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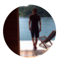

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# Systematic revision of *Nacella* (Patellogastropoda: Nacellidae) based on a complete phylogeny of the genus, with the description of a new species from the southern tip of South America

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True limpets of the genus *Nacella* (Patellogastropoda: Nacellidae) include at least 11 nominal species distributed in different provinces of the Southern Ocean. Here, we present new molecular analyses and a comprehensive morphological revision of *Nacella* confirming the validity of all the currently recognized species, but with important amendments to the published distributions of several. We also show that specimens collected along two fjords in the Beagle Channel, southern South America, constitute a new taxon: ***Nacella yaghana* sp. nov**. The phylogenetic position of this new taxon in our molecular tree reveals that it represents an ancestral South American lineage of *Nacella*, markedly separated from the previously recognized and evolutionary recent Magellanic radiation. In addition, this new *Nacella* species was clearly distinguished from the rest of the species by morphological comparisons, including shell characteristics, radular-tooth shape and configuration, as well as by the coloration pattern of the mantle tentacles. This study provides new evidence about the evolutionary history of this important Southern Ocean, marine, near-shore benthic group and the role of the Antarctic Circumpolar Current in the biogeography of the genus.

ADDITIONAL KEYWORDS: Antarctica – biogeography – *COI* mtDNA – Miocene – molecular phylogeny – Mollusca – morphology – Patagonia – phylogenetic systematic – rRNA.

## INTRODUCTION

Patellogastropods or 'true limpets' are some of the most ubiquitous molluscan components of marine littoral hard-substrate communities (Powell, 1973; Branch, 1985; Ponder & Lindberg, 1997; Fernández & Castilla,

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2005; Lindberg, 2008). This clade includes some of the best-studied intertidal model organisms in ecology, physiology, behaviour, reproduction and systematics (Coleman *et al.*, 2006; Lindberg, 2008; Burgos-Rubio *et al.*, 2015). They differ from other gastropods in key morphological characteristics, such as radular/gill morphology, shell geometry and crystalline microstructure (Ridgway *et al.*, 1998; Koufopanou *et al.*, 1999; Nakano & Ozawa, 2007; Lindberg, 2008). In general, true limpets have been classified based on external characteristics; however, such features are extremely variable and overlapping in several groups, which have led to major taxonomic uncertainties (Ridgway *et al.*, 1998; Harasewych & McArthur, 2000; Nakano & Sasaki, 2011). In addition, their simple morphologies and anatomies have led taxonomists to underestimate the actual diversity of the group (Lindberg, 2008).

The development of molecular techniques has become fundamental to further understand and resolve the evolutionary history of patellogastropods (Ponder & Lindberg, 1997; Koufopanou *et al.*, 1999; Harasewych & McArthur, 2000; McArthur & Harasewych, 2003; Nakano & Ozawa, 2004, 2007; Nakano & Sasaki, 2011). In the last molecular revision of the group, Nakano & Sasaki (2011) recognized seven families: Lottidae, Acmaeidae, Pectinodontidae, Patellidae, Lepetidae, Eoacmaeidae and Nacellidae. Moreover, the most recent taxonomic overview of the gastropods proposed major changes to their classification: Patellogastropoda is ranked as a subclass that includes a single order Patellida, which in turn is divided into three superfamilies (with constituent families): (1) Eoacmaeoidea (Eoacmaeidae), (2) Patelloidea (Patellidae) and (3) Lottioidea (Lottidae, Acmaeidae, Lepetidae, Neolepetopsidae, Pectinodontidae and Nacellidae) (Bouchet *et al.*, 2017).

A key diagnostic feature of nacellid limpets is the presence of a very long and coiled radula, up to five times the length of that of other patellogastropods (Powell, 1973). The Nacellidae includes tropical/temperate *Cellana*, Antarctic/sub-Antarctic *Nacella* and, possibly, the South Australian endemic *Naccula* (Nakano & Sasaki, 2011). *Nacella* is the only patellogastropod genus largely restricted to Antarctic and sub-Antarctic waters and differs from *Cellana* in the gill cordon, which is interrupted by the head in *Cellana*, but is continuous in *Nacella*. At the same time, members of *Nacella* are the only patellogastropod that possesses an epipodial fringe, a scalloped lamellate flange that occupies a mid position between the edge of the foot and the gill cordon (Powell, 1973). The most recent complete taxonomic review of *Nacella* is that of Powell (1973), although there have been earlier (e.g. Gmelin, 1791; Reeve, 1855; Rochebrune & Mabille, 1889; Pilsbry, 1891) and more recent partial revisions of the group (Castellanos & Landoni, 1988; Forcelli, 2000; Valdovinos & Rüth, 2005; de Aranzamendi *et al.*, 2009; González-Wevar *et al.*, 2011a).

Members of *Nacella* are key inter- and subtidal macro-invertebrates across different provinces of the Southern Ocean, including temperate and sub-Antarctic areas of South America and the Falkland/Malvinas Islands, maritime Antarctica and geographically isolated sub-Antarctic islands, including Marion, Crozet, Kerguelen, Heard, Macquarie and Campbell (Fig. 1). The species *N. delesserti* (Philippi, 1849), *N. macquariensis* Finlay, 1926 and *N. terroris* (Filhol, 1880) are endemic to Marion, Macquarie and Campbell Islands, respectively. *Nacella kerguelenensis* (Smith, 1879) and *N. edgari* (Powell, 1957) are sympatric on the Kerguelen and Heard Islands (Powell, 1973; Cantera & Arnaud, 1985; Troncoso *et al.*, 2001; González-Wevar *et al.*, 2017). The Antarctic limpet *N. concinna* (Strebel, 1908) is restricted to maritime Antarctica and nearby sub-Antarctic islands, including South Georgia, South Sandwich and Bouvet (Powell, 1973). Finally, *Nacella clypeater* (Lesson, 1831) expands the distribution of the genus north of 30°S along the Chilean coast (Valdovinos & Rüth, 2005), following the cold Humboldt Current System.

The morphological diversity recorded in the Magellanic region has led to a confusing nomenclatural history. Powell (1973) recognized five species: *N. deaurata* (Gmelin, 1791), *N. flammea* (Gmelin, 1791), *N. fuegiensis* (Reeve, 1855), *N. magellanica* (Gmelin, 1791), and *N. mytilina* (Helbling, 1779); and he treated *N. delicatissima* (Strebel, 1907) as an ecomorph of *N. deaurata*. At the same time, he considered *N. chiloensis* (Reeve, 1855) and *N. venosa* (Reeve, 1855) as subspecies of *N. magellanica*. However, in a subsequent morphological revision of South American nacellids, Valdovinos & Rüth (2005) considered there were seven valid Magellanic species, viewing *N. fuegiensis* as a synonym of *N. magellanica*. Nevertheless, during the last decade, molecular-based and geometric morphometric analyses distinguished only four closely related Magellanic species (de Aranzamendi *et al.*, 2009; González-Wevar *et al.*, 2011a), namely Powell's (1973) species with the additional synonymy of *N. fuegiensis* with *N. deaurata*. González-Wevar *et al.* (2010, 2011a) showed that this Magellanic diversification is evolutionarily recent. Moreover, in a recent molecular-based study, González-Wevar *et al.* (2017) revealed the presence of a new lineage from the southern tip of South America.

Here, we present a detailed revision of *Nacella*, including the description of the new South American species. Through a significant sampling effort, especially in South America, we also revise the accepted distribution of all the species in the genus, making some important amendments to previous published records.

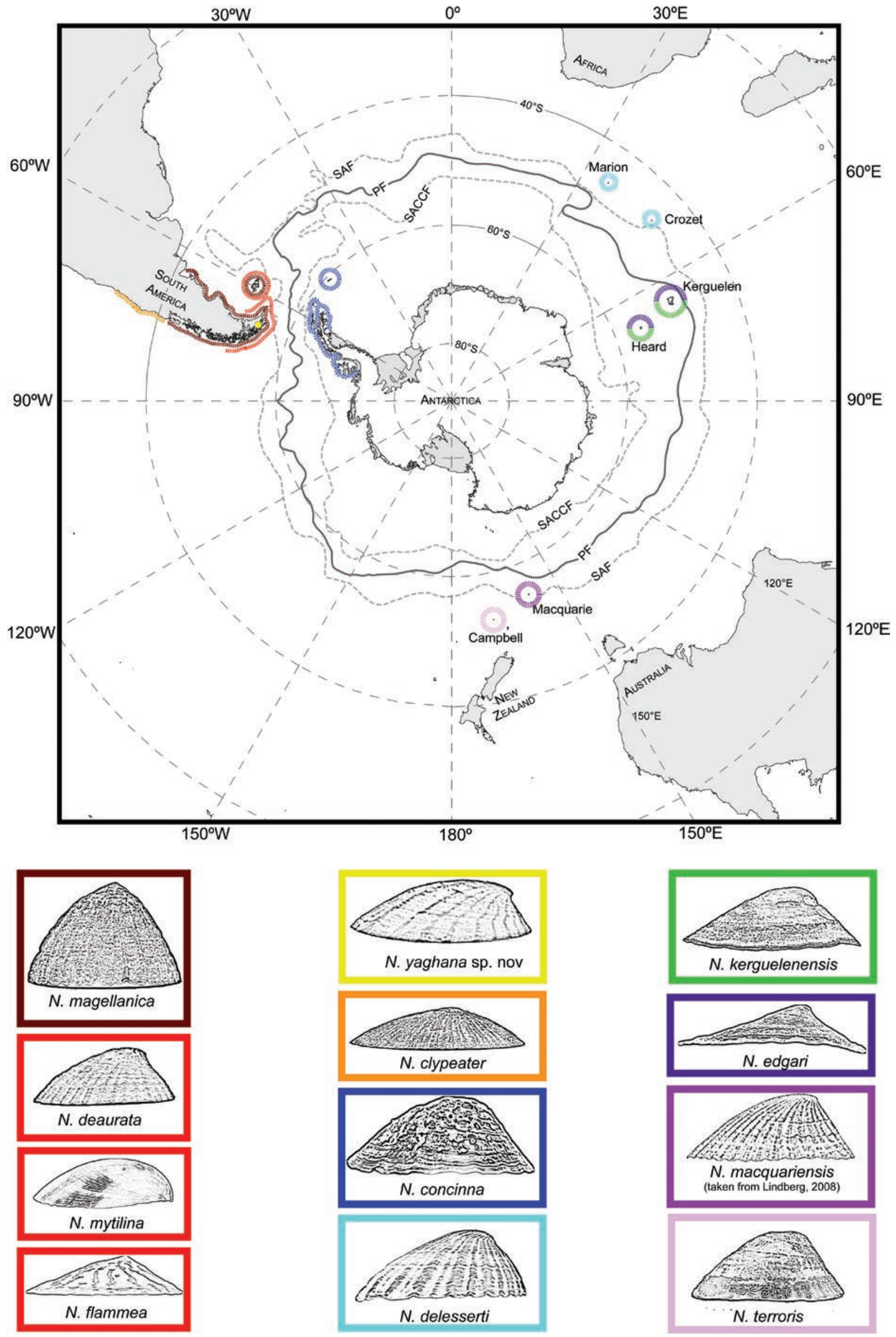

**Figure 1.** Distribution of *Nacella* in different provinces of the Southern Ocean, including South America, maritime Antarctica and sub-Antarctic Islands. Major ocenographic currents and sudivisions includes SAACF = Southern ACC Front, PF = Polar Front, and SAF = sub-Antarctic Front. Coloured areas show the distribution of the analysed species.

## MATERIAL AND METHODS

### Taxon sampling

*Nacella* specimens were collected between 2006 and 2017 from different localities and provinces across the Southern Ocean (Fig. 1). Individuals were identified following Powell (1973), Valdovinos & Rüth (2005) and González-Wevar *et al.* (2011a). All specimens were fixed in ethanol (99%) for further molecular analyses. Phylogenetic recontructions included a total of 113 individuals, ten specimens per species, with the exception of *N. terroris* where the number of individuals was restricted to three. Shells, living and fixed animals were also photographed for morphological revisions. Non-type material examined is available at the Universidad de Magallanes collection and their respective vouchers and accession numbers are listed in Supporting Information, Table S1. We also include in the analyses ten specimens of the new Magellanic lineage, described below as *Nacella yaghana* sp. nov. This new taxon exhibits key *Nacella* features (i.e. the epipodial fringe and a long and coiled radula), but it does not resemble any described species.

### Shellmorphology,anatomyandradularmorphology

Shell diameter, height, thickness, colour and sculpture, as well as coloration of the head, foot, mantle tentacles and cephalic tentacles, were examined for each taxon, with the exception of *N. macquariensis* from Macquarie Island. Radular teeth of *Nacella yaghana* sp. nov. were dissected and placed in Proteinase K for 6 h before rinsing in distilled water. Finally, the radular morphology was examined by scanning electron microscopy (SEM) and compared to previous radular analyses of other Magellanic species (Valdovinos & Rüth, 2005). The configuration of the radular sac was observed using a binocular microscope. In the other species examined, the radula teeth were placed in household bleach for 20 s, rinsed in distilled water and photographed using stereomicroscopy.

### DNA preparation, PCR amplification and sequence editing

DNA was extracted from the mantle following a standard salting-out method (Aljanabi & Martínez, 1997). A fragment of the mitochondrial cytochrome *c* oxidase subunit I (*COI*) gene was amplified using universal (Folmer *et al.*, 1994) and specific primers (González-Wevar *et al.*, 2010). Similarly, a fragment of the nuclear 28S rRNA gene was amplified using universal primers LSU5' (Littlewood *et al.*, 2000) and LSU 1600R (Williams *et al.*, 2003). PCR mixture preparations and temperature parameters were done following González-Wevar *et al.* (2017). PCR amplicons were purified using QIAquick Gel Extraction Kit (QIAGEN) and sequenced in both directions at Macrogen Inc. (Seoul, South Korea). Forward and reverse sequences of each gene were assembled independently and edited using GENEIOUS 5.1.7 (Kearse *et al.*, 2011). Multiple alignments were obtained using MUSCLE (Edgar, 2004) and optimized by eye. Base composition of nucleotide of sequences was analysed with MEGA 7 (Kumar *et al.*, 2016).

### Phylogenetic reconstructions

Phylogenies were reconstructed using three different methods: maximum parsimony (MP), maximum likelihood (ML) and Bayesian Inference (BA). Before performing the reconstructions, we executed a saturation test for both genetic markers using DAMBE v.5 (Xia, 2013). These analyses recorded little saturation in the analysed fragments. Nucleotide substitution models for ML and BA analyses were determined separately for each gene with the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC), respectively, implemented in the model selected by jmodeltest2 (Darriba *et al.*, 2012). For tree-rooting purposes we also include in the analyses available sequences of two *Cellana* species (*C. nigrolineata* and *C. radiata orientalis*) and one outgroup (*Patella vulgata*). MP analyses were carried out using PAUP* (Swofford, 2002) following González-Wevar *et al.* (2010). The GTR+I+G (*COI*) and the GTR+G (28S rRNA) substitution models were used for ML and BA reconstructions in PhyML (Guindon & Gascuel, 2003) and MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001), respectively. Non-parametric bootstrap (BS) analyses were used to determine nodal support for both the MP and ML, using the full heuristic search option over 1000 pseudo-replicates (Felsenstein, 1981). Bayesian Inference analyses were performed to obtain posterior probabilities for the nodes in phylogenetic trees. Posterior probability values of sampled trees were obtained using the Metropolis coupled Monte-Carlo algorithm (MCMC) implemented in MrBayes. A total of four chains were run twice in parallel for $10^8$ generations and trees were sampled every 1000 generations. Stationarity in the analyses was inferred when the average standard deviation of split frequencies was less than 0.01 (Huelsenbeck & Ronquist, 2001). The first 10% of the trees were discarded as burn-in and Bayesian posterior probabilities (BPP) were estimated as the percentage of trees that showed a particular node. Posterior probability density of the combined tree and log files was summarized as a maximum clade credibility tree using TreeAnnotator (http://beast.bio.ed.ac.uk/TreeAnnotator) and then visualized with FigTree v.1.4 (http://tree.bio.ed.ac.uk/software/figtree/).

# RESULTS

## SYSTEMATICS

### CLASS GASTROPODA CUVIER, 1795

### SUBCLASS PATELLOGASTROPODA LINDBERG, 1986

### ORDER PATELLIDA VON IHERING, 1876

### SUPERFAMILY LOTTIOIDEA GREY, 1840

### FAMILY NACELLIDAE THIELE, 1891

### GENUS *NACELLA* SCHUMACHER, 1817

*Nacella* Schumacher, 1817: 179. Type species (by monotypy) *Nacella mytiloides* Schumacher, 1817 (= *Patella mytilina* Helbling, 1779).
*Patinigera* Dall, 1905: 53. Type species (by original designation) *Patella magellanica* Gmelin, 1791. New Synonymy.

*Revised diagnosis:* The shell is of medium to moderately large size and the thickness varies from hard and robust in some species (*N. magellanica*, *N. deaurata*, *N. delesserti*, *N. terroris*, *N. concinna* and *N. clypeater*) to thin and fragile in others (*N. kerguelenensis*, *N. flammea*, *N. edgari*, *N. yaghana* sp. nov. and *N. mytilina*). The shell morphology is typically elliptical, high-arched, with the apex strongly curved forward and downward, sometimes almost at the anterior end. The surface of the shell varies from very smooth (e.g. *N. mytilina*) to strongly radially ridged (e.g. *N. magellanica*). The external shell colour is pale-olive to brownish, the apex coppery; the inside is silvery iridescent to reddish bronze.

