10A). *Siphonaria lateralis* showed two main haplotypes, one of them present in the three localities for which there is molecular information (Fig. 10A). No association between haplotypes and collection site could be found for any of the species.

DISCUSSION

Out of the nine *Siphonaria* species reported from southern South America, including the Argentinean and Magellanic biogeographic provinces, our study has confirmed the presence of only three species, including the one here described as *S. fuegiensis*. Several other names have been used for specimens from this area, for the following reasons: (1) some species were described based on only a few shells and disregarding the intraspecific variability of previously described species (such as seems to be the case for *S. antarctica* and *S. magellanica*) and (2) names from other geographic areas were wrongly applied to Magellanic specimens, based on their morphological similarities (e.g. *S. tristensis* and *S. macgillivrayi*). The three species recognized as valid have here been characterized using an integrative approach that considers morphological, anatomical, radular and molecular information. The general shell outline, the position of the apex, the shell sculpture, the morphology of the epiphallus, the site of the junction of the ovispermiduct and duct of the bursa with the epiphallus, and the degree of development of the rachidian tooth all proved to be useful characters for distinguishing these species. *Siphonaria lessonii* is the most variable species; although morphological variability has been discussed in some previous studies, it had never been considered in the context of molecular studies. The information from the present study allows the range of variability of this species to be established, thus confirming its wide distributional range. It cannot be ruled out that Pacific records from Chiloé, Chile, north to Paita, Perú, correspond to another 'cryptic' species, such as recently found in the same region for the bivalve *Perumytilus purpuratus* (Trovant *et al*., 2014). Núñez *et al*. (2015) reported the existence of two distinct 'mitochondrial lineages' of *S. lessonii*: an 'Atlantic' clade present in the southwestern Atlantic and Beagle Channel, and a 'Pacific' clade encompassing specimens from central Chile and three (out of the 14 specimens they studied) from Puerto Madryn, in the southwestern Atlantic. The haplotype network obtained herein is very similar to that obtained by those authors for the 'Atlantic' clade, with one central, very frequent haplotype and several other haplotypes differing by one to three steps. However, none of our specimens from Puerto Madryn (or any other locality we sampled) appear to be as distant as those belonging to the 'Pacific' clade of Núñez *et al.* (2015). Unfortunately, the sequences from this previous study are not available to date in GenBank (accessed 1 May 2015) and therefore we could not include specimens from central Chile in our molecular analysis. Núñez *et al.* (2015) interpreted the existence of two lineages as evidence of Pacific-Atlantic geographic isolation after the glaciation periods that affected the region throughout the Pleistocene. However, all our specimens from Isla Lilihuapi (42°S), Chile, share haplotypes with our Atlantic specimens. This suggests that the two lineages of Núñez *et al.* (2015) could actually reflect disjunction between the Magellanic and Perú-Chilean provinces (at about 42°S).

Dayrat *et al.* (2014) reported a genetic distance of 6.9% between their '*S. lateralis*' units 5 and 6 (here identified as *S. lateralis* and *S. fuegiensis* n. sp.). The topologies obtained here by ML and BI were coincident with that obtained by these authors. The distance value obtained here by addition of new sequences is slightly higher (7.3%) than theirs, but the observed reciprocal monophyly and extremely low within-group distances allow us to confirm them as two distinct species. Although Dayrat *et al.* (2014) did not find any clear morphological differences between the specimens they studied within '*S. lateralis*' units 5 and 6, our material revealed several distinctive morphological, anatomical and radular characters.

Three gaps in present taxonomic knowledge have become evident from our study. First, the doubtful identity of records from central Chile north to Perú, which have been assigned by some authors to '*S. lessonii*', but might actually correspond to another species (*S. laeviuscula*, *S. tenuis* and/or *S. lineolata*). Adequate material from the Perú-Chilean province was not available for the present study, so it has not been possible to clarify the identity of these specimens. Further taxonomic study of the *Siphonaria* species occurring in that area would allow a re-analysis of the phylogeographic context proposed by Núñez *et al.* (2015). Second, there is a need for confirmation of the identity of the specimens from the Australia-New Zealand-Kerguelen region previously assigned to *S. lateralis*, and for the study of the relation of these records with the other species described from

