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Neither slugs nor snails: a molecular reappraisal of the gastropod family Velutinidae

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The systematics of the marine mollusc family Velutinidae has long been neglected by taxonomists, mainly because their often internal and fragile shells offer no morphological characters. Velutinids are usually undersampled owing to their cryptic mantle coloration on the solitary, social or colonial ascidians on which they feed and lay eggs. In this study, we address the worldwide diversity and phylogeny of Velutinidae based on the largest molecular dataset (313 specimens) to date, accounting for > 50% of the currently accepted genera, coupled with morphological and ecological data. Velutinids emerge as a diverse group, encompassing four independent subfamily-level lineages, two of which are newly described herein: **Marseniopsinae subfam. nov.** and **Hainotinae subfam. nov.** High diversity was found at genus and species levels, with two newly described genera (***Variolipallium* gen. nov.** and ***Pacifica* gen. nov.**) and ≥ 86 species in the assayed dataset, 58 of which are new to science (67%). Velutinidae show a remarkable morphological plasticity in shell morphology, mantle extension and chromatic patterns. This variability is likely to be the result of different selective forces, including habitat, depth and trophic interactions.

ADDITIONAL KEYWORDS: biodiversity – cryptic species – Gastropoda – host–parasite systems – mimicry – molecular systematics – new genera – taxonomic revision.

INTRODUCTION

Our knowledge of the diversity of extant animals is constrained by several factors, including the physical size, abundance and habitat accessibility of the taxa involved. The choice of a group as a study target can be influenced by its commercial interest, charisma or

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aesthetics. These factors have produced an uneven knowledge of global biodiversity, with some taxa that are well known because of human curiosity and attention (e.g. birds and mammals), whereas others stand as long neglected (e.g. invertebrates and fungi) (Troudet *et al.*, 2017; Hochkirch *et al.*, 2021).

In gastropod systematics, shell morphology is an important source of diagnostic characters and a general criterion for certain groups. Empty shells are far more common than living molluscs, and molluscs are among the best-known marine invertebrates (Bouchet, 2006). As a drawback, the taxonomy of groups with fragile, vestigial and/or internal shells has been harder to address historically, and their diversity is poorly documented.

The caenogastropod superfamily Velutinoidea Gray, 1840 comprises > 460 accepted extant species, currently classified into three families: Triviidae Troschel, 1863 (293 species), Eratoidae Gill, 1871 (69 species) and Velutinidae Gray, 1840 (99 species). Species included in this superfamily share a number of features, the most consistent of which is an echinospira larva (planktotrophic, with a double larval shell: the outer shell being periostracal and planispiral, not calcified and unusually large for a larval shell; the inner shell helicoid and calcified), in addition to a trophic association with tunicates on which they feed, an oval, bipectinate osphradium and a closed vas deferens (Wilson, 1998). Although triviids (false cowries or bean cowries) and eratoids (eratos), with their cowry-like shells, are relatively well studied, velutinids, possessing fragile, ear-like, often internal shells, have garnered comparatively little attention.

Velutinidae are currently classified in two subfamilies (Bouchet *et al.*, 2017): Velutininae Gray, 1840 and Lamellariinae d'Orbigny, 1841. In Velutininae, snail shells range from thin and enclosed by the mantle (as in *Onchidiopsis* Bergh, 1853) to exposed and with a velvety periostracum (as in *Velutina* J. Fleming, 1820). Lamellariinae, instead, possess a thin to very thin shell covered by a thin periostracum that is entirely or almost entirely enveloped by the large fleshy mantle.

Currently, there are six genera included in Lamellariinae, ten in Velutininae and three that are not assigned to a subfamily, namely *Lamellariopsis* Vayssière, 1906 (two species), *Marseniella* Bergh, 1886 (one species) and *Torellivelutina* J. H. McLean, 2000 (one species) (see Table 1 for details).