*Remarks:* Based on shell morphology, the genus *Nacella* has traditionally been divided into *Nacella* s. str. and the subgenus *Patinigera* (Powell, 1973). Members of *Nacella* s. str. are characterized by a thin and fragile shell, they inhabit seaweeds and are restricted to southern South America (*N. mytilina*) and the Kerguelen Islands (*N. kerguelenensis*), whereas the remaining species were included in *Patinigera* and exhibit solid shells, are typical inter- and subtidal rocky dwellers, grazers and are broadly distributed in the Southern Ocean. Nevertheless, the distinction between *Nacella* and *Patinigera* was not corroborated by molecular analyses; indeed, the respective type species are very closely related (González-Wevar *et al.*, 2010, 2011a, 2017; this study).

### *NACELLA YAGHANA* GONZÁLEZ-WEVAR & NAKANO SP. NOV.

(FIG. 2)

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*Material examined*

*Holotype:* NSMT-Mo 78800, about 140 km west of Puerto Williams (54°56’50.17”S, 67°39’44.48”W), Beagle Channel, Chile, 14-09-2013, collection Mathias Hüne.

*Paratypes:* NSMT-Mo 78801, Paratype 2, NSMT-Mo 78802; Paratype 3: MNHNCL-MOL 15968; Paratype 4: MNHNCL-MOL 15969; Paratype 5: MNHNCL-MOL 15970.

*Diagnosis*

*Shell:* The shell shape and sculpture are relatively constant in the analysed individuals from the Pía and Garibaldi Fjords, Beagle Channel, southern South America (Fig. 2A–C). The species exhibits a conical morphology, dorsally raised with a moderately thin and translucent shell. The anterior part of the animal is laterally compressed (Fig. 2D–F). It has a medium shell size (maximum length 60 mm) with a medium profile. The apex is positioned near the anterior end. The anterior slope is slightly concave, while the lateral and posterior slopes are convex (Fig. 2A–C). The surface is almost smooth. The exterior colour is olive to bluish olive, reddish brown at the apex, with radial brown/purple rays (Fig. 2A–F). The muscle-scar areas inside the shell are reddish brown. The intermediate area between the muscle scar and shell margin is silvery grey. The shells exhibit narrow olive interior margins and the presence of external purple-brown radial rays.

*External anatomy:* The ventral area of the foot is grey and the epipodial fringe is recognizable. The mantle fold is thick and dun-brown coloured. The mantle tentacles alternate three shorter with one larger with no pigmentation (Fig. 2G). The cephalic tentacles are dorsally pigmented (black) (Fig. 2G).

*Radula:* The radula is typical of *Nacella*, with a very weak and small medium-central vestigial plate between long first laterals. The first lateral teeth are set close together on the anterior edge of the basal plates, long and sharp pointed, with two cusps (Fig. 2H). The second laterals are broader, wider spaced with four cusps (Fig. 2H). There are two pairs of marginal teeth with spoon-like cusps (Fig. 2H, J, K).

*Radula sac:* The radula sac is medium in length, extending backwards towards the anterior third of the visceral cavity and turning into an inverse S in the anterior part of the visceral mass.

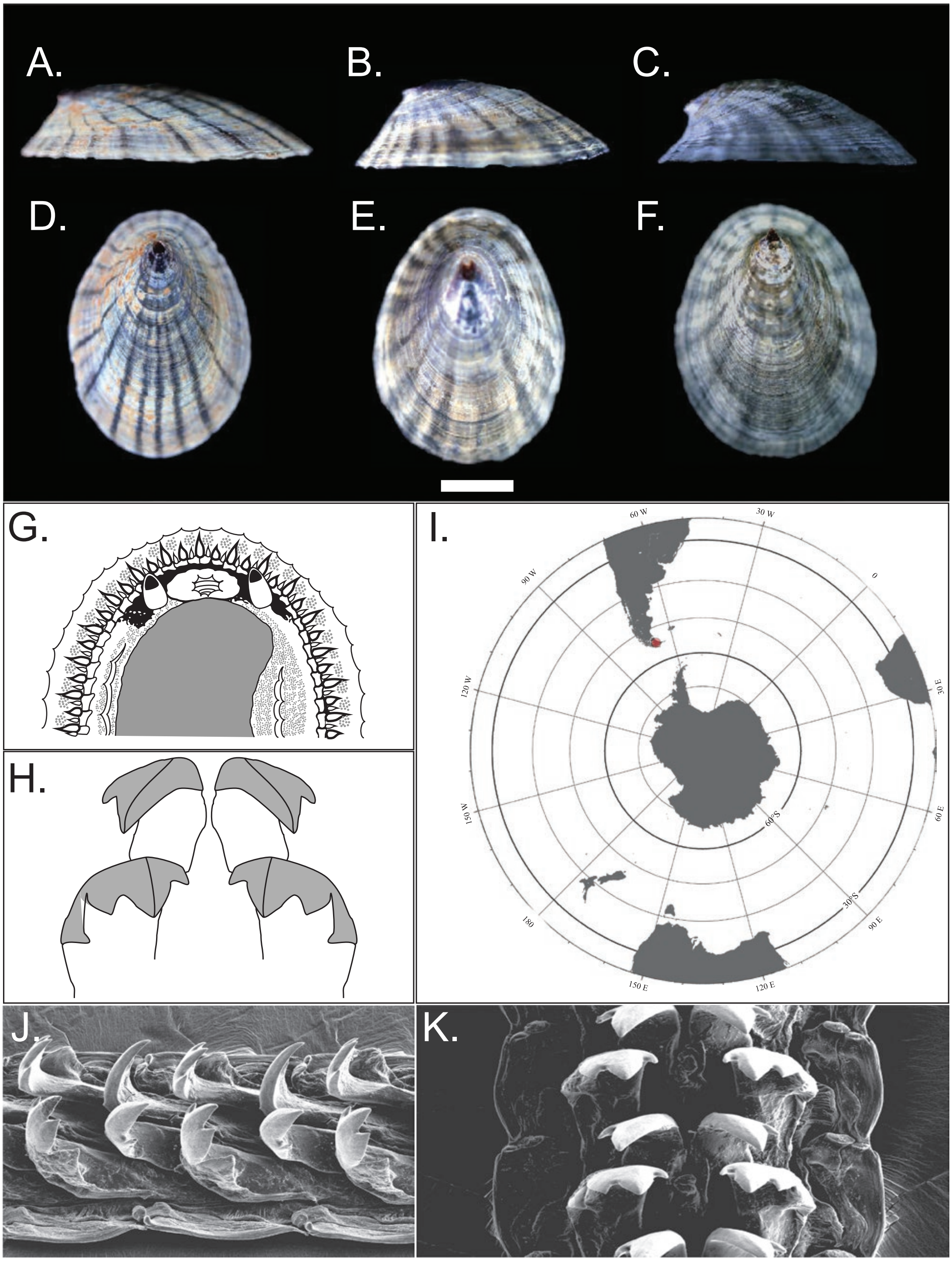

**Figure 2.** ***Nacella yaghana* sp. nov.** Pía and Garibaldi fjords, Beagle Channel, southern South America. Scale bar = 1.0 cm for all unless specified otherwise. A, B = Pía Fjord, C = Garibaldi Fjord. A–F, shell morphology and coloration of ***Nacella yaghana* sp. nov.** A–C, lateral view. D–F, dorsal view. G, mantle tentacles, cephalic tentacles and foot colorations. H, radula. I, distribution. J–K, radular morphology (SEM).

*Holotype dimensions:* Length 25.6 mm, width 18.8 mm and height 6.0 mm.

*Depositories:* Holotype NSMT-Mo 78800. NSMT: National Museum of Nature and Science, formerly National Science Museum, Tokyo, Japan. Paratypes NSMT-Mo78801, NSMT-Mo 78802, MNHNCL-MOL 15968, MNHNCL-MOL 15969, MNHNCL-MOL 15970. NHNM: Museo Nacional de Historia Natural, Chile.

*Type locality:* Pía Fjord (54°49'36.81" S, 69°39'11.81" W), Beagle Channel, Chile (Fig. 2I).

*Habitat:* Rocky intertidal to subtidal shores of Pía and Garibaldi Fjords.

*Material studied:* Pía Fjord (54°49'36.81"S, 69°39'11.81"W) *N* = 50; Garibaldi Fjord (54°43'20.63"S, 69°57'48.27"W) *N* = 50.

*Etymology:* The type locality of this species is part of the traditional territory of the Yagán (Yaghan) people, recognized as the southernmost indigenous population in the world. They were traditionally nomadic hunter-gatherers, whose women would collect shellfish by diving.

*Comments:* Shell shape, coloration and thickness differ from other Patagonian species of the genus (*N. magellanica*, *N. deaurata*, *N. mytilina* and *N. flammea*), and particularly those inhabiting intertidal rocky ecosystems. Although *N. yaghana* sp. nov. resembles *N. mytilina* in terms of shell-shape, thickness, architecture and overall morphology, its coloration is a mixture of that found in *N. flammea* (subtidal) and *N. deaurata* (intertidal). Strebel (1907) described *Nacella cymbularia*, regarded since Powell (1973) as a synonym of *N. mytilina*, which externally resembles *N. yaghana* sp. nov. in the morphology of the shell. However, Strebel (1907 taf. III, fig. 42) reported that *N. cymbularia* exhibits black mantle tentacles, whereas we observed those in *N. yaghana* sp. nov. to be white. At the same time, *N. cymbularia* was recorded from different parts of Patagonia (i.e. Strait of Magellan, Tierra del Fuego and Navarino Island), but not from Garibaldi and the Pía Fjords. Our significant sampling efforts in the Magellanic region show that *N. yaghana* sp. nov. is restricted to Pía and the Garibaldi Fjords, where it co-exists with *N. magellanica* and *N. deaurata*. No record of *N. mytilina* or *N. flammea* exists for these fjords.

### *NACELLA CLYPEATER* (LESSON, 1831)

(FIG. 3)

*Patella clypeater* Lesson, 1831: 419; Reeve, 1854: pl. 16, figs A, B; Huppé, 1854: 259.
*Nacella* (*Patinella*) *clypeater* – Pilsbry, 1891: 122.
*Patinigera clypeata* – Dell, 1964: 273.
*Nacella* (*Patinigera*) *clypeater* – Powell, 1973: 193, pl. 175, figs 1, 2; Ramírez, 1981: 52; Valdovinos & Ruth, 2005: 504.
*Nacella clypeater* – Aldea & Valdovinos, 2005: 369; González-Wevar *et al.*, 2010: 116; 2017: 863.

*Material studied:* Coquimbo (29°58'04.68" S, 71°22'00.79"W) *N* = 40; Valparaíso (33°00'56.98"S, 71°33'39.62"W) *N* = 25; Pichilemu (34°25'29.96"S, 72°02'39.31"W) *N* = 20; Tubul (37°13'11.09"S, 73°26'35.55"W) *N* = 35; Mehuín (39°26'39.04"S, 73°13'52.63"W) *N* = 25; La Misión (39°47'44.48"S, 73°23'59.17"W) *N* = 40; Pucatrihue (40°32'39.92"S, 73°43'16.68"W) *N* = 25.

*Shell:* The shell shape and sculpture are relatively constant in the analysed individuals from different localities along the Chilean Central coast (Fig. 3A–F). The species exhibits a conical morphology, dorsally depressed with a relatively thick and non-translucent shell (Fig. 3A–C). The anterior part of the animal is laterally compressed (Fig. 3D–F). The shell is large (maximum length 120 mm) with a low profile. The apex is situated at the anterior 30% of the shell. The anterior slope of the shell is slightly concave, while the lateral and the posterior slopes are convex (Fig. 3A–C). The aperture of the shell is circular. The surface of the shell is sculptured with fine, rounded near-radial ribs and concentric growth lines beginning below the apex. The margin of the shell is relatively even. The external coloration varies (grey, green and brown) with clear white, yellow and creamy ribs. The internal part of the shell exhibits silvery to pale bronze, with a brown spot that corresponds to the impression of the body.

*External anatomy:* The ventral area of the foot and the mantle fold are creamy white coloured and the epipodial fringe is recognizable. The mantle fold is thin and bordered by a black narrow line. Mantle tentacles are in alternate series of three short ones and a slightly longer one and lack pigmentation (Fig. 3G). The cephalic tentacles are not pigmented (Fig. 3G).

*Radula:* See Valdovinos & Rüth (2005) (Fig. 3H).

*Distribution:* Pacific margin of the Chilean coast between 42°S and 30°S (Fig. 3I).

*Habitat:* Low intertidal and subtidal rocky shores between 0 to 20 m depths.

*Comments:* Field observation along the Chilean coast shows that *N. clypeater* exhibits a patchy distribution being highly abundant in some localities and completely absent at others. In fact, Aguilera (2011), in a rocky intertidal trophic study across the Chilean coast, did

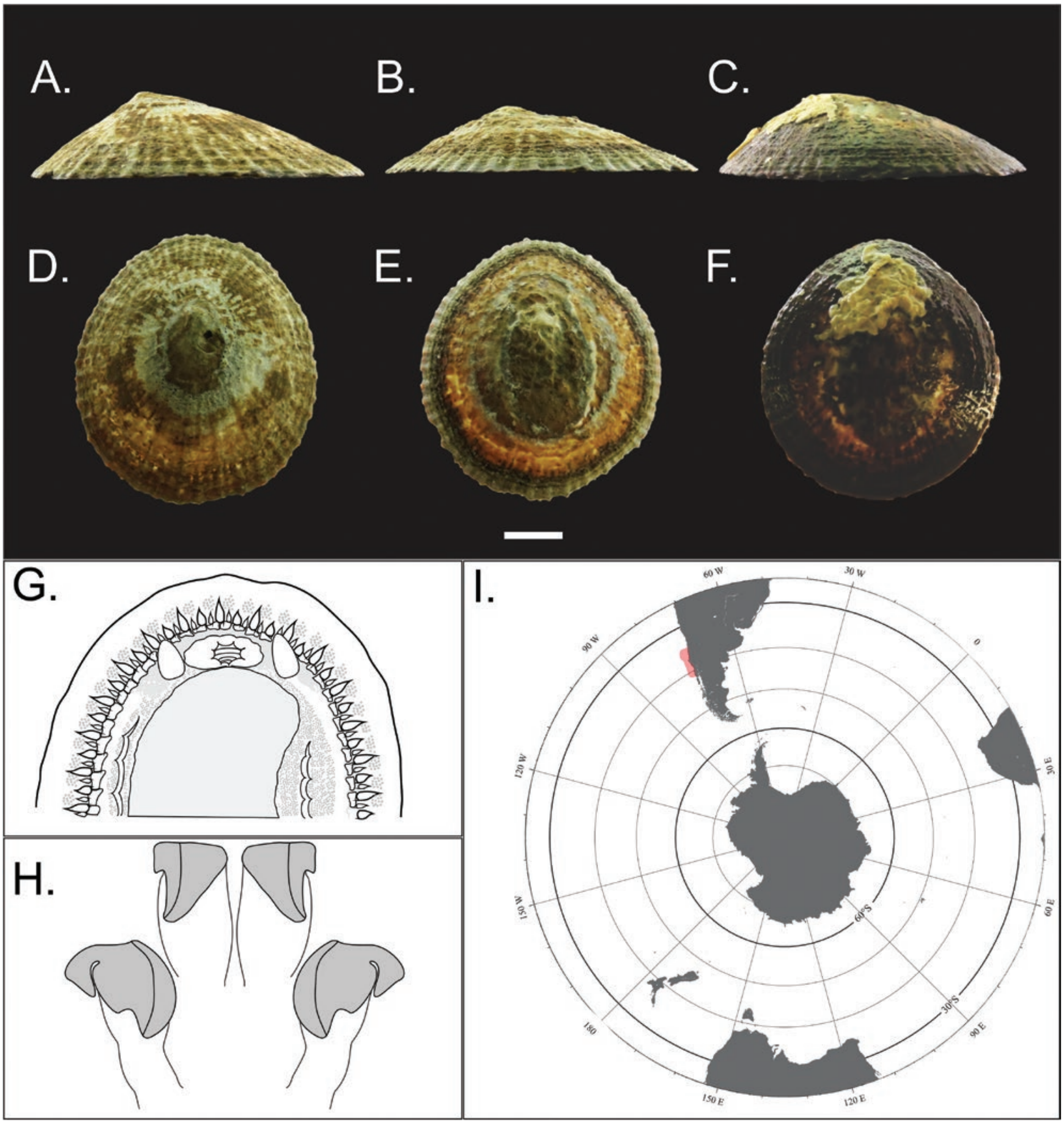

**Figure 3.** *Nacella clypeater*, Central Chile, South America. Scale bar = 1.0 cm for all unless specified otherwise. A = La Misión, B = Tubul, C = Coquimbo. A–F, shell morphology and coloration of *Nacella clypeater*. A–C, lateral view. D–F, dorsal view. G, mantle tentacles, cephalic tentacles and foot coloration patterns. H, radula. I, distribution.

not record the presence of *N. clypeater* and, therefore, considered it as an uncommon inter- subtidal species. Population-based analyses in the species suggest that *N. clypeater* represents a single genetic unit across its distribution and exhibits extremely low levels of mtDNA (*COI*) genetic diversity across its distribution (unpublished data).

### *Nacella magellanica* (Gmelin, 1791)

(Fig. 4)

*Patella magellanica* Gmelin, 1791: 3703; Reeve, 1854: pl. 10, figs 19A, B; Carcelles, 1950: 52, pl. 1, fig. 12.
*Patella atramentosa* Reeve, 1854: pl. 17, fig. 41A, B.
*Patella venosa* Reeve, 1854: pl. 10, fig. 18A–C.
*Patella chiloensis* Reeve, 1855: pl. 33, fig. 98A, B.
*Patella meridionales* Rochebrune & Mabille, 1885: 109.
*Patella metallica* Rochebrune & Mabille, 1885: 109.
*Patella pupillata* Rochebrune & Mabille, 1885: 110.
*Patella tincta* Rochebrune & Mabille, 1885: 110.
*Patinella aenea* var. *magellanica* – Pilsbry, 1891: 119, pl. 44, figs 9, 12, 15, 16; pl. 43, figs 1, 6.
*Patinella magellanica atramentosa* – Strebel, 1907: 146, pl. 6, figs 86, 88; pl. 7, figs 91, 92, 94, 95.
*Patinella aenea* var. *minor* Strebel, 1907: 137, pl. 5, fig. 67a–d.