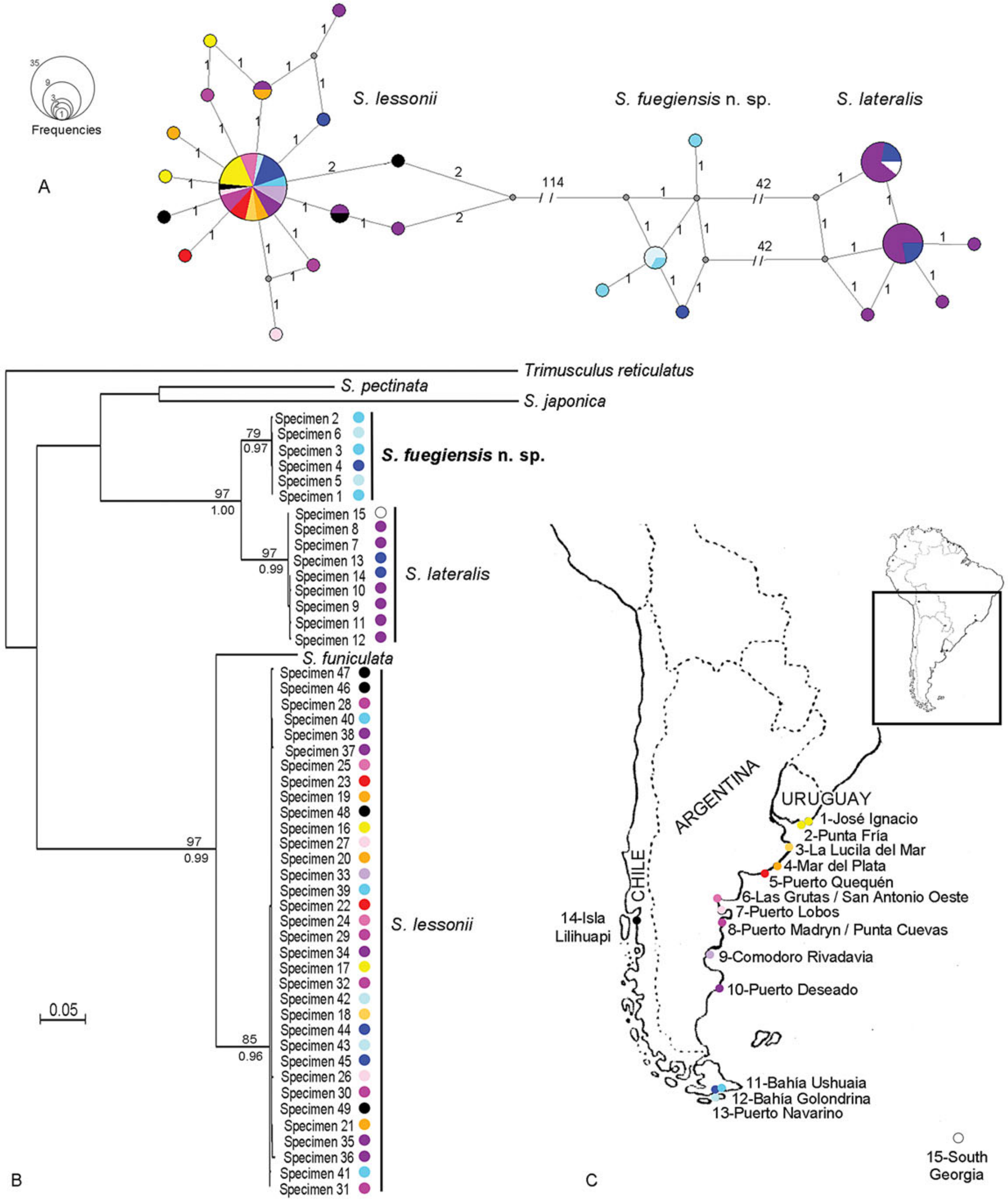

Figure 10. Molecular analysis of *Siphonaria lessonii*, *S. lateralis* and *S. fuegiensis* n. sp. **A.** Haplotype network; circle diameter is proportional to haplotype frequency, as shown in scale drawn next to figure; number of substitutions are indicated on branches. **B.** ML phylogeny, indicating bootstrap values (above node) and Bayesian posterior probabilities (below node); values less than 75/0.75 are not shown. The designation of the specimens corresponds with those indicated in Supplementary Material, Table S5. **C.** Sampled localities, showing colour conventions used in **A**, **B**.

that area. Third, the finding of *S. fuegiensis* n. sp. living sympatrically with the other two species included in this study, opens the possibility that its geographic distribution could be wider than currently known. We have here reported previous misidentifications that actually correspond to this species, and have seen lots in museum collections where the species was mixed with others. This suggests that the presence of *S. fuegiensis* in other localities could be passing unnoticed.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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