Velutinidae are known from all oceans and biogeographical provinces, but knowledge of their anatomy and biology is largely based on the Atlantic species of *Lamellaria* Montagu, 1816, *Marsenina* Gray, 1850 and *Velutina*, the Antarctic *Marseniopsis* Bergh, 1886 and the Indo-West Pacific *Coriocella* Blainville, 1824 (Wilson, 1998). The gradual loss of the protection offered by an external shell in this family seems to have been counterbalanced by the secretion of deterrent chemical compounds, found in species both with and without an external shell, such as *Velutina velutina* (O. F. Müller, 1776), *Lamellaria perspicua* (Linnaeus, 1758) and *Marseniopsis mollis* (E. A. Smith, 1902) (Thompson, 1960; McClintock *et al.*, 1994). These chemicals can be found on the surface of the animal and induce an avoidance response in potential predators (e.g. sea stars and sea anemones). However, it is not clear whether these compounds are produced directly by velutinid glands or if they are secondary metabolites acquired from the ascidians on which they feed (Thompson, 1960; McClintock *et al.*, 1994).

Velutinids are known to feed and lay eggs on tunicates that can be solitary, social and compound (or colonial); yet detailed information about species-specific associations is scarce, also as a consequence of

Table 1. Number of known extant species of the family Velutinidae, according to MolluscaBase (2022)

Subfamily	Genus	Number of species
Lamellariinae d'Orbigny, 1841	*Calyptoconcha* Bouchet & Warén, 1993	1
	Coriocella Blainville, 1824	8
	Hainotis F. Riedel, 2000	1
	Lamellaria Montagu, 1816	24
	Mysticoncha J. K. Allan, 1936	2
	Pseudosacculus Hirase, 1928	1
Velutininae Gray, 1840	*Cartilagovelutina* Golikov & Gulbin, 1990	3
	Ciliatovelutina Golikov & Gulbin, 1990	4
	Cilifera Golikov & Gulbin, 1990	1
	Limneria H. Adams & A. Adams, 1851	3
	Marsenina Gray, 1850	7
	Marseniopsis Bergh, 1886	9
	Onchidiopsis Bergh, 1853	17
	Piliscus Lovén, 1859	3
	Pseudotorellia Warén, 1989	1
	Velutina J. Fleming, 1820	10
Not assigned	*Lamellariopsis* Vayssière, 1906	2
	Marseniella Bergh, 1886	1
	Torellivelutina J. H. McLean, 2000	1
	Total	**99**

the challenging systematics of both the gastropods and the tunicates. Three main feeding strategies have been described: *Lamellaria diegoensis* Dall, 1885 rasping through the ascidian tunic and extracting zooids via suction (Lambert, 1980); and *Velutina velutina* feeding on the surface of the tunic of ascidians with the radula (possibly eating epibionts) or drilling a hole in the tunic, inserting the proboscis and consuming the internal organs (Sargent *et al.*, 2019). As a result, velutinids have been treated historically as predators (e.g. Fretter & Graham, 1962; Lambert, 1980; Sargent *et al.*, 2019), parasites (Dias & Martins Delboni, 2008) or 'symbionts *sensu lato*' (Queiroz & Sales, 2016) of ascidians. Indeed, it can be said that velutinids act as predators of the single zooids in a colony, as grazers of the whole colony and as parasites when drilling a hole into the ascidian tunic either to feed on internal tissue or to lay eggs (or even as symbionts, if we consider that it has not been shown whether this interaction affects hosts fitness negatively). Acknowledging the complexity of their trophic and reproductive ecology, for simplicity we will here refer to velutinids as carnivorous parasites.

The velutinid mantle often mimics the ascidian host in both colour and pattern, often with spots resembling the oral apertures of colonial ascidians (Fig. 1A). Individuals of the same species (*Lamellaria mopsicolor* Ev. Marcus, 1958) can display different mantle features related to the appearance of their ascidian host (Dias & Martins Delboni, 2008). This observation led to the hypothesis that the pigments of the ascidian are incorporated into the mantle of the velutinid feeding on them. However, a 7-day host-shift experiment in an aquarium did not result in a colour change in the velutinid mantle, suggesting either that colour incorporation would be a process lasting longer or that colour patterns have a strictly genetic basis (Dias & Martins Delboni, 2008). Cases of velutinids resembling the surrounding rocky or algal substrate or even showing a barnacle-like dorsal pattern (e.g. in *Lamellaria perspicua*, Cornwall, UK) have also been described (Fig. 1D; Thompson, 1973).