*Patinella chiloensis* – Strebel, 1907: 151, pl. 7, figs 89, 90.
*Patinella venosa* – Strebel, 1907: 150, pl. 7, fig. 93.
*Patinigera magellanica* – Powell, 1951: 81; Dell, 1964: 273; Castellanos & Landoni, 1988: 22, pl. IV, figs 1, 2.
*Patinigera chiloensis* – Dell, 1964: 273.
*Patinigera magellanica venosa* – Dell, 1964: 273.
*Nacella* (*Patinigera*) *magellanica magellanica* – Powell, 1973: 198, pl. 73, figs 14, 15; pl. 178, figs 1, 2; Ramírez, 1981: 54; Linse, 1999: 400; Aguirre, 2003: 14; Aguirre, Richiano & Sirch, 2006: 252; Aguirre *et al.*, 2009: 423.
*Nacella* (*Patinigera*) *magellanica venosa* – Powell, 1973: 198, pl. 180, figs 3, 4; Ramírez, 1981, 54; Linse, 1999: 400.
*Nacella magellanica* – Guzmán, 1978: 205; Ríos & Gerdes, 1997: 49; Adami & Gordillo, 1999: 186; Ríos & Mutscke, 1999: 196; Bazterrica *et al.*, 2007: 22; Yoon *et al.*, 2007: 64; González-Wevar *et al.*, 2010: 116; 2011a: 1937; 2012a: 448; 2012b: 139; 2017: 863; Aldea & Rosenfeld, 2011: 117; de Aranzamendi, Bastidas & Gardenal, 2011: 2405; 2014: 53; Rosenfeld, Marambio & Aldea, 2013: 11, 2016: 77; Rosenfeld *et al.*, 2015: 62; 2018: 1; Andrade & Brey, 2014: 65; Andrade *et al.*, 2016: 2286.
*Nacella* (*Patinigera*) *magellanica chiloensis* – Ramírez, 1981: 55.
*Nacella* (*Patinigera*) *magellanica* – Guzman & Rios, 1987: 159; Mutshke *et al.*, 1998: 8; Reid & Osorio, 2000: 118; fig. 2L–O; Malanga *et al.*, 2005:551; Valdovinos & Rüth, 2005: 509 (in part), fig. 6A; de Aranzamendi *et al.*, 2009: 1, fig. 2A–O; Thatje & Rios, 2010: 97.
*Nacella* (*Patinigera*) *chiloensis* – Valdovinos & Rüth, 2005: 497.
*Nacella* (*Patinigera*) *venosa* – Valdovinos & Rüth, 2005: 510.
*Nacella venosa* – González-Wevar *et al.*, 2011a: 1937.
*Nacella chiloensis* – González-Wevar *et al.*, 2011a: 1937.
*Nacella magallanica* [*sic*.] – Ojeda *et al.*, 2014: 504.

*Material studied:* Puerto Montt; Reloncaví Fjord (41°28’32.78” S, 72°55’15.04” W) *N* = 30; Metri, Reloncaví Fjord (41°35’37.30” S, 72°42’42.80” W) *N* = 25; Ancud, Chiloé Island (41°53’00.69” S, 73°49’52.29” W) *N* = 25; Concoto Island, Pacific Patagonia (44°14’41.60” S, 73°37’05.68” W) *N* = 35; Puerto Aguirre, Pacific Patagonia (45°09’57.09” S, 73°32’27.07” W) *N* = 25; Costa Channel, Pacific Patagonia (45°48’05.79” S, 74°44’28.52” W) *N* = 40; Serrano Channel, Pacific Patagonia (46°26’45.22” S, 73°47’44.12” W) *N* = 30; Wager Island, Pacific Patagonia (47°48”33.22” S, 75°00’45.33” W) *N* = 30; Madre de Dios Island, Pacific Patagonia (50°07’09.82” S, 75°15’24.79” W) *N* = 20; London Island, Pacific Patagonia (54°40’00.30” S, 72°03’58.67” W) *N* = 30; Carlos III Island, Strait of Magellan (53°38’55.41” S, 72°15’31.04” W) *N* = 30; Port Famine, Strait of Magellan (53°36’34.07” S, 70°55’53.40” W) *N* = 50; Otway Sound, Strait of Magellan (52°56’13.10” S, 71°11’39.07” W) *N* = 30; Chabunco, Strait of Magellan (52°59’14.66” S, 70°48’44.43” W) *N* = 30; Laredo Bay, Strait of Magellan (52°56’59.14” S, 70°48’03.96” W) *N* = 30; Possession Bay, Strait of Magellan (52°13’55.50” S, 69°17’50.71”W) *N* = 30; Santa María Bay, Tierra del Fuego (53°19’29.86” S, 70°22’34.30” W) *N* = 60; Caleta River, Tierra del Fuego (53°51’45.32” S, 70°19’54.11” W) *N* = 60; Pía Fjord, Beagle Channel (54°49’36.81” S, 69°39’11.31” W) *N* = 40; Garibaldi Fjord, Beagle Channel (54°43’20.63” S, 69°57’48.27” W) *N* = 50; Wulaia Bay (54°59’20.30” S, 68°09’02.97” W) *N* = 25; Tekenika Bay (55°03’24.66” S,68°07’52.22” W) *N* = 30; Orange Bay (55°27’21.44” S, 68°04’02.33” W) *N* = 30; Virginia Bay, Beagle Channel (54°54’16.95” S, 67°56’05.35” W) *N* = 30; Puerto Williams, Beagle Channel (54°56’04.95” S, 67°36’48.33” W) *N* = 26; Lapataia Bay, Beagle Channel (54°50’58.94” S, 68°28’41.95” W) *N* = 30; Hornos Island, Cape Horn (55°58’38.36” S, 67°16’36.39” W) *N* = 30; Diego Ramírez Island, Cape Horn (56°30’08.86” S, 68°43’38.85” W) *N* = 25; Puerto Deseado, Atlantic Patagonia (47°45’16.17” S, 65°52’17.58” W) *N* = 25; Comodoro Rivadavia, Atlantic Patagonia (45°51’52.17” S, 67°28’25.50” W) *N* = 26; Hookers Point, Falkland/Malvinas Islands (51°42’09.60” S, 57°46’07.49” W) N = 50.

*Shell:* The shell shape and sculpture are very variable in this species (de Aranzamendi *et al.*, 2009; González-Wevar *et al.*, 2011a) (Fig. 4A–C). The species exhibits a conical morphology, dorsally raised with a very thick and non-translucent shell (Fig. 4A–F). The anterior part of the animal is laterally compressed (Fig 4D–F). The shell is large (maximum length 140 mm), with a high profile. The apex is situated at the anterior 40–50% of the shell’s length (Fig. 4A–F). All the slopes of the shell are convex (Fig. 4A–C). The aperture of the shell is oval. The surface of the shell is sculptured with raised angular primary radial ribs, weaker secondary ones and concentric growth lines across the interspaces. The margin of the shell is highly crenulated. The external coloration of the shell is very variable in the species across its distribution (pale reddish brown, white with dark lines, grey, green and brown). The primary and secondary ribs are brown ash-coloured to dark brown, with clearer interspaces. The internal part of the shell has soft metallic brown coloration with dark lines corresponding to external colour patterns, bordered by a white/brown halo.

*External anatomy:* The ventral area of the foot is light grey and the epipodial fringe is recognizable. The mantle fold is thick and dun-brown coloured.

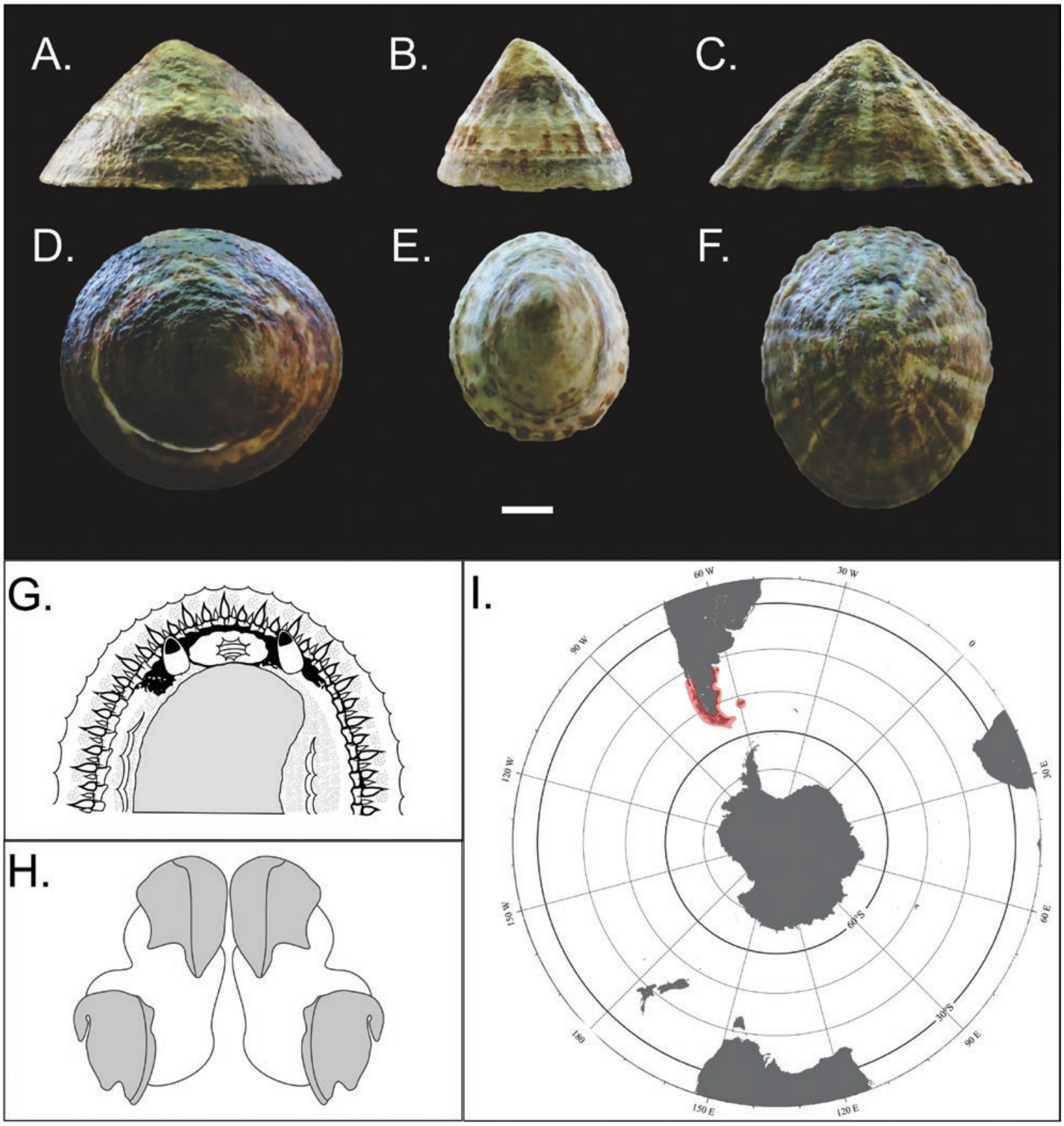

**Figure 4.** *Nacella magellanica*, Patagonia, South America. Scale bar = 1.0 cm for all unless specified otherwise. A = Chiloé, B = Port Famine, C = Falkland/Malvinas Islands. A–F, shell morphology and coloration of *Nacella magellanica*. A–C, lateral view. D–F, dorsal view. G, mantle tentacles, cephalic tentacles and foot coloration patterns. H, radula. I, distribution.

The mantle tentacles are in alternate series of three white shorter and a white longer one and are absent of pigmentation (Fig. 4G). The cephalic tentacles are dorsally pigmented with a black line (Fig. 4G).

*Radula:* See Valdovinos & Rüth (2005) (Fig. 4H).

*Distribution:* Magellanic province. Pacific Patagonia from Chiloé Island to Cape Horn. Atlantic Patagonia from Tierra del Fuego to the Río Negro Province. Falkland/Malvinas Islands (Fig. 4I).

*Habitat:* High and medium intertidal rocky ecosystem between 0 and 25 m depths.

*Comments:* The species is highly abundant, with a continuous distribution along Pacific Patagonia from Chiloé Island to Cape Horn, including fjords and channels, the Strait of Magellan and Tierra del Fuego, Cape Horn, Hornos Islands and Diego Ramírez Islands (Guzman, 1978; Rios & Gerdes, 1997; Linse, 1999; Reid & Osorio, 2000; Aldea & Rosenfeld, 2011; Gonzalez-Wevar *et al.*, 2012a; Ojeda *et al.*, 2014; Rosenfeld *et al.*, 2015). In the Atlantic, *N. magellanica* is also highly abundant up north to the Río Negro Province. However, along the Atlantic coast the distribution and abundance of *N. magellanica* depends on the availability of suitable rocky habitats (Bazterrica *et al.*, 2007; de Aranzamendi *et al.*, 2009, 2011, 2014). Similarly, *N. magellanica* is highly abundant in the Falkland/Malvinas Islands. *Nacella magellanica* comprises a single genetic unit throughout Pacific (González-Wevar *et al.*, 2012a) and Atlantic (de Aranzamendi *et al.* 2009, 2011) Patagonia, with Falkland/Malvinas Islands populations detectably different (González-Wevar *et al.*, 2012a). Molecular and geometric morphometric comparisons showed that *N. chiloensis* and *N. venosa* are synonyms of *N. magellanica* (González-Wevar *et al.*, 2011a).

### *NACELLA DEAURATA* (GMELIN, 1791)

(FIG. 5)

*Patella aenea* Martyn, 1784: pl. 1, fig. 17 (invalid).
*Patella deaurata* Gmelin, 1791: 3719; Strebel, 1907: 137, pl. 5, figs 62, 65, 68, 70; pl. 6, figs 76, 81; Carcelles, 1950: 52, pl. 1, fig. 13.
*Patella varicosa* Reeve, 1854: pl. 11, fig. 21A–C.
*Patella fuegiensis* – Reeve, 1855; pl. 28, fig. 73A, B; Rochebrune & Mabille, 1885: 95.
*Nacella strigatella* Rochebrune & Mabille, 1885: 110.
*Nacella* (*Patinella*) *aenea* – Pilsbry, 1891: 118, pl. 46, figs 28, 36.
*Patinella delicatissima* – Strebel, 1907: 145; pl. 5, figs 71, 72, 74, 75; Strebel 1908: pl. 1, figs 75, 75A.
*Helcioniscus benneti* – Preston, 1913: 221, pl. 4, fig. 7.
*Patella delicatissima* – Melvill & Standen, 1914: 114; Carcelles, 1950: 52, pl. 1, fig. 14.
*Nacella* (*Patinigera*) *aenea* – Wenz, 1938: 328, fig. 401.
*Patinigera aenea* – Powell, 1951: 82.
*Patinigera fuegiensis* – Powell, 1955: 67.
*Patinigera delicatissima* – Powell, 1951: 82; Dell, 1964: 273; Castellanos & Landoni, 1988: 24, pl. IV, fig. 4; Aguirre, 2003: 20.
*Patinigera deaurata* – Dell, 1964: 273; Aguirre *et al.*, 2006: 251.
*Nacella* (*Patinigera*) *fuegiensis* – Powell, 1973: pl. 177, figs 1, 2; Ramírez, 1981: 53.
*Nacella* (*Patinigera*) *deaurata deaurata* – Powell, 1973: 195; Ramírez, 1981: 56; Linse, 1999: 400.
*Nacella* (*Patinigera*) *deaurata* form *delicatissima* – Powell, 1973: 195; pl. 178, figs 3, 4; Ramirez, 1981: 57; Linse, 1999: 400.
*Nacella* (*Patinigera*) *delicatissima* – Cantera & Arnaud, 1985: 34; Valdovinos & Rüth, 2005: 506; de Aranzamendi *et al.*, 2009.
*Nacella* (*Patinigera*) *deaurata* – Morriconi & Calvo, 1993: 135; Mutschke *et al.*, 1998: 8; Morriconi, 1999; 417; Malanga *et al.*, 2005: 551; Valdovinos & Rüth, 2005: 505, fig. 5A; de Aranzamendi *et al.*, 2009: 1; Aguirre *et al.*, 2009: 252; Thatje & Rios, 2010: 97.
*Nacella deaurata* – Rios & Gerdes, 1997: 50; Adami & Gordillo, 1999: 186; Ríos & Mutschke, 1999: 196; Aguirre *et al.*, 2009: 419; González-Wevar *et al.*, 2010: 116; 2011a: 1937; 2017: 864; Aldea & Rosenfeld, 2011; 117; Ojeda *et al.*, 2014: 504; Rosenfeld *et al.*, 2013: 11; 2015b; 55; 2016: 77; 2017: 4; 2018: 1.
*Nacella* (*Patinigera*) *fugiensis* [*sic.*] – Linse, 1999: 400.
*Nacella* (*Patinigera*) *magellanica* – Valdovinos & Rüth, 2005: 509 (in part, not of Helbling).
*Nacella delicatissima* – Aguirre *et al.*, 2006: 252; Aguirre *et al.*, 2009: 454; González-Wevar *et al.*, 2011a: 1937.
*Nacella fuegiensis* – González-Wevar *et al.*, 2011a: 1937.

*Material studied:* London Island, Pacific Patagonia (54°40’00.30” S, 72°03’58.67” W) *N* = 30; Carlos III Island, Strait of Magellan (53°38’55.41” S, 72°15’31.04” W) *N* = 20; Port Famine, Strait of Magellan (53°36’34.07” S, 70°55’53.40” W) *N* = 50; Otway Sound, Strait of Magellan (52°56’13.10” S, 71°11’39.07” W) *N* = 30; Chabunco, Strait of Magellan (52°59’14.66” S, 70°48’44.43” W) *N* = 30; Laredo Bay, Strait of Magellan (52°56’59.14” S, 70°48’03.96” W) *N* = 50; Possession Bay, Strait of Magellan (52°13’55.50” S, 69°17’50.71” W) *N* = 30; Santa María Bay, Tierra del Fuego (53°19’29.86” S, 70°22’34.30” W) *N* = 60; Caleta River, Tierra del Fuego (53°51’45.32” S, 70°19’54.11” W) *N* = 60; Pía Fjord, Beagle Channel (54°49’36.81” S, 69°39’11.31” W) *N* = 40; Garibaldi Fjord, Beagle Channel (54°43’20.63” S, 69°57’48.27” W) *N* = 30; Wulaia Bay (54°59’20.30” S, 68°09’02.97” W) *N* = 40; Tekenika Bay (55°03’24.66” S, 68°07’52.22” W) *N* = 30; Orange Bay (55°27’21.44” S, 68°04’02.33” W) *N* = 30; Virginia Bay, Beagle Channel (54°54’16.95” S, 67°56’05.35” W) *N* = 40; Puerto Williams, Beagle Channel (54°56’04.95” S, 67°36’48.33” W) *N* = 26; Lapataia Bay, Beagle Channel (54°50’58.94” S, 68°28’41.95” W) *N* = 40; Hookers Point, Falkland/Malvinas Islands (51°42’09.60” S, 57°46’07.49” W) *N* = 50.

*Shell:* Shell shape and sculpture are very variable (de Aranzamendi *et al.*, 2009) (Fig. 5A–C). The species exhibits a conical morphology, dorsally raised shell, which is thick and non-translucent (Fig. 5A–F). The anterior part of the animal is laterally compressed (Fig. 5D–F). It has a large shell (maximum length 120 mm), which has a medium profile. The apex is located at the anterior 30–40% of the shell’s length (Fig. 5A–F). All the slopes of the shell are convex (Fig. 5A–C). The aperture is oval to oblong. The surface of the shell is sculptured with numerous broad radial ribs and clearly defined concentric growth lines from the central zone towards the margin. The margin of the shell margin is highly crenulated. The external coloration of the shell is very variable across its distribution (pale reddish, brown, green with a bronze apex, grey, brown). The

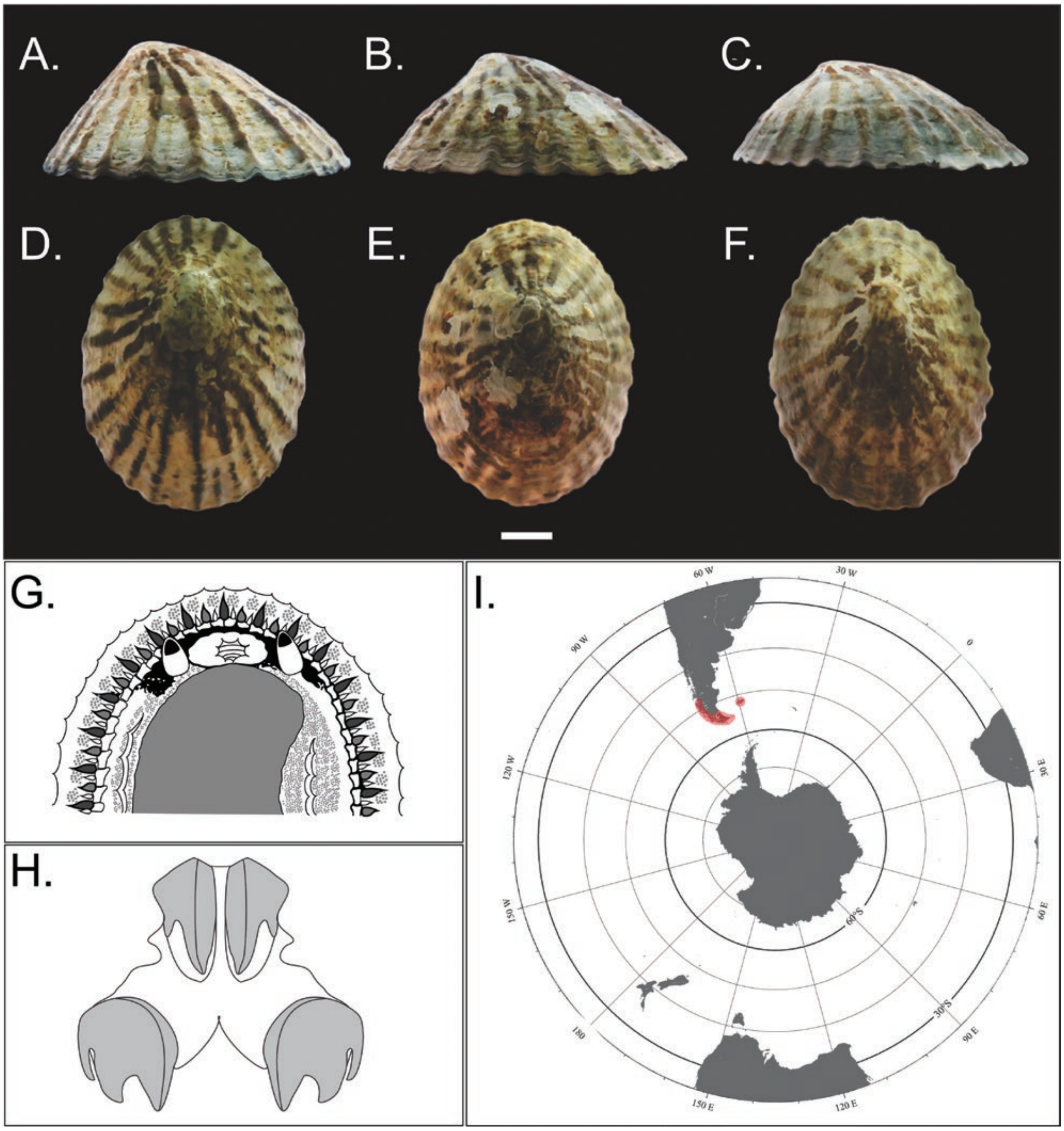

**Figure 5.** *Nacella deaurata*, Patagonia, South America. Scale bar = 1.0 cm for all unless specified otherwise. A = Port Famine, B = Navarino Island, C = Falkland/Malvinas. A–F, shell morphology and coloration of *Nacella deaurata*. A–C, lateral view. D–F, dorsal view. G, mantle tentacles, cephalic tentacles and foot coloration patterns. H, radula. I, distribution.

primary and secondary ribs are dark brown with clearer interspaces. The internal part of the shell has a soft metallic grey/brown interior with dark lines corresponding to external colour patterns, bordered by a white/brown halo.

*External anatomy:* The ventral area of the foot is grey and the epipodial fringe is recognizable. The mantle fold is thick and cream-coloured. The mantle tentacles are in an alternated series of three shorter pigmented ones (white/black/white) and a black longer one (Fig. 5G). The cephalic tentacles are dorsally pigmented with a black line (Fig. 5G).

*Radula:* See Valdovinos & Rüth (2005) (Fig. 5H).

*Distribution:* Magellanic province. Pacific Patagonia: from Guarello Island (50°S) to Cape Horn. Atlantic Patagonia: Tierra del Fuego. Falkland/Malvinas Islands (Fig. 5I).

*Habitat:* Medium and low intertidal, subtidal rocky ecosystem between 0 and 40 m depths.

*Comments:* Our extensive sampling effort across Pacific Patagonia suggests that *N. deaurata* occurs in this region from Guarello Island (50°S) to Cape Horn. In the Atlantic coast this species was reported north up to Mar del Plata province (Morris & Rosenberg, 2005). However, according to de Aranzamendi *et al.* (2009) the distribution of the species in the Atlantic is restricted to Tierra del Fuego. This species is also abundant in the Falkland/Malvinas Islands. Molecular analyses suggest that *N. deaurata* represents a single genetic unit along Pacific (González-Wevar *et al.*, 2011a) and Atlantic (de Aranzamendi *et al.*, 2009, 2011) Patagonia. Molecular and geometric morphometric comparisons (González-Wevar *et al.*, 2011a) showed that *N. fuegiensis* is a synonym of *N. deaurata*. Similarly, molecular analyses indicate that *N. delicatissima* represents particular morphotypes of *N. deaurata* (*contra* de Aranzamendi *et al.*, 2009). Molecular analyses (unpublished data) indicate that *N. deaurata* exhibits marked levels of population genetic differentiation between Patagonia and the Falkland/Malvinas Islands.

### *NACELLA MYTILINA* (HELBLING, 1779)

(FIG. 6)

*Patella mytilina* Helbling, 1779: 104, pl. 1, figs 5, 6; Gmelin, 1791: 3698; Strebel, 1907: 113, pl. 3, fig. 44; pl. 4, figs 49, 51, 55, 57A, 59.
*Patella mytiliformis* Lightfoot, 1786: 42.
*Patella conchacea* Gmelin, 1791: 3708.
*Nacella mytiloides* Schumacher, 1817: 179.
*Patella cymbularia* Lamarck, 1819: 335; Mermod, 1950: 700, fig. 11.
*Patella cymbuloides* Lesson, 1830: 422.
*Patella hyalina* Philippi, 1845: 59.
*Patella vitrea* Philippi, 1845: 60.
*Patella cymbium* Philippi, 1845: 60.
*Nacella mytilina* – Dall, 1870: 274; Rochebrune & Mabille, 1889: 97; Pilsbry, 1891: 115, pl. 50, figs 32–39; Pelseneer, 1903: 6; Smith, 1905: 336; Thiele, 1912: 234; Melvill & Standen, 1914: 114; Carcelles, 1950: Vol. 2: 52; Powell, 1951: 80; Dell, 1964: 273; Powell, 1973, 192: Vol. 3, 191, pl. 173, figs 1, 2; Castellanos & Landoni 1988: pl. IV, figs 9, 10; Ríos & Gerdes 1997: 51; Mutshke *et al.* 1998: 8; Ríos *et al.*, 2007: 100; de Aranzamendi *et al.*, 2009: 1; González-Wevar *et al.*, 2010: 116; 2011a: 1937; 2016a: 1; 2017: 863; Rosenfeld *et al.*, 2015: 55; 2016: 76.
*Nacella compressa* Rochebrune & Mabille, 1889: 98, pl. 5, fig. 9.
*Nacella falklandica* Preston, 1913: 221, pl. 4, fig. 6.
*Nacella* (*Nacella*) *mytilina* – Wenz, 1938: 217, fig. 400; Carcelles & Williamson, 1951: 257; Carcelles, 1953: 164, pl. 1, fig. 11; Ramírez, 1981: 51; Valdovinos & Rüth, 2005: 499, fig. 2A.
*Nacella* (*Patinigera*) *mytilina* [*sic.*] – Linse, 1999: 400.
*Nacella mytelina* [*sic.*] Adami & Gordillo, 1999: 186.

*Studied material:* Tamar Island, Strait of Magellan (52°53’48.04” S, 73°47’15.03” W) $N = 20$; Duntze Sound, Strait of Magellan (54°19’22.32” S, 73°48’12.11” W) $N = 20$; London Island, Pacific Patagonia (54°40’00.30” S, 72°03’58.67” W) $N = 24$; Carlos III Island, Strait of Magellan (53°38’55.41” S, 72°15’31.04” W) $N = 50$; Port Famine, Strait of Magellan (53°36’34.07” S, 70°55’53.40” W) $N = 50$; Carrera Point, Strait of Magellan (53°35’10.92” S, 70°55’24.14” W) $N = 30$; Otway Sound, Strait of Magellan (52°56’13.10” S, 71°11’39.07” W) $N = 25$; Chabunco, Strait of Magellan (52°59’14.66” S, 70°48’44.43” W) $N = 30$; Laredo Bay, Strait of Magellan (52°56’59.14” S, 70°48’03.96” W) $N = 30$; Possession Bay, Strait of Magellan (52°13’55.50” S, 69°17’50.71” W) $N = 30$; Santa María Bay, Tierra del Fuego (53°19’29.86” S, 70°22’34.30” W) $N = 40$; Caleta River, Tierra del Fuego (53°51’45.32” S, 70°19’54.11” W) $N = 30$; Virginia Bay, Beagle Channel (54°54’16.95” S, 67°56’05.35” W) $N = 30$; Puerto Williams, Beagle Channel (54°56’04.95” S, 67°36’48.33” W) $N = 35$; Hookers Point, Falkland/Malvinas Islands (51°42’09.60” S, 57°46’07.49” W) $N = 40$.

*Shell:* The shell shape and sculpture are relatively variable in the analysed individuals across the species’ distribution (Fig. 6A–C). The species exhibits a conical morphology, oblique with a very thin and translucent shell (Fig. 6A–F). The anterior part of the animal is laterally compressed (Fig. 6D–F). It has a medium shell size (maximum length 90 mm) and a medium profile. The apex is situated at the anterior 10% of the shell’s length, anteriorly directed and curved toward the border. The anterior slope of the shell is concave, while the posterior and lateral ones are convex (Fig. 6A–F). The aperture of the shell is oval to oblong. The surface of the shell has a sculpture of a few radial ribs, more obvious in the anterior zone, and concentric growth lines, which increase in thickness towards the shell margin. The margin of the shell is relatively even. The external coloration varies (pearly cream, yellow and light brown with darker tones towards the margin with a brown/red apex). The internal part of the shell is simple with white nacreous coloration.

*External anatomy:* The ventral area of the foot varies from dark grey to black and the epipodial fringe is highly recognizable (Fig. 6G). The mantle fold is narrow and cream-coloured. The mantle tentacles are in alternated series of three white shorter ones and a white longer one (Fig. 6G). Nevertheless, some individuals also exhibit a configuration of three shorter (white/black/white) and a black longer one. The cephalic tentacles are dorsally pigmented with a black line (Fig. 6G)

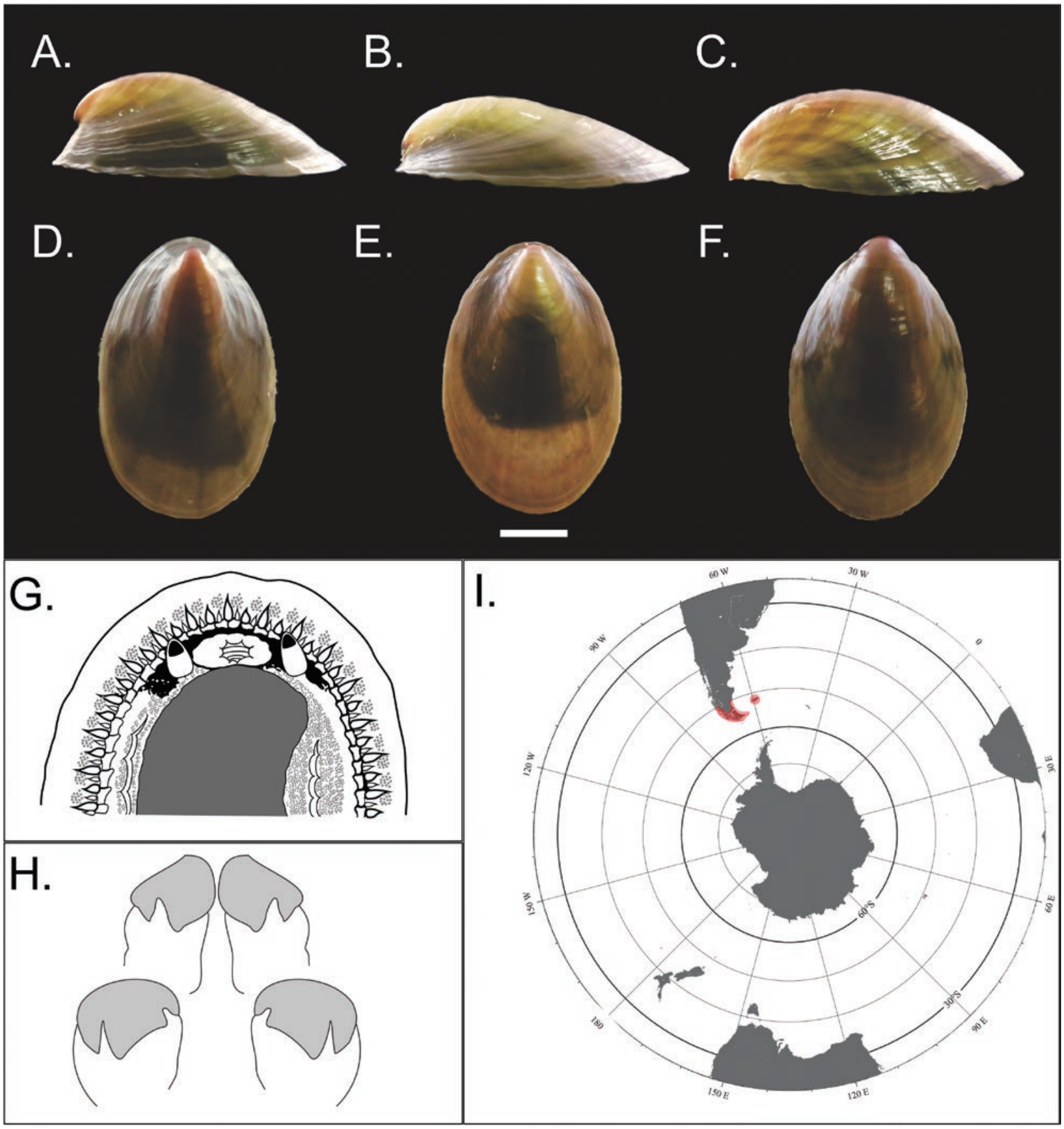

**Figure 6.** *Nacella mytilina*, Patagonia, South America. Scale bar = 1.0 cm for all unless specified otherwise. A = Port Famine, B = Navarino Island, C = Falkland/Malvinas Islands. A–F, shell morphology and coloration of *Nacella mytilina*. A–C, lateral view. D–F, dorsal view. G, mantle tentacles, cephalic tentacles and foot coloration patterns. H, radula. I, distribution.