Most species of Velutinidae are gonochoristic, but simultaneous hermaphroditism is reported in a few velutinine genera (*Marsenina*, *Onchidiopsis* and *Velutina*; Wilson, 1998). Larval development in velutinids has been reported to involve a long-lived planktotrophic larval stage (Hain & Arnaud, 1992; Wilson, 1998), but a reduction of the duration of the planktonic phase for some Antarctic species is assumed owing to protoconch morphology and morphometry (Fassio *et al.*, 2019).

Taxonomic study of Velutinidae is particularly challenging owing to the frequent absence of

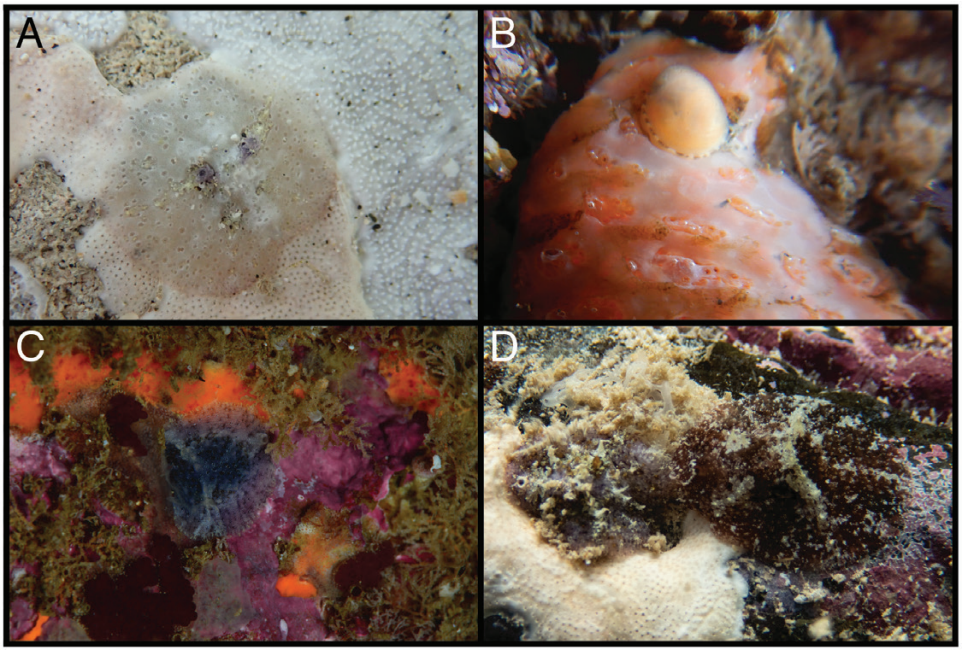

Figure 1. Velutinids in their habitats. A, *Marsenia* sp. on ascidians, Sal Island, Cape Verde. B, *Limneria prolongata* (NCT VePrSSAR8202020a) on *Aplidium californicum* (Ritter & Forsyth, 1917), Arch Rock, Brookings, OR, USA. C, *Lamellaria latens* complex (ZMBN 127500) on hard substrate, Egersund, Litle Svetlingen, Rogaland, Norway. D, two *Marsenia* sp. on hard substrate, Sal Island, Cape Verde. Photograph credits: A, D, Leopoldo E. Moro Abad; B, Nancy Treneman; C, ZMBN, Anders Schouw.

diagnostic shell features and a high degree of convergence in mantle shape and colour patterns. Indeed, Forbes & Hanley (1853: 354) wrote about the genus *Lamellaria*: 'The species of this genus are extremely difficult of distinction, in consequences of the close similarity of shells. At present it is impossible to say how many forms there are even in Europe. A careful examination and delineation of the animals […] will be necessary before we can arrive at a sound judgement respecting them.' A century and a half later, few works have attempted to revisit the systematics of this family (e.g. Behrens, 1980; Gulbin & Golikov, 1997, 1998, 1999, 2000, 2001; Behrens *et al.*, 2014; Fassio *et al.*, 2019). Fassio *et al.* (2019) showed that the bipartite subfamily classification does not conform to a molecular phylogenetic hypothesis for the group, highlighting the unsatisfactory state of velutinid systematics and suggesting that internal relationships needed to be redefined. Species delimitation based on shell features is severely hampered by the lack of informative characters in the thin, fragile and almost featureless shells and the highly variable mantle shape, texture and host associations (e.g. Behrens, 1980). All these issues make integrative taxonomy the only viable approach to address the species diversity and systematics of the group (Fassio *et al.*, 2019).