*Radula:* See Valdovinos & Rüth (2005) (Fig. 6H).

*Distribution:* Magellanic province. Pacific Patagonia: from Guarello Island (50°S) to Cape Horn (56°S). Atlantic Patagonia: Tierra del Fuego to Puerto Deseado (47°S). Falkland/Malvinas Islands (Fig. 6I).

*Habitat: Nacella mytilina* is regularly found on macroalgae (*Macrocystis*, *Gigartina* and *Lessonia*; Rosenfeld *et al.*, 2015) but in some localities individuals can also be found on inter- and subtidal rocks.

*Comments:* The previously recognized distribution of *N. mytilina* included the Magellanic province and the Kerguelen Archipelago (Powell, 1955, 1957, 1973; Cantera & Arnaud, 1985; Troncoso *et al.*, 2001), as well as Antarctica (Castellanos & Landoni, 1988). Cantera & Arnaud (1985) treated *N. kerguelenensis* from the Kerguelen Islands as a junior synonym of *N. mytilina*. However, recent multi-locus molecular analyses have demonstrated that kelp-associated *N. mytilina*-like individuals from the Kerguelen Islands represent a particular morphotype of *N. kerguelenensis*, which is genetically distinct from *N. mytilina* (González-Wevar *et al.*, 2017). At the same time, no confirmed record exists for *N. mytilina* in Antarctica or in peri-Antarctic islands, such as South Shetlands Islands or South Orkneys. Accordingly, the distribution of *N. mytilina* is restricted to southern South America and the Falkland/Malvinas Islands. As recorded for other Patagonian marine invertebrates (Leese *et al.*, 2008; González-Wevar *et al.*, 2012a, 2018), *N. mytilina* exhibits population-level genetic differentiation between Pacific Patagonia and the Falkland/Malvinas Islands (González-Wevar *et al.*, 2016a).

### *NACELLA FLAMMEA* (GMELIN, 1791)

(FIG. 7)

*Patella flammea* Gmelin, 1791: 3716, pl. 5, fig. 42.
*Patinella flammea* – Strebel, 1907: 145, pl. 5, fig. 73.
*Nacella* (*Patinigera*) *flammea* – Powell, 1973: 197, pl. 181; Mutschke *et al.*, 1988: 8; Ramírez, 1981: 57; Linse, 1999: 400; Valdovinos & Rüth, 2005: 508, fig. 5C; González-Wevar *et al.*, 2010: 116.
*Nacella flammea* – Ríos & Gerdes, 1997: 51; Ríos & Mutschke, 1999: 196; de Aranzamendi *et al.*, 2009: 1; González-Wevar *et al.*, 2011a: 1937; 2017: 863; Rosenfeld *et al.*, 2015: 55; 2016: 77.

*Material studied:* Melimoyu (43°03'33.63" S, 73°15'12.55" W) *N* = 25; Port Famine, Strait of Magellan (53°36'34.07" S, 70°55'53.40" W) *N* = 50; Laredo Bay, Strait of Magellan (52°56'59.14" S, 70°48'03.96" W) *N* = 30; Tekenika Bay (55°03'24.66" S, 68°07'52.22" W) *N* = 40; Puerto Williams, Beagle Channel (54°56'04.95" S, 67°36'48.33" W) *N* = 40; Hookers Point, Falkland/Malvinas Islands (51°42'09.60" S, 57°46'07.49" W) *N* = 25.

*Shell:* The shell shape and sculpture are relatively constant in the analysed individuals (Fig. 7A–C). The species exhibits a conical morphology, dorsally depressed with a thin and relatively translucent shell (Fig. 7A–F). The anterior part of the animal is laterally compressed (Fig. 7D–F). It has a medium shell size (maximum length 80 mm) and a low profile. The apex is situated at the anterior 30–40% of the shell's length. All the slopes of the shell are regularly straight (Fig. 7A–F). The aperture of the shell is oval to oblong. The surface of the shell is sculptured with radial ribs, more obvious in the anterior zone, and concentric growth lines, which increase in thickness towards the shell margin. The margin of the shell is relatively even. The external coloration is quite constant in the analysed individuals with a white coloration pattern with light brown/grey/purple rays. Some rays beginning below the apical zone, others at the margin. The internal part of the shell exhibits a nacreous halo and a dun-brown spot corresponding to the animal's body impression. *Nacella flammea* individuals exhibit similar internal and external coloration patterns.

*External anatomy:* The ventral area of the foot is white to light grey and the epipodial fringe is recognizable (Fig. 7G). The mantle fold is thick and creamy coloured. The mantle tentacles are in alternated series of three white shorter ones and a light grey longer one (Fig. 7G). The cephalic tentacles are not pigmented (Fig. 7G).

*Radula:* The first lateral teeth are set close together on the anterior edge of the basal plates, long and sharp pointed, with two cusps. The second laterals are broader, wider spaced, with three short cusps (Fig. 7H).

*Distribution:* Magellanic province. Pacific Patagonia: from Melimoyu (44°S) to Cape Horn (56°S). Atlantic Patagonia: Tierra del Fuego. Falkland/Malvinas Islands (Fig. 7I).

*Habitat:* Subtidal rocky ecosystem between 5 and 40 m.

*Comments:* Field observations along the Magellanic province reveal that *N. flammea* exhibits a patchy distribution, being highly abundant in some localities and completely absent at others. Nevertheless, preliminary population-based analyses of the species suggest that it represents a single genetic unit across its distribution (unpublished data). This revision extends the known northern limit of this species to the Melimoyu Islands (44°03'33.63" S, 73°15'12.55" W).

### *NACELLA CONCINNA* (STREBEL, 1908)

(FIG. 8)

*Patella polaris* Hombron & Jacquinot, 1841: 191 (not of Röding, 1798); Martens & Pfeffer, 1886: 101, pl. 2, figs 11–13; Melvill & Standen, 1907: 124.
*Nacella polaris* – Pilsbry, 1891: 120, pl. 49, figs 21–27; Lamy, 1906: 10, Lamy, 1911: 26.
*Nacella aenea* var. *polaris* – Pelseneer, 1903: 14.
*Patinella polaris* – Strebel, 1908: 81, pl. 5, figs 79–82.
*Patinella polaris* var. *concinna* Strebel, 1908: 81, pl. 5, fig. 77.
*Lepeta depressa* Hedley, 1916: 42, pl. 6, fig. 64; Arnaud, 1972: 114; Dell, 1972: 32, figs 19, 24–25; Egorova, 1982: 14, fig. 75.
*Nacella* (*Patinigera*) *polaris* – David, 1934: 127; Zelaya, 2005: 111, fig. 2.
*Patinigera polaris* – Powell, 1951: 82; Walker, 1972: 49; Castellanos & Landoni, 1988: 25, pl. 4, fig. 8.
*Patinigera polaris concinna* – Powell, 1951: 83; Castellanos & Landoni, 1988: 26, pl. 4, fig. 5.
*Nacella* (*Patinigera*) *concinna* – Powell, 1973: 193–195, pl. 175, figs 1–5; Picken, 1980: 71; Ramírez 1981: 58; 71; Picken & Allan, 1983: 273; Brêthes *et al.*, 1984: 161; González-Wevar *et al.*, 2010: 116; González-Wevar *et al.*, 2011b: 220.

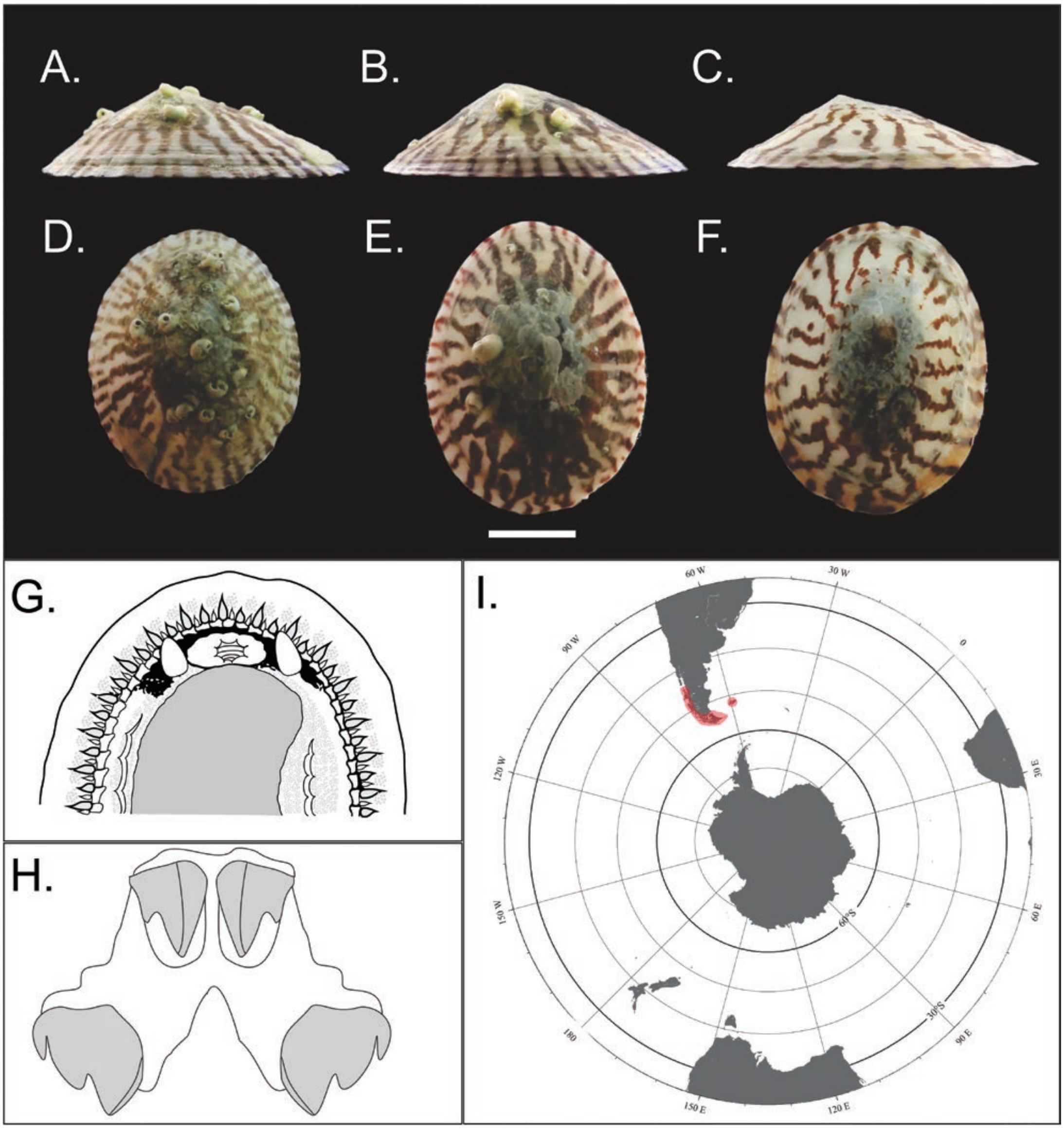

**Figure 7.** *Nacella flammea*, Patagonia, South America. Scale bar = 1.0 cm for all unless specified otherwise. A = Melimoyu, B = Port Famine, C = Falkland/Malvinas Islands. A–F, shell morphology and coloration of *Nacella flammea*. A–C, lateral view. D–F, dorsal view. G, mantle tentacles, cephalic tentacles and foot coloration patterns. H, radula. I, distribution.

*Patinigera polaris polaris* – Castellanos & Landoni, 1988; 26, pl. 4, fig. 8.
*Nacella concinna* – Beaumont & Wei, 1991: 443; Linse *et al.*, 2006: 997; de Aranzamendi *et al.*, 2008: 875; Hoffman *et al.*, 2010a: 287; 2010b: 765; 2011: 55; 2012a: 922; 2012b: 1; 2013: 1; González-Wevar *et al.*, 2013: 5221; 2017: 863; Rosenfeld *et al.* 2017: 3.
*Nacella* cf. *concinna* – Hain & Melles, 1994: 36, fig. 4.1.
*Nacella polaris concinna* – Aldea, Olabarria & Troncoso, 2008: 355; Aldea & Troncoso, 2009; 49, fig. 2.
*Nacella polaris polaris* – Aldea *et al.*, 2008: 49, fig. 3.

*Material studied:* Rothera Station, Adelaide Island, Antarctic Peninsula (67°34’03.17” S, 68°07’17.40” W) *N* = 50; South Bay, Anvers Island (64°53’21.55” S, 63°35’43.44” W) *N* = 40; Yelcho Station, Doumer Island, Palmer Archipelago, Antarctic Peninsula (64°53’34.29” S, 63°35’09.04” W) *N* = 40; Covadonga Bay, Antarctic Peninsula (63°19’13.96” S, 57°53’54.15” W) *N* = 50, James Ross Island, East Antarctic Peninsula (63°55’14.33” S, 57°15’54.22” W) *N* = 40, Hannah Point, Livingstone Island, South Shetland Islands (62°39’11.31” S, 60°36’55.44” W) *N* = 40; Fildes

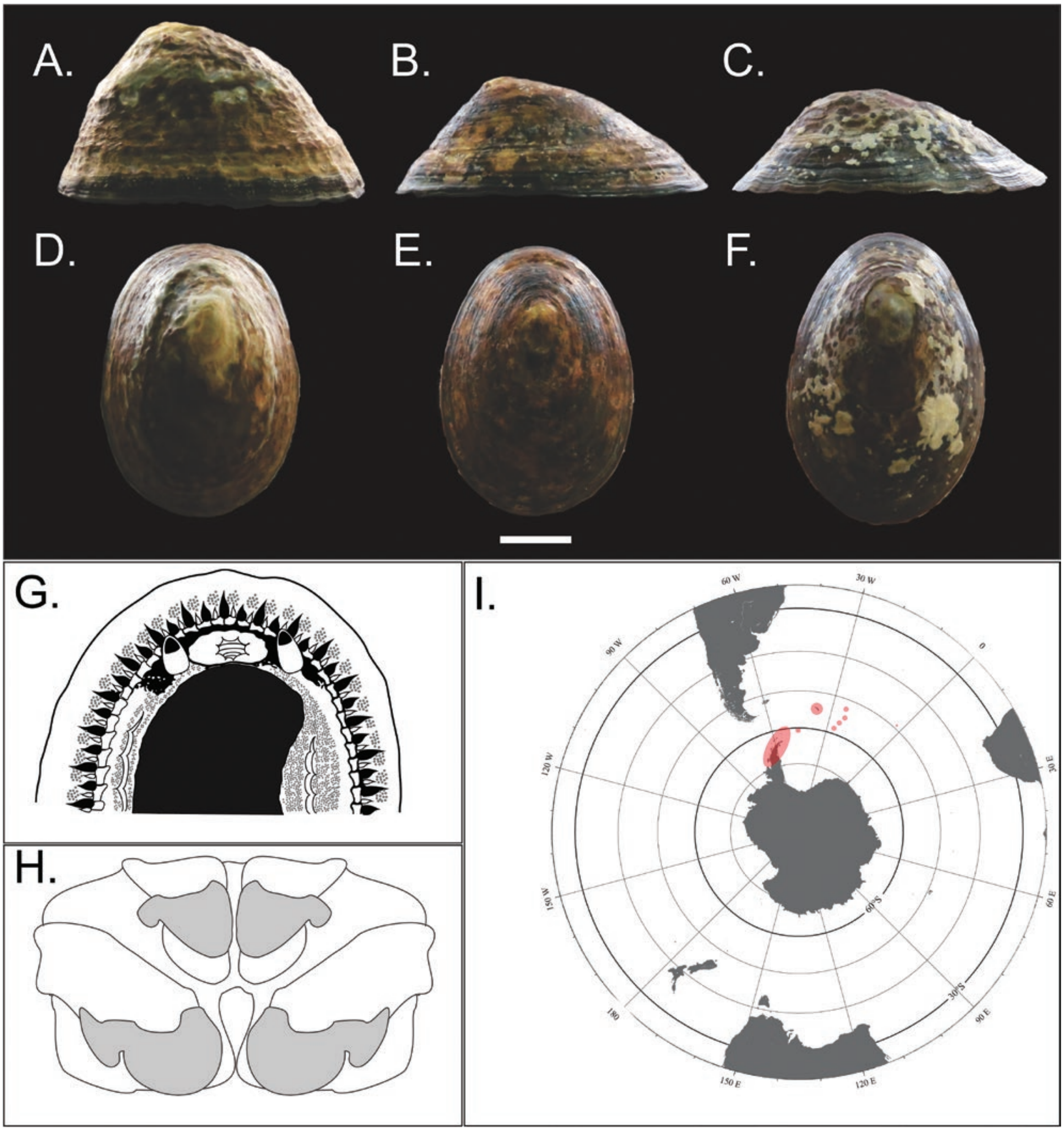

**Figure 8.** *Nacella concinna*, maritime Antarctica. Scale bar = 1.0 cm for all unless specified otherwise. A = Fildes Bay, South Shetland Islands, B = Marguerite Bay, Anvers Island, C = South Georgia. A–F, shell morphology and coloration of *Nacella concinna*. A–C, lateral view. D–F, dorsal view. G, mantle tentacles, cephalic tentacles and foot coloration patterns. H, radula. I, distribution.

Bay, King George Island, South Shetland Islands (62°12'28.68" S, 58°57'24.89" W) *N* = 80, Admiralty Bay, King George Island, South Shetland Islands (62°05'14.40" S, 58°27'29.57" W) *N* = 80; Deception Island (62°55'14.52" S, 60°35'14.62" W) *N* = 50; Elephant Island (61°05'12.24" S, 55°20'22.54" W) *N* = 29; South Orkney Island (60°44'20.03" S, 44°44'17.05" W) *N* = 26; Signy Island, South Orkneys Islands (60°43'22.22" S, 45°35'16.14" W) *N* = 30; South Georgia (54°17'00.11" S, 36°29'13.04" W) *N* = 100.

*Shell:* The shell shape and sculpture are very variable (Beaumont & Wei, 1991; de Aranzamendi *et al.*, 2008; Hoffman *et al.*, 2010b; González-Wevar *et al.*, 2011b) (Fig. 8A–C). The species exhibits a conical morphology, dorsally raised, with a thick and non-translucent shell (Fig. 8A–F). The anterior part of the animal is laterally compressed (Fig. 8D–F). It has a large shell (maximum length 120 mm) and a variable profile (Fig. 8A–C). The apex is situated at the anterior 30–40% of the shell's length (Fig. 8A–C). All the slopes of the shell are convex (Fig. 8D–F). The aperture of the shell is oval. The surface of the shell is sculptured with weak primary radial ribs, weaker secondary ones and concentric growth lines. The margin of the shell is highly crenulated. The external coloration is very variable (pale brownish/green/grey to dark brown and black). The internal part of the shell varies from creamy nacreous to dark bronzy-brown with dark lines corresponding to external colour patterns.

*External anatomy:* The ventral area of the foot is black and the epipodial fringe is highly recognizable. The mantle fold is thick and dun-brown coloured. The mantle tentacles are in alternate series of a single black longer tentacle and three shorter ones (white/black/white) (Fig. 8G). The cephalic tentacles are dorsally pigmented with a black line (Fig. 8G).

*Radula:* The first lateral teeth are set close together on the anterior edge of the basal plates, of medium length and with two spoon-like cusps. The second laterals are broader, wider spaced, with two spoon-like cusps. One of them is very small and the other is bigger and broader (Fig. 8H).

*Distribution:* Maritime Antarctica, including ice-free rocky ecosystems of the Antarctic Peninsula, the South Shetland Islands, South Georgia, South Orkneys, Bouvet, Elephant Island, Seymour Island, Paulet Island, Wander Island, Anvers Island and Peterman Island (Fig. 8I).

*Habitat:* Intertidal and subtidal between 0 and 150 m depths.

*Comments:* The Antarctic limpet represents a single genetic population along maritime Antarctica (González-Wevar *et al.*, 2011b, 2013, 2016b, 2017), but this population differes markedly from those from South Georgia (González-Wevar *et al.*, 2013). The inter- and subtidal morphotypes were once regarded as separate subspecies, *N. polaris polaris* and *N. polaris concinna* (Powell, 1951). Nevertheless, genetic comparisons using allozymes (Beaumont & Wei, 1991), mtDNA (González-Wevar *et al.*, 2011b, 2013, 2016b) and AFLPs (Hoffman *et al*., 2010b) confirmed that these forms represent a single evolutionary unit. Accordingly, shell height, shape and sculpture differences in the Antarctic limpet represent phenotypic plasticity in the species.

### *NACELLA DELESSERTI* (PHILIPPI, 1849)

(FIG. 9)

*Patella delesserti* Philippi, 1849: 9, pl. 1, fig. 5.
*Patella ferruginea* Reeve, 1854: 425, pl. XVII, fig. 40a–c.
*Nacella* (*Patinigera*) *delesserti* – Powell, 1973: 196; Cantera & Arnaud, 1985: 34.
*Nacella delesserti* – Blankley & Branch, 1984: 171; Blankley & Branch, 1985: 259; Hodgson & Bernard, 1989: 145; González-Wevar *et al.*, 2016b: 77; 2017: 863.

*Material studied:* Trypot Beach, Marion Island (46°52’33.91” S, 37°51’51.40” E) *N* = 50; Ships Cove, Marion Island (46°51’16.22” S, 37°50’42.36” E) *N* = 40; Crozet Islands (46°25’34.25” S, 51°51’42.50” E) *N* = 50.

*Shell:* The shell shape and sculpture are relatively constant (Fig. 9A–C). The species exhibits a conical morphology, dorsally raised, with a very thick and non-translucent shell (Fig. 9A–F). The anterior part of the animal is laterally compressed (Fig. 9D–F). It has a medium-sized shell (maximum length 80 mm) and exhibits a variable profile. The apex is situated at the anterior 25–35% of the shell’s length (Fig. 9D–F). All the slopes of the shell are convex (Fig. 9A–C). The aperture of the shell is oval. The surface of the shell exhibits low radial folds and lamellar growth lines. The margin of the shell is highly crenulated. The external coloration of the shell is relatively constant in the species: grey to white, with dark (brown and black) primary radial ribs. The internal part of the shell has a soft metallic-white coloration, with dark lines corresponding to external colour patterns, bordered by a white/brown halo.

*External anatomy:* The ventral area of the foot is black and the epipodial fringe is highly recognizable. The mantle fold is thick and dun-brown coloured. The mantle tentacles are in alternate series of three shorter pigmented ones (white/black/white) and black longer one (Fig. 9G). The cephalic tentacles are dorsally pigmented with a black line (Fig. 9G).

*Radula:* The first lateral teeth are set close together on the anterior edge of the basal plates, long and very sharp, with two cusps. The second laterals are broader, wider spaced, with four very sharp cusps (Fig. 9H).

*Distribution:* Marion, Prince Edward and Crozet Islands (Fig. 9I).

*Habitat:* High and medium intertidal rocky ecosystem between 0 and 30 m depths.

*Comments: Nacella delesserti* was first reported at Crozet Islands by Cantera & Arnaud (1985), a finding we confirm here. These authors also reported the species from South Georgia, but our sample of >150 individuals consisted only of *N. concinna*. Zelaya (2005) also failed to find *N delesserti* at South Georgia. Hence, we consider *N. delesserti* to be restricted to Marion and Crozet Islands. Phylogenetic reconstructions placed *N. delesserti* as the sister species of *N. concinna*, their separation occurring around 0.35 Mya (González-Wevar *et al.*, 2017). The

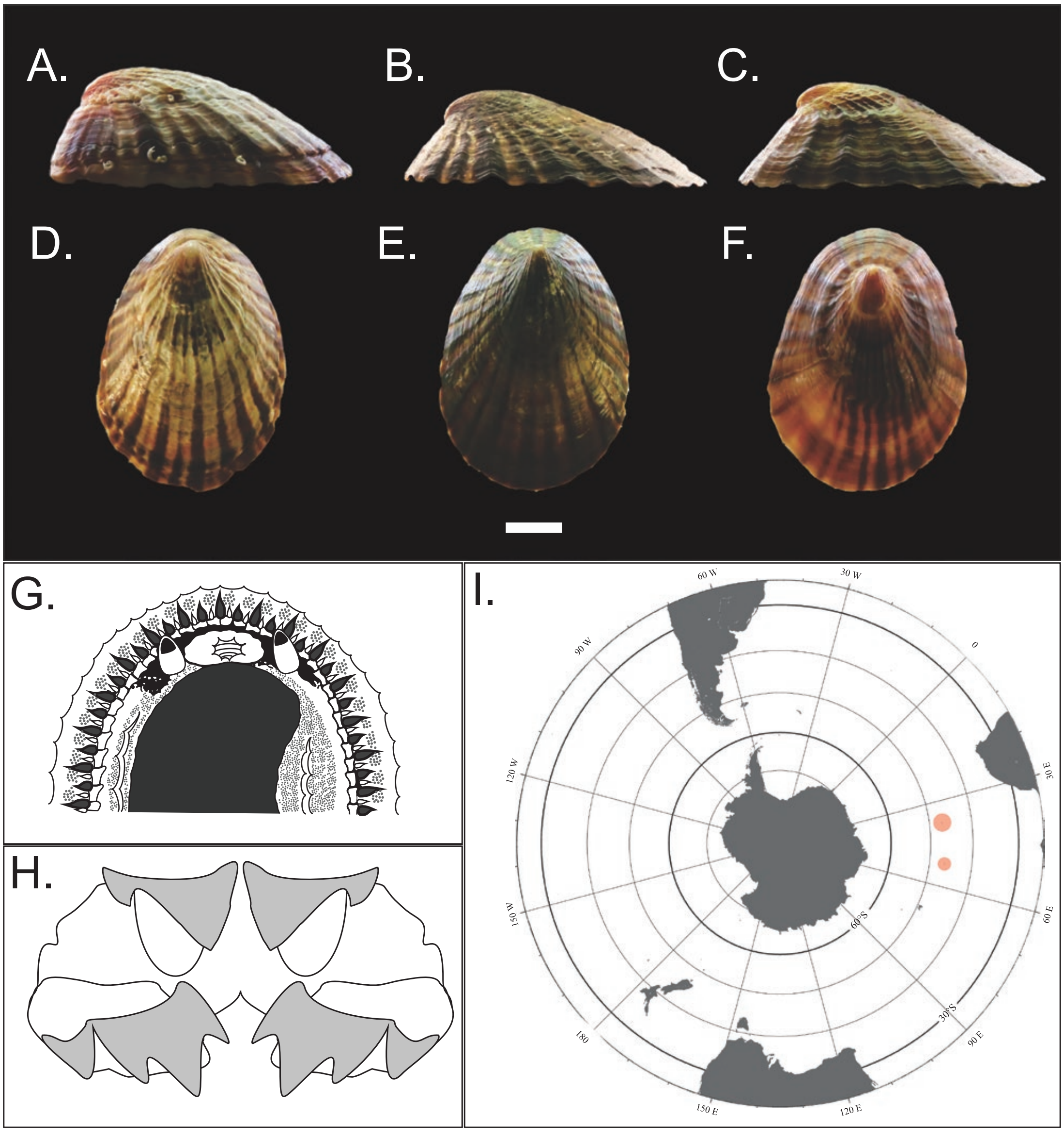

**Figure 9.** *Nacella delesserti*, Marion and Crozet Islands, sub-Antarctic Indian Ocean. Scale bar = 1.0 cm for all unless specified otherwise. A = Trypot Beach, Marion Island B = Ships Cove, Marion Island, C = Crozet Islands. A–F, shell morphology and coloration of *Nacella delesserti*. A–C, lateral view. D–F, dorsal view. G, mantle tentacles, cephalic tentacles and foot coloration patterns. H, radula. I, distribution.

presence of *N. delesserti* at sub-Antartctic Marion and Crozet Islands is thus the result of evolutionarily recent long-distance dispersal from maritime Antarctica. *Nacella delesserti* showed very low levels of genetic diversity that constitute evidence of recent postglacial expansion in Marion Island. Due to the exceptional high density and biomass of *N. delesserti* on Marion Island rocky shores, it plays an important role in the organization of intertidal and shallow-water benthic communities (Blankley & Branch, 1985).

### *NACELLA KERGUELENENSIS* (SMITH, 1879)

(FIG. 10)

*Patella* (*Patinella*) *kerguelenensis* Smith, 1879: 177, pl. 19, figs 13, 13a.
*Patella* (*Nacella*) *mytilina* – 181, not of Helbling.
*Patella kerguelenensis* – Watson, 1886: 27.
*Nacella kerguelenensis* – Pilsbry, 1891: 121, pl. 49, figs 7, 8; Hedley, 1916: 44; Dell, 1964: 276; Powell, 1973: 192, pl. 173, figs 3, 4; Cantera & Arnaud, 1985: 33; González-Wevar *et al.*, 2010: 116; 2017: 862.

*Patinella kerguelenensis* – Strebel, 1908: 83.
*Nacella mytilina* – Thiele, 1912: 234, Powell, 1951: 80; 1973: 192 (in part, not of Helbling).
*Patinigera* cf. *kerguelenensis* – Powell, 1955: 69.
*Patinigera kerguelenensis* – Powell, 1957: 126.
*Nacella* (*Patinigera*) *mytilina* – Cantera & Arnaud, 1985: 33 (not of Helbling)
*Nacella* cf. *mytilina* – Troncoso *et al.*, 2001: 88 (not of Helbling).

*Material studied:* Port-aux-Français, Kerguelen Islands (49°21'09.84" S, 70°13'05.89" E) *N* = 50; Port Christmas, Kerguelen Islands (48°41'40.22" S, 69°01'15.54" E) *N* = 60; Fjord des Portes Noires, Kerguelen Islands (49°29'47.32" S, 69°08'06.70" E) *N* = 50; Îles du Prince-de-Monaco, Kerguelen Islands (49°36'47.24" S, 69°14'11.38" E) *N* = 30; Baie des Cascades, Kerguelen Islands (49°10'02.31" S, 70°08'53.33" E) *N* = 30; Atlas Cove, Heard Island (53°01'27.99" S, 73°23'46.95" E) *N* = 10.

*Shell:* The shell shape and sculpture are very variable in the species and two different morphotypes have been recorded at Kerguelen Islands: (1) a kelp-dweller (Fig. 10A) and (2) a hard-substrate morphotype (Fig. 10B, C). The shell and the sculpture of the hard-substrate morphotype are relatively constant in the analysed individuals, which exhibit a conical morphology, dorsally raised, with a very thick and non-translucent shell. The anterior part of the animal is laterally compressed (Fig. 10A–D). The shell is large (maximum length 120 mm) and has a medium profile. The apex is located at the the anterior 30% of the shell. All the slopes of the shell are convex. The aperture of the shell is oval. The surface of the shell is sculptured with weak radial folds. The margin of the shell is very crenulated. The external coloration varies from purplish brown to grey/white and the apex is reddish bronze. The internal part of the shell varies from light brown to purple with a metallic lustre and dark lines corresponding to external colour patterns bordered by a white/grey halo.

The shell of the kelp-dweller morphotype resembles *N. mytilina* from the Magellanic province. This morphotype is conical, dorsally raised, with a very thin and translucent shell. The shell is of medium size (maximum length 60 mm), with a low profile. The apex is situated at the anterior 20% of the shell, anteriorly directed and curved toward the border, and obtuse. The anterior slope is concave, while the posterior and lateral ones are convex. The aperture is oval. The surface of the shell is sculptured with a few radial ribs, more obvious in the anterior zone, with concentric growth lines. The margin of the shell is relatively even. The external and internal coloration of the shell is purple to brown, with darker tones toward the apex.

*External anatomy (for both morphotypes):* The ventral area of the foot is dark grey to black and the epipodial fringe is highly recognizable. The mantle fold is thick and dun-brown coloured. The mantle tentacles are in alternated series of three shorter pigmented ones (white/black/white) and a black longer one (Fig. 10G). The cephalic tentacles are dorsally pigmented with a black line (Fig. 10G).

*Radula:* The first lateral teeth are set close together on the anterior edge of the basal plates, long and sharp pointed, with two cusps. The second laterals are broader with four sharp cusps (Fig. 10H).

*Distribution:* Kerguelen and Heard Islands (Fig. 10I). *Nacella kerguelenensis* is highly abundant and exhibits a continuous distribution in the Kerguelen Archipelago. The species is also broadly distributed on Heard Island.

*Habitat:* The species occurs in the high and medium intertidal rocky ecosystem down to 40 m depths; it is also abundant grazing on macroalgae.

*Comments:* As previously mentioned, the kelp-associated morphotype of *N. kerguelenensis* exhibits major parallels in terms of shell morphology, thickness and sculpture, as well as habitat preferences with the Patagonian *N. mytilina*. Recent molecular analyses determined that this kelp-associated morphotype at Kerguelen Islands fell within the genetic diversity recorded in *N. kerguelenensis* (González-Wevar *et al.*, 2017). Accordingly, *N. kerguelenesis* is restricted to Kerguelen and Heard Islands (González-Wevar *et al.*, 2010, 2017, this revision).

### *NACELLA EDGARI* (POWELL, 1957)

(FIG. 11)

*Patella* (*Patinella*) *fuegiensis* – Smith, 1879: 180, pl. 19, figs 14, 14a (not of Reeve).
*Nacella fuegiensis* – Pilsbry, 1891: 121, pl. 49, figs 28, 29, 30, 31 (not of Reeve).
*Nacella* (*Patinigera*) *fuegiensis* – Thiele, 1912: 234 (not of Reeve).
*Patinigera fuegiensis edgari* Powell, 1957: 127, pl. 2, figs 5, 6; Powell, 1960: 129.
*Nacella* (*Patinigera*) *edgari* – Powell, 1973: 196, pl. 179, figs 3, 4; Cantera & Arnaud, 1985: 35; Troncoso *et al.*, 2001: 88.
*Nacella* (*Patinigera*) *macquariensis* – Powell, 1973: 196 (in part, not of Finlay).