In this study, we explore the diversity and phylogenetic relationships of Velutinidae with the largest molecular dataset yet assembled, including 313 specimens representing > 50% of the currently accepted genera and covering much of the worldwide geographical distribution of this family.

MATERIAL AND METHODS

Material examined

The dataset consists of 313 specimens belonging to ten of the 19 accepted extant genera of Velutinidae (MolluscaBase, 2021): *Limneria* H. Adams & A. Adams, 1851, *Marsenina* Gray, 1850, *Marseniopsis* Bergh, 1886, *Onchidiopsis* Bergh, 1853 and *Velutina* J. Fleming, 1820 (Velutininae); *Calyptoconcha* Bouchet & Warén, 1993, *Coriocella* Blainville, 1824, *Hainotis* F. Riedel, 2000 and *Lamellaria* Montagu, 1816 (Lamellariinae); and *Lamellariopsis* Vayssière, 1906 (not assigned to a subfamily).

Specimens from all biogeographical realms (following Spalding *et al.*, 2007), except the Arctic and temperate South Africa, were included in our dataset, covering the worldwide distribution of the family. A total of 228 specimens were collected by the authors (NCT, Nancy Treneman personal collection) or kindly provided by colleagues from the Muséum national d'Histoire naturelle, Paris (MNHN), the National Museum of Natural History, Washington, DC (USNM), the Natural History Museum of Los Angeles County (LACM), the Instituto Español de Oceanografía, Vigo, the University Museum of Bergen (ZMBN), the Department of Biology and Biotechnologies 'Charles Darwin' of Sapienza University of Rome (BAU), the National Institute of Water and Atmospheric Research, New Zealand (NIWA) and the CEAMARK Program (CE). Whole specimens were almost invariably preserved in 95–98% ethanol, when possible at –20 °C. In some cases, in order to increase the ratio between the volumes of ethanol and tissue (generally kept 5:1 or higher), a clip of the foot was fixed separately (see Puillandre *et al.*, 2014). Six sequences were produced by the Ocean Genomic Legacy Center (OGL; Explore Northeastern, https://ogl.northeastern.edu), one by Giulia Furfaro (University of Salento, Italy) and the others at the Molecular Systematic Laboratory of the Department of Biology and Biotechnologies 'Charles Darwin' (Sapienza University of Rome, Italy).

Sequences of 85 additional specimens were downloaded from GenBank or BOLD, including the sequences from two species of Triviidae [*Trivia arctica* (Pulteney, 1799) and *Trivia monacha* (da Costa, 1778)] used as outgroups. For voucher numbers, collecting localities, sequence details and GenBank/BOLD accession numbers, see the Supporting Information (Table S1).

Molecular analyses and sequence alignment

Whole genomic DNA was extracted from a tissue clip of the foot using an optimized 'salting out' protocol modified from Aljanabi *et al.* (1997). Tissues were incubated overnight on a thermo-block at 55–60 °C with 430 µL of PK buffer and 20 µL of proteinase K (20 mg/mL). After incubation, tubes were mixed by inversion, centrifuged (10 min at 16 060 g), and the supernatants were transferred to fresh tubes. Next, 160 µL of 5 M NaCl was added. The tubes were mixed by inversion, centrifuged (10 min at 16 060 g), and the supernatants were transferred to fresh tubes. Then 500 µL of cold isopropanol was added. The tubes were mixed by gentle inversion and centrifuged (10 min at 16 060 g). The tubes were emptied, and the pellets were washed with 1000 µL of 80% ethanol, mixed by gentle inversion and centrifuged (5 min at 16 060 g). Lastly, the tubes were emptied, and the pellets were dried at 65 °C and resuspended in 50 µL of TE buffer.

In the case of old and/or poorly or improperly preserved material, the EZNA Mollusc DNA kit (Omega BIO-TEK) was used for DNA extraction, with optional steps to increase DNA yield as follows: incubation overnight at 50 °C on an agitation plate; column equilibration following the manufacturer's

instructions; and a first elution step with 50 µL of the provided elution reagent, followed by a second elution step using the first eluate.

Two mitochondrial and two nuclear markers were amplified. A 658 bp region of *COI* was amplified using several different primer pairs [LCO1490 and HCO2198 (Folmer *et al.*, 1994); jgLCOI and jgHCO (Geller *et al.*, 2013); and CoxAF and CoxAR (Colgan, 2003)]. When amplification of this region failed, possibly owing to DNA degradation, a minibarcode region of ~350 bp was amplified, replacing the forward primer with the internal primer mlCOIintF (Leray *et al.*, 2013). A ~700 bp region of the 16S rRNA gene was amplified with the primers 16SA (Palumbi, 1996) and CGLeuR (Hayashi, 2003) or 16SH (Espiritu *et al.*, 2001). Concerning nuclear genes, a ~800 bp region of the 28S rRNA gene was amplified with primers C1 and D2 (Jovelin & Justine, 2001), and a ~450 bp region of the second internal transcribed spacer (ITS2) was amplified with primers ITS-3d and ITS-4r (Oliverio *et al.*, 2002).

Polymerase chain reactions were performed with 1–3 µL of undiluted DNA template in a 25 µL reaction volume, including 2.5–3 µL of 10× NH_4 reaction buffer, 2.5–3 µL of 50 mM $MgCl_2$ solution, 0.15–0.2 µL of BIOTAQ DNA polymerase, 0.4 µL of each 25 pM primer solution, 1 µL of 10% bovine serum albumin solution and 0.5 µL of 10 mM nucleotide mix solution. The PCR conditions were as follows: initial denaturation (4 min at 94 °C); 35 cycles of denaturation (30 s at 94 °C), annealing (40 s at 48–52 °C for *COI* and 16S; 40 s at 58–62 °C for 28S and ITS2) and extension (1 min at 72 °C); and final extension (10 min at 72 °C). For difficult samples, PCR conditions for the *COI* molecular marker using universal primers followed a 'touchdown' profile modified from Desjardins *et al.* (2007): 24 cycles of denaturation (30 s at 94 °C), annealing (30 s at 50 °C, −0.4 °C per cycle) and extension (1 min at 72 °C, +2 s per cycle); 12 cycles of denaturation (30 s at 94 °C), annealing (30 s at 40 °C) and extension (2 min at 72 °C, +3 s per cycle); and final extension (10 min at 72 °C). For amplification of the minibarcodes, the 'touchdown' profile described by Leray *et al.* (2013) was used, or a version slightly modified as follows: initial denaturation (2 min at 94 °C); ten cycles of denaturation (10 s at 94 °C), annealing (30 s at 56 °C, −1 °C per cycle) and extension (1 min at 72 °C); 24 cycles of denaturation (10 s at 94 °C), annealing (30 s at 46 °C) and extension (1 min at 72 °C); and final extension (5 min at 72 °C).

The PCR products were purified using ExoSAP-IT (USB Corporation) and sequenced at Macrogen, Inc.

The sequences were aligned with MAFFT v.7 online (Katoh & Standley, 2013; Katoh *et al.*, 2019) using the E-INS-i algorithm (16S and ITS2) and the G-INS-i algorithm (*COI* and 28S).

Species delimitation

To assess velutinid species diversity, we adopted an integrative taxonomy approach for large datasets (Puillandre *et al.*, 2012). At first, each specimen was assigned to a candidate species based on pairwise *COI* genetic distances using an ascendent hierarchical clustering algorithm implemented in the program ASAP (assemble species by automatic partitioning; Puillandre *et al.*, 2020). ASAP analysis was conducted on the *COI* ingroup dataset after removal of 13 short minibarcode sequences (Kimura two-parameter substitution model, with other parameters as default; for a list of the removed specimens, see Supporting Information, Table S1). These hypothetical species were then tested further for reciprocal monophyly using the phylogenetic reconstruction obtained with the combined genetic dataset (see below for details of phylogenetic analyses) and integrated with information about their morphology and geographical range.

Pairwise *COI* genetic distances were calculated using MEGA v.11 (Kimura two-parameter substitution model, pairwise deletion, with other parameters as default; Tamura *et al.*, 2021).

Phylogenetic reconstruction

Phylogenetic analyses were performed on the four single-gene datasets (*COI* partitioned by codon, 16S, 28S and ITS2) and on the combined dataset (*COI* + 16S + 28S + ITS2) with both maximum likelihood (ML) and Bayesian inference (BI). The best-fitting nucleotide substitution models for each partition were chosen with PAUP4 (Swofford, 2003) using the Bayesian information criterion (BIC; *COI*, first codon position of the open reading frame = TrN+I+G; *COI*, second codon position = HKY+I+G; *COI*, third codon position = GTR+G; 16S = TrN+I+G; 28S = GTR+I+G; and ITS2 = HKY+G).

Maximum likelihood analyses were done using IQ-TREE (Trifinopoulos *et al.*, 2016), with 10 000 ultrafast bootstrap replicates for node support. Bayesian inference analyses were performed using MrBayes v.3.2.6 (Ronquist & Huelsenbeck, 2003) with an eight-chain Markov chain Monte Carlo (MCMC), run in parallel for 5×10^7 generations, with trees sampled every 1000 generations and a burn-in of 25%. MrBayes analyses were run on the CIPRES Science Gateway (Miller *et al.*, 2010). We evaluated convergence of each analysis using Tracer v.1.7.1 (Rambaut *et al.*, 2018) to ensure that effective sampling size (ESS) values were > 200.

Nodes were considered supported for Bayesian posterior probability (PP) values ≥ 0.95. The same threshold (95%) was used for the ultrafast bootstrap

(UFb) value obtained from the ML analyses, as suggested by the authors of IQ-TREE (Minh *et al.*, 2013).

Phylogenetic trees were visualized using FIGTREE v.1.4.4 (Rambaut, 2018).

MORPHOLOGICAL ANALYSES

The morphology of the shell, radula, jaws and soft parts was examined for at least three specimens for each genus-level clade and integrated with published data when available [with the exception of *Hainotis sharonae* (Willett, 1939), for which only published data were used]. When available, the coloration of the living animal was noted. Alcohol-preserved specimens were observed and dissected under a Wild M6 dissection microscope. For gonochoristic genera, specimens were sexed based on the presence or absence of a penis. Radulae, jaws and shells were observed with a scanning electron microscope (SEM). Radulae and jaws were dissected from the buccal masses, cleaned with 20% NaOH solution, rinsed in distilled water, air dried and coated with gold at the Laboratory of Electron Microscopy (Department of Earth Science, Sapienza University of Rome) and at the AMOBIO Unit (Stazione Zoologica Anton Dohrn, Italy). Scanning electron microscopic observations of radulae, jaws and larval shells were made with a Hitachi TM3000 SEM at the Laboratory of Technological and Functional Analyses of Prehistoric Artefacts (Department of Classics, Sapienza University of Rome). Shell photographs were taken at the Zoological Museum (Sapienza University of Rome, Italy) under a ZEISS Axio Zoom V16 microscope using an Axiocam 208 colour.

TAXONOMIC REVISION

Genus and subfamily names were assigned to each clade based, as far as possible, on the position in the tree of the type species or genus; when this was not possible, taxonomic recognition was based on diagnostic morphological characters. Given that velutinid species descriptions from the 19th and 20th centuries were frequently based on elusive diagnostic characters (such as mantle colour and shell shape; see Fassio *et al.*, 2019), we were not able to ascribe several clades to nominal species. In some cases, in order to reflect the uncertainty of the identification better, we have preceded the specific name of the taxon with the Latin 'cf.' (*confere*).

RESULTS

MOLECULAR DATASET

The molecular dataset was composed of 290 *COI*, 199 16S, 73 28S and 135 ITS2 sequences. There was some relevant type material among the specimens for which molecular sequencing failed; therefore, those specimens have been investigated here based only on morphology, namely: *Djiboutia verrucosa* Vayssière, 1912 (holotype *MNHN-IM-2000-35926*), *Lamellariopsis aurora* Hedley, 1916 (syntype C.46801.003), *Marsenina liouvillei* Vayssière, 1917 (syntype MNHN-IM-2000-34139), *Marseniopsis charcoti* Vayssière, 1917 (holotype *MNHN-IM-2000-34137*), *Marseniopsis antarctica* Vayssière, 1906 (holotype *MNHN-IM-2000-34135*) and *Lamellariopsis turqueti* Vayssière, 1906 (holotype *MNHN-IM-2000-34136*). Among the successfully sequenced specimens, the following merit a special mention: the holotype of *Coriocella