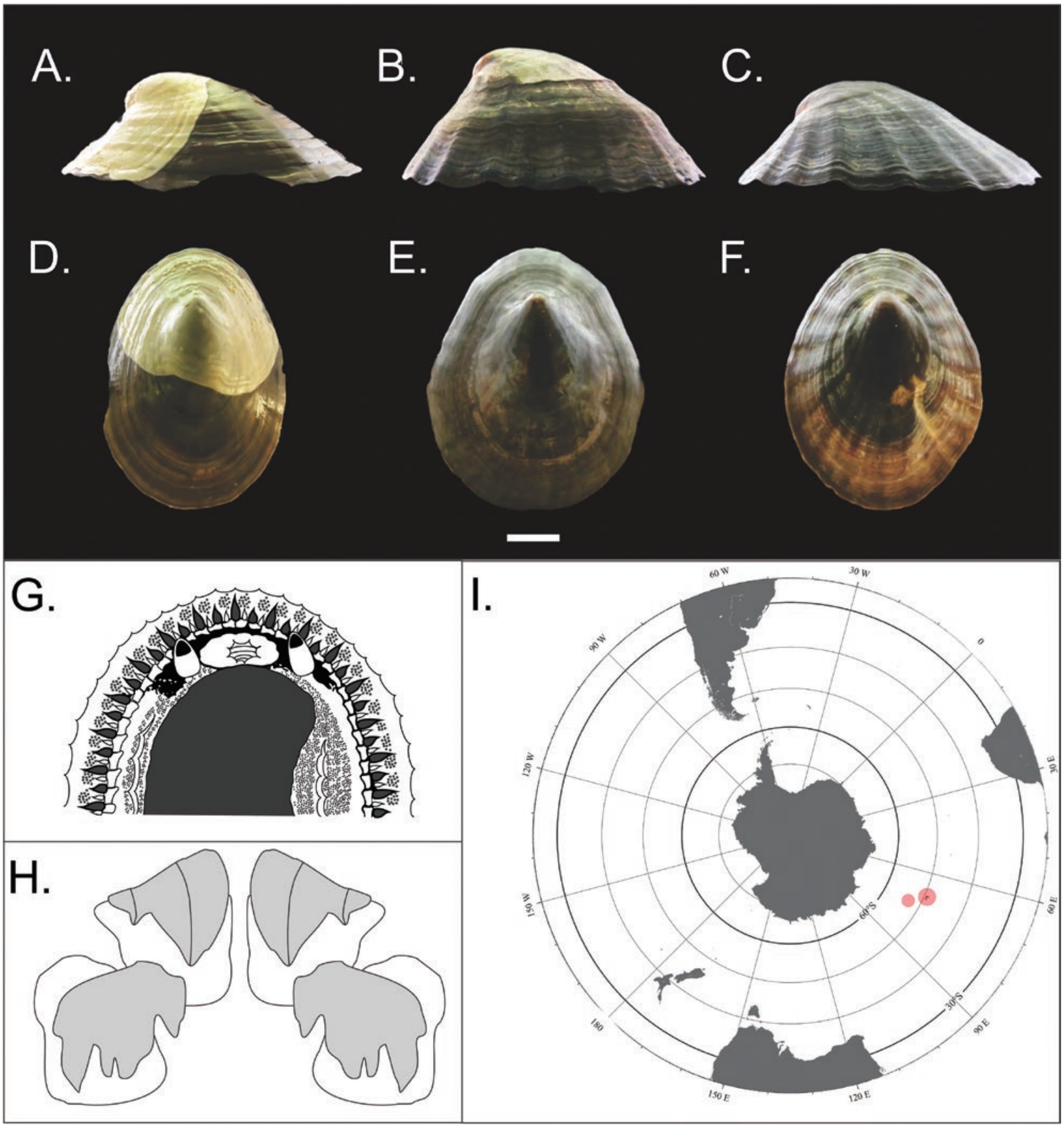

**Figure 10.** *Nacella kerguelenensis*, Kerguelen and Heard Islands, sub-Antarctic Indian Ocean. Scale bar = 1.0 cm for all unless specified otherwise. A = Port-aux-Français, Kerguelen Island, B = Baie des Cascades, Kerguelen Island, C = Atlas Cove, Heard Island. A–F, shell morphology and coloration of *Nacella kerguelenensis*. A–C, lateral view. D–F, dorsal view. G, mantle tentacles, cephalic tentacles and foot coloration patterns. H, radula. I, distribution.

*Nacella* cf. *macquariensis* – González-Wevar *et al.*, 2010: 116 (not of Finlay).
*Nacella edgari* – González-Wevar *et al.*, 2016b: 2; 2017: 862.

*Material studied:* Port-aux-Français, Kerguelen Islands (49°21’09.84” S, 70°13’05.89” E) *N* = 40; Port Christmas, Kerguelen Islands (48°41’40.22” S, 69°01’15.54” E) *N* = 50; Fjord des Portes Noires, Kerguelen Islands (49°29’47.32” S, 69°08’06.70” E) *N* = 30; Îles du Prince-de-Monaco, Kerguelen Islands (49°36’47.24” S, 69°14’11.38” E) *N* = 50; Baie des Cascades, Kerguelen Islands (49°10’02.31” S, 70°08’53.33” E) *N* = 30; Atlas Cove, Heard Islands (53°01’27.99” S, 73°23’46.95” E) *N* = 5.

*Shell:* The shell shape and sculpture are variable in the species and two different morphologies were recorded at Kerguelen (Fig. 11A, B) and Heard Islands (Fig. 11C), respectively. Individuals from the Kerguelen Islands exhibit a conical morphology, dorsally depressed, with a thin and translucent

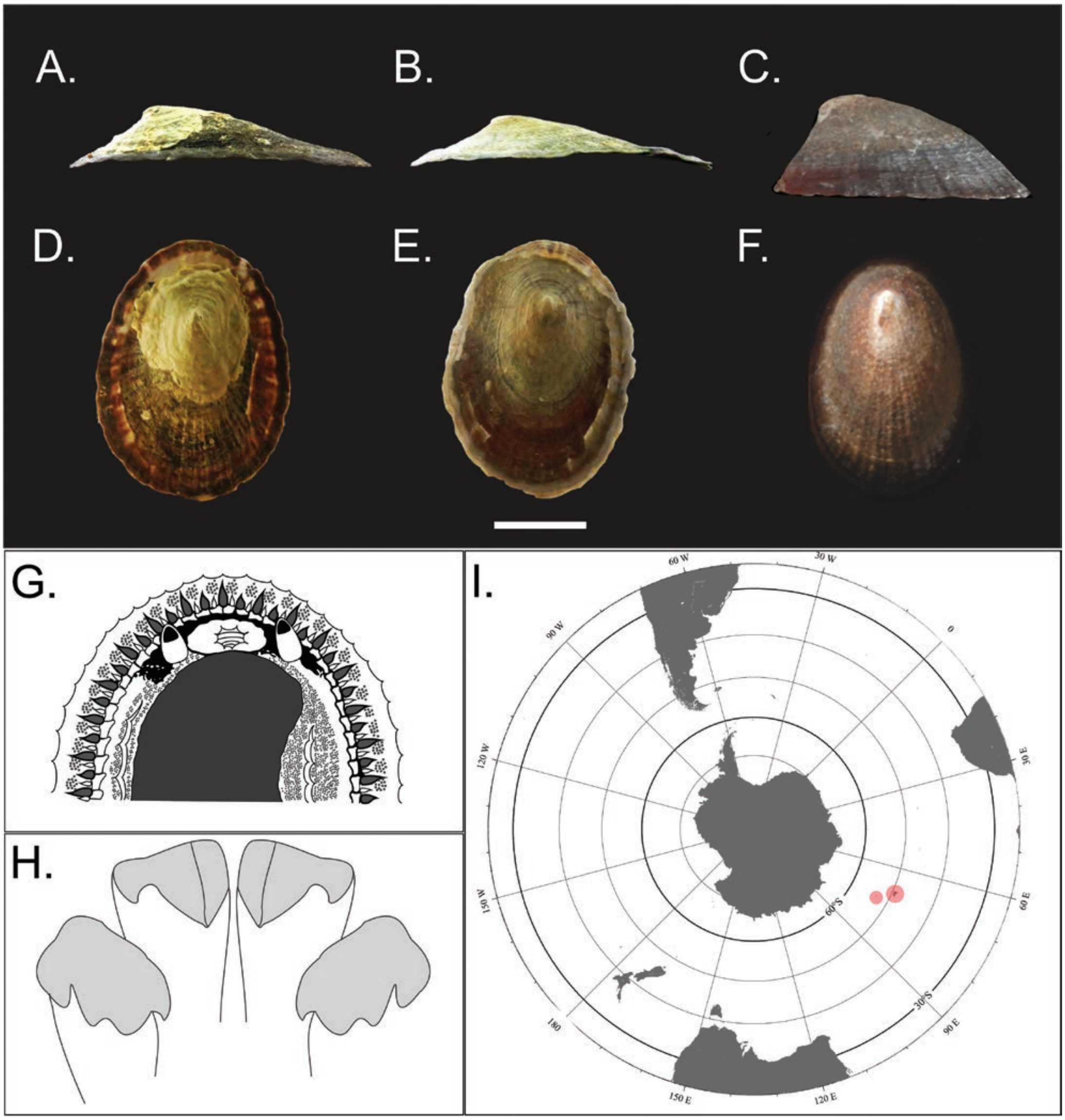

**Figure 11.** *Nacella edgari*, Kerguelen and Heard Islands, sub-Antarctic Indian Ocean. Scale bar = 1.0 cm for all unless specified otherwise. A = Port-aux-Français, Kerguelen Island, B = Îles du Prince-de-Monaco, Kerguelen Island, C = Atlas Cove, Heard Island. A–F, shell morphology and coloration of *Nacella edgari*. A–C, lateral view. D–F, dorsal view. G, mantle tentacles, cephalic tentacles and foot coloration patterns. H, radula. I, distribution.

shell. The anterior part of the animal is laterally compressed (Fig. 11D–F). The shell is of medium size (maximum length 80 mm) and has a low profile. The apex is located at the anterior 20–30% of the shell. All the slopes of the shell are concave. The aperture is oval. The whole surface is crowded with concentric lamellae that undulate as they cross the radials. The margin of the shell is very crenulated. The external coloration varies in the species across its distribution (brown, grey and purple) and the apex has a bronze coloration. The interior part of the shell is iridescent bluish grey with dark lines, corresponding to external colour patterns bordered by a white/grey halo.

The morphology of *N. edgari* at Heard Island was relatively constant in the analysed individuals ($N = 5$) with a conical form, dorsally raised, very thick and not translucent. The anterior part of the animal is laterally compressed. The shell is of medium size (maximum length 80 mm) and has a medium profile. The apex is situated at the anterior 30–40% of the shell's length. All the slopes of the shell are convex. The aperture of the shell is oval. The surface of the shell consists of low radial folds and lamellar growth lines. The margin of the shell is very crenulated. External coloration varies from brown to reddish. The internal part of the shell has iridescent bluish grey coloration with dark lines corresponding to external colour patterns bordered by a white/grey halo.

*External anatomy:* The ventral area of the foot is black and the epipodial fringe is highly recognizable. The mantle fold is thick and dun-brown coloured. The mantle tentacles are in alternate series of three white shorter and a white longer one and are absent of pigmentation (Fig. 11G). The cephalic tentacles are dorsally pigmented with a black line (Fig. 11G).

*Radula:* The first lateral teeth are set close together on the anterior edge of the basal plates, of medium length and sharp pointed, with two cusps. The second laterals are broader, wider spaced with four short cusps (Fig. 11H).

*Distribution:* Kerguelen and Heard Islands (Fig. 11I).

*Habitat:* This species occurs from high and medium intertidal rocky shores down to 30-m depths; the species is also regularly found on macroalgae (Powell, 1955, 1957)

*Comments:* In the original description of the radula from Kerguelen Islands individuals (under the name *Patella fuegiensis*) Smith (1879) describes:

> Teeth of the lingual ribbon slightly hooked, in pairs, scarcely diverging; the central pairs two-pronged, the inner prong much the larger, spear-head shaped; the lateral pairs alternating with the central ones are four-pronged, the innermost prong smallest, the next two subequal, and the outside one situated nearly at right angles to the rest of the tooth, about the same size or a trifle larger.

This radular teeth configuration highly resembles our observations of the radula of *N. edgari*. At the same time, the lateral and dorsal patterns of shell morphology recorded in *Patella fuegiensis* from Kerguelen by Smith (1879) are very similar to those observed in *N. edgari*. Accordingly, individuals identified as *Nacella fuegiensis* from Kerguelen should be treated as *N. edgari*. Powell (1957) commented that the adults of *N. edgari* have a very thin and fragile shell, and live closely associated to 'kelps'. Recent multi-locus reconstructions indicate that *N. edgari* from the Kerguelen Islands and *N.* cf *macquariensis* from Heard Island (González-Wevar *et al.*, 2010) represent the same evolutionary unit (González-Wevar *et al.*, 2017). Moreover, *Nacella* individuals from Macquarie Island fell within a different and endemic lineage, *N. macquariensis*, closely related to *N. edgari* (Kerguelen and Heard Islands) and to *N. terroris* (Campbell Island). Therefore, the colonization of both sub-Antarctic Australia/New Zealand islands, Macquarie and Campbell, constitutes a recent off-shoot from a geographically distant Kerguelenian *Nacella* lineage. Accordingly, *N. edgari* is currently restricted to Kerguelen and Heard Islands where, it coexists with *N. kerguelenensis*.

### *NACELLA MACQUARIENSIS* FINLAY, 1926

*Nacella fuegiensis* – Suter, 1913: 77 (not of Reeve).
*Nacella delesserti* – Hedley 1916: 42, pl. 6, figs 65–69 (not of Philippi).
*Nacella macquariensis* Finlay, 1926: 337; Lindberg, 2008: 272; González-Wevar *et al.*, 2017: 862.
*Patinigera macquariensis* – Powell, 1955: 68; Dell, 1964: 274.
*Nacella* (*Patinigera*) *macquariensis* – Powell, 1973: 199 (in part), pl. 182, figs 1, 2.

*Material studied:* For this revision we only had access to tissue samples obtained from ten individuals collected at Garden Cove (54°29'59.15" S, 158°56'09.38" E), Macquarie Island.

*Shell:* According to Powell (1973), the shell of this species is moderately large, up to 63 mm in length, strong but of light build. Its shape is narrowly ovate and elevated but varying to rather broadly ovate and depressed. The sculpture consists of 32 to 35 broadly rounded, primary radial ribs, plus narrower secondary intermediate radials, mostly over the posterior half of the shell. The whole surface is crowded with low concentric growth lamellae that do not thicken to any extent on the crest of the radials. The external colour is olive to chestnut-brown; internally, it is diffused and strongly rayed in bronzy reddish brown, the spatula being well-marked, variously blotched with reddish brown, and often almost completely white-callused.

*Distribution:* Macquarie Island.

*Habitat:* This species occurs from the high and medium intertidal rocky ecosystem down to 25 m.

*Comments:* Multi-locus mtDNA and nucDNA reconstructions indicate that *Nacella macquariensis* from Macquarie Island represents a separate, diagnosable taxonomic unit, closely related to *N. edgari* (Kerguelen and Heard Islands) and *N. terroris* (Campbell Island). Accordingly, the distribution of *N. macquariensis* is restricted to the Macquarie Islands and the species is not present at Kerguelen and Heard (*contra* Powell, 1973).

### *NACELLA TERRORIS* (FILHOL, 1880)

(FIG. 12)

*Patella terroris* Filhol, 1880: 1095; Filhol, 1885: 529.
*Nacella* (*Patinigera*) *illuminata* Suter, 1913: 77.

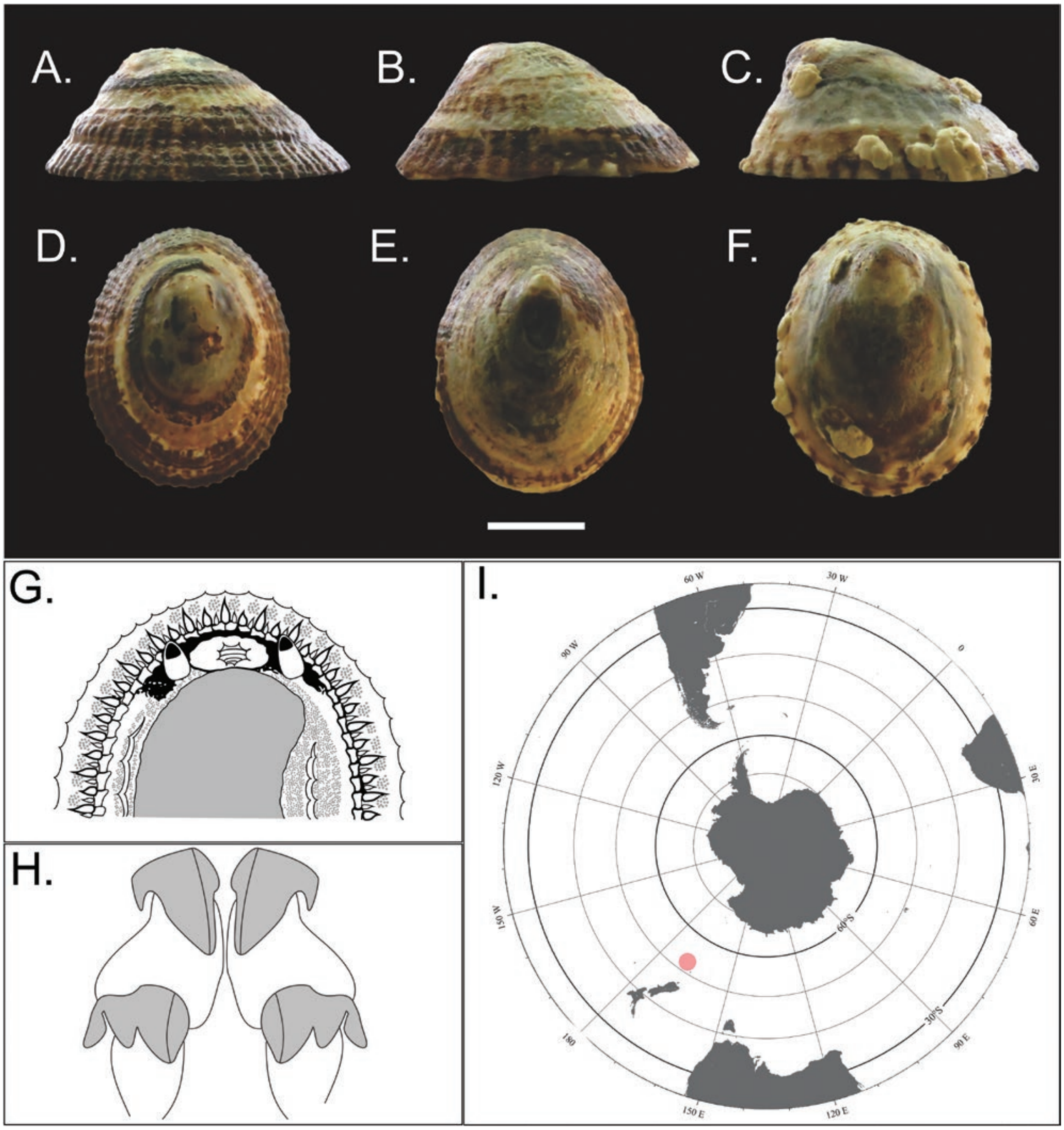

**Figure 12.** *Nacella terroris*, Campbell Island, sub-Antarctic New Zealand. Scale bar = 1.0 cm for all unless specified otherwise. A–C, Perseverance Harbour, Campbell Island. A–F, shell morphology and coloration of *Nacella terroris*. A–C, lateral view. D–F, dorsal view. G, mantle tentacles, cephalic tentacles and foot coloration patterns. H, radula. I, distribution.

*Patinigera terroris* – Powell, 1955: 69.
*Nacella* (*Patinigera*) *terroris* – Powell, 1973: 200, pl. 182, figs 3, 4; Powell, 1979: 42, pl. 15, 16.
*Nacella terroris* – González-Wevar *et al.*, 2017: 862.

*Material studied:* Perseverance Harbour, Campbell Island (52°33'02.14" S, 169°09'08.38" E) $N = 3$.

*Shell:* The shell shape and sculpture are constant in the three analysed specimens (Fig. 12A–C). The species exhibits a conical morphology, dorsally raised, with a very thick and non-translucent shell (Fig. 12A–F). The anterior part of the animal is laterally compressed (Fig. 12D–F). The shell is of medium size (maximum length 80 mm) and exhibits a high profile. The apex is situated at the anterior 40% of the shell. All the slopes are convex (Fig. 12A–C). The aperture is oval. The surface of the shell is sculptured with raised angular primary radial ribs, weaker secondary ones and concentric growth lines that are visible in the interspaces. The margin of the shell is crenulated. The external coloration is pale reddish-brown and grey. The primary and secondary ribs are red-brown to ash-coloured to dark brown with clearer interspaces. The internal part of the shell has a soft metallic-brown coloration with dark lines corresponding to external colour patterns, bordered by a white/brown halo.

*External anatomy:* The ventral area of the foot is grey and the epipodial fringe is quite recognizable. The mantle fold is thin and dun-brown coloured. The mantle tentacles are not pigmented and in alternate series of three white and a white longer one (Fig. 12G). The cephalic tentacles are dorsally pigmented with a black line (Fig. 12G).

*Radula:* The first lateral teeth are set close together on the anterior edge of the basal plates, long and sharp pointed, with two long cusps. The second laterals are broader, wider spaced with three short cusps (Fig. 12H).

*Distribution:* Campbell Island, sub-Antarctic New Zealand (Fig. 12I).

*Habitat:* Low intertidal and subtidal rocky ecosystem down to 30 m.

*Comments:* Multi-locus phylogenetic reconstructions recognized *N. terroris* from Campbell Island as a distinct taxonomic unit, closely related to Macquarie Island's *N. macquariensis* and to *N. edgari* from Kerguelen and Heard Islands. Phylogenetic relationships and divergence time estimates indicate that *Nacella* species from New Zealand (*N. terroris*) and Australia (*N. macquariensis*) constitute a recent offshoot from the Kerguelen Archipelago (González-Wevar *et al.*, 2017).

## MOLECULAR ANALYSES

As previously demonstrated (Nakano & Ozawa, 2004, 2007; González-Wevar *et al.*, 2010, 2017), the monophyly of Nacellidae (*Nacella* + *Cellana*), as well as the molecular distinction and the sister relationship between *Nacella* and *Cellana*, were highly supported (Fig. 13). Within *Nacella*, no topological inconsistencies were detected when comparing mitochondrial and nuclear markers. Phylogenetic reconstructions recognized the division of *Nacella* into two main clades. The first (I) includes South American lineages, while the second (II), those from maritime Antarctica and sub-Antarctic islands (Fig. 13).

In South America, main clade I includes individuals of the new Magellanic lineage (a) *N. yaghana* sp. nov. (Fig. 13). All the analysed specimens from Pía and Garibaldi Fjords, Beagle Channel, fell within a clearly resolved, reciprocal monophyletic clade and, therefore, represent a new previously unrecognized *Nacella* species here described (Fig. 13). Lineage (b) includes all the individuals of *N. clypeater* collected along Central Chile in the Pacific margin of South America between 42°S and 30°S (Fig. 13). Finally, lineage (c) represents the most diverse South American group and includes Magellanic species: *N. deaurata*, *N. flammea*, *N. magellanica* and *N. mytilina*. As observed in previous studies (González-Wevar *et al.*, 2010), mitochondrial DNA reconstructions recognized the reciprocal monophyly of *N. mytilina* and *N. flammea*, but failed to recover that between *N. deaurata* and *N. magellanica*. However, 28S rRNA and the concatenated analyses (Fig. 13) recovered the reciprocal monophyly of all four Magellanic species with strong support. Accordingly, the current diversity of *Nacella* in South America includes three lineages (a–c) and six species (*N. clypeater*, *N. deaurata*, *N. flammea*, *N. magellanica*, *N. mytilina* and *N. yaghana* sp. nov.).

The second main clade II includes *Nacella* species from sub-Antarctic islands and from maritime Antarctica (Fig. 13). Lineage (d) includes the species *N. edgari* (Kerguelen and Heard Islands), *N. macquariensis* (Macquarie Island) and *N. terroris* (Campbell Island). All the methods and molecular markers recognized *N. edgari* as a monophyletic unit, including individuals previously labelled *N.* cf. *macquariensis* from Heard Island (González-Wevar *et al.*, 2010) (Fig. 13). At the same time, the species *N. macquariensis* (Macquarie Island) and *N. terroris* (Campbell Island) are both monophyletic and form a clade closely related to *N. edgari* (Fig. 13). Lineage (e) includes individuals of *N. kerguelenensis* (Kerguelen and Heard Islands), but this species was not found at Macquarie Island as reported by Powell (1973). Interestingly, high levels of genetic divergence characterize the sympatric species *N. kerguelenensis* and *N. edgari*. In fact, molecular divergence between these sympatric species are similar to those recorded between Antarctic and sub-Antarctic lineages of the genus (González-Wevar *et al.*, 2012b, 2016b). Finally, lineage (f) includes the Antarctic limpet *N. concinna* and its sister species *N. delesserti* from the sub-Antarctic Marion and Crozet Islands (Fig. 13). Accordingly, the diversification of *Nacella* in the Kerguelen Plateau and New Zealand Islands includes two main lineages (d and e) and four species (*N. edgari*, *N. kerguelenensis*, *N. macquariensis* and *N. terroris*) while maritime Antarctica encompasses a single lineage (f) with two sister species (*N. concinna* and *N. delesserti*).

## DISCUSSION

New multi-locus phylogenetic reconstructions and morphological revision in *Nacella* recognized 12 reciprocally monophyletic species across different provinces of the Southern Ocean. As previously

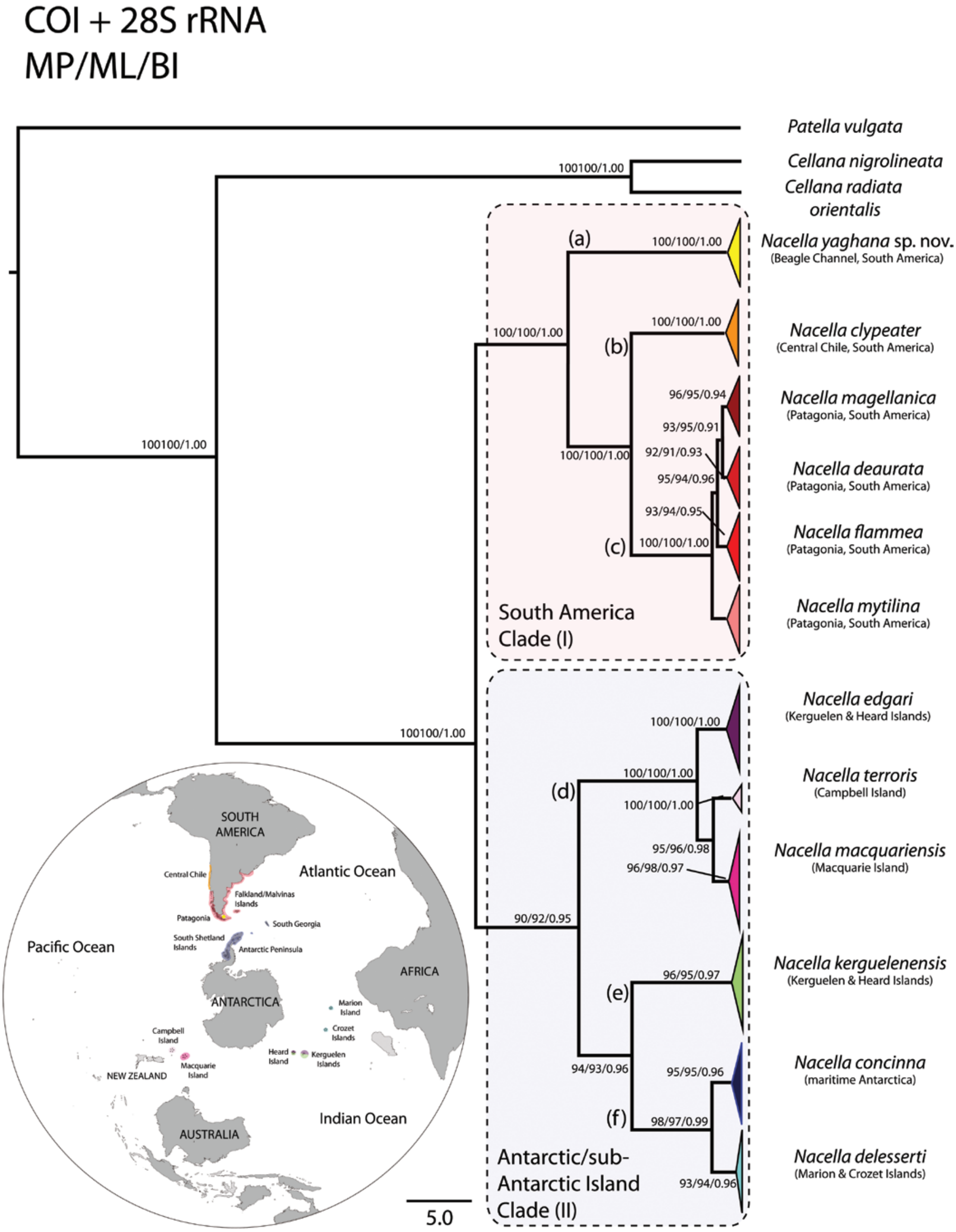

**Figure 13.** Evolutionary relationships of sampled *Nacella* (Nacellidae) based on the concatenated datasets of the cytochrome *c* oxidase subunit I (659 bp) and the 28S rRNA (839 bp) genes. Bayesian maximum clade credibility tree of *Nacella* relationships based on mtDNA (*COI*) and nucDNA (28S rRNA) sequences. Bootstrap support values for MP, ML and Bayesian posterior probabilities are shown above the nodes (in that order). Maps and colours indicate major sampled areas.

demonstrated (González-Wevar *et al.* 2010, 2017), the distinction of the subgenus *Patinigera* within *Nacella* was not supported. The type species of *Patinigera*, *N. magellanica* and the type species of *Nacella*, *N. mytilina*, are very closely related and fell within the evolutionarily recent diversification of the genus in Patagonia. The major conchological differences within *Nacella* that led to this subdivision seem to be related to habitat preferences. Thick-shelled *Patinigera* species are usually associated with inter- and subtidal hard substratum ecosystems, while thin-shelled *Nacella* forms are usually kelp-associated species. Similar morphological differences between kelp- and rock-dwelling species have been recorded in other patellogastropod groups, such as *Helcion* (Graham & Fretter, 1947; Weber *et al.*, 1997) and *Notoacmaea* (Nakano & Spencer, 2007). Hence, *Patinigera* does not represent a valid taxonomic rank and it should be synonymized with *Nacella*.

The morphological revision in *Nacella* corroborates previous studies (Powell, 1973; Forcelli, 2000; Valdovinos & Rüth, 2005) of the genus in recording a high degree of inter- and intraspecific variation. In general, intertidal *Nacella* individuals (i.e. *N. magellanica*, *N. deaurata*, *N. delesserti*, *N. concinna* and *N. kerguelenensis*) tend to exhibit high shell profiles, whereas subtidal ones (i.e. *N. clypeater*, *N. flammea*, *N. kerguelenensis* and *N. concinna*) exhibited lower contours. Such inter- and subtidal morphological differences have also been recorded as intraspecific variability within particular species of *Nacella*, such as *N. concinna*, *N. deaurata* and *N. kerguelenensis*. On thermally stressful rocky shores, small, slow-moving ectotherms like limpets exhibit morphological characteristics, including high-spired and heavily ridged shells, which seem to reduce the possibility of reaching stressful or lethal body temperatures (Nakano & Ozawa, 2005; Harley *et al.*, 2009). Similarly, individuals of *Patella* species living high on the shore tend to be higher spired than conspecific individuals living lower on the shore (Ebling *et al.*, 1962). Comparable observations have been also recorded for *Cellana* across its distribution in different biogeographic provinces (Bird, 2011; Reisser *et al.*, 2012).

In this study, we present the description of a new lineage from the southern tip of South America, *Nacella yaghana* sp. nov. Molecular comparisons with all the extant species of the genus recognized this taxon as a new South American representative, currently restricted to particular fjords in the Beagle Channel. Together with this narrow distribution, several key morphological characteristics of *N. yaghana* sp. nov. are substantively different from those recorded in the rest of *Nacella* representatives, especially those from Patagonia. In addition, this revision of *Nacella* proposes several amendments to the geographical ranges of several taxa, particularly those from sub-Antarctic islands and Patagonia (Supporting Information, Table S2).

Evolutionary studies of the Southern Ocean benthic marine biota have demonstrated the long-term influence of the Antarctic Circumpolar Current (ACC) upon the biogeographical patterns (Waters, 2007; Strugnell *et al.*, 2008; Griffiths *et al.*, 2009; Wilson *et al.*, 2009; González-Wevar *et al.*, 2010, 2012b; 2017; Nikula *et al.*, 2010; Downey *et al.*, 2012; Near *et al.*, 2012; Cumming *et al.*, 2014; Poulin *et al.*, 2014; Griffiths & Waller, 2016; Moon *et al.*, 2017). Divergence time estimates and lineage-through-time plots in the genus (González-Wevar *et al.*, 2017) suggest that the diversification of *Nacella* in the Southern Ocean occurred long after the physical separation of the continental landmasses or to the onset of the ACC (Zachos *et al.*, 2001; Pfuhl & McCave, 2005; Scher & Martin, 2006; Scher *et al.*, 2015). Consequently, biogeographical patterns in this high-latitude limpet genus are not a consequence of tectonic-related vicariant processes, but seem to be related to major climatic/oceanographic shifts following the middle Miocene Climatic Transition (MMCT), a period associated with the full development of a deep Antarctic Circumpolar Current (Dalziel *et al.*, 2013). This process may have played a key role in the subsequent Southern Ocean's cryosphere expansion (Lear *et al.*, 2000; Zachos *et al.*, 2001; Mackensen, 2004; Verducci *et al.*, 2009), probably associated with an intensification of the ACC (Flower & Kennett, 1994; Lewis *et al.*, 2008). Major changes in the latitudinal position of the ACC and the strengthening of this current following the MMCT may have favoured the colonization of geographical distant provinces of the Southern Ocean. Otherwise, and as supported by diversification rates estimations in *Nacella* (González-Wevar *et al.*, 2017), the establishment of a strong, deep ACC that acted as an effective barrier may explain the Late Miocene to Early Pliocene simultaneous diversification of the genus in different provinces of the Southern Ocean.

The earliest species attributed to *Nacella* is the extinct *N. reicheae* from the Late Oligocene of southern Peru (DeVries, 2008) and the earliest recorded *Cellana* is the Oregonian *C. ampla* from the Late Eocene (Lindberg & Hickman, 1986). These dates are congruent with our previous time-calibrated phylogeny, which suggests that *Nacella* and *Cellana* separated between the Late Eocene and Mid Oligocene (González-Wevar *et al.*, 2017). DeVries (2008) also recorded a *Nacella* from the Late Early Miocene of Chiloé and a radiation of five species, all of them extinct, from the Pliocene of southern Peru. One of the latter, *N. oblea*, he considered to be very close to the extant *N. clypeater*. Consequently, DeVries (2008) argued that tropical and western South America was the region where the first *Nacella* appeared. The timing of the split leading to *N. yaghana* sp. nov., however, is earlier than the Peruvian Pliocene radiation and we suggest that clade I had a southern origin in South America, and that the Peruvian Pliocene species arose from colonization via the cold Humboldt Current northward. Whether or not the origin of the genus as a whole also occurred in higher latitudes is less clear, but a similar scenario could apply. As noted by DeVries (2008), *Nacella* species do not often fossilize and hence the absence of high-latitude Oligocene and Miocene fossils need not indicate such species did not exist.

Anthropogenic climate change is predicted to be a major cause of species extinctions during the next 100 years and the restricted distribution of *N. yaghana* sp. nov. to particular fjords (Pía and Garibaldi) of the Beagle Channel raises several questions about the fate of this taxon. Further studies about the species' biology, physiology, ecology, habitat selection preferences and reproduction are required in order to provide fundamental information about how it meets its requirements for survival and how it will respond to future changes in the environments.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

**Table S1.** Patellogastropod species, specimens, sampling localities, and accession numbers for mitochondrial DNA (*COI*) and nuclear DNA (28S rRNA) sequences.
**Table S2.** Described distributions of *Nacella* species through time with amendments to new information. In order to assemble this table we include only those nominal species that were validated in the complete revision of *Nacella* by Powell (1973), as well as recent phylogenetic and phylogeographic data concerning the relationships within the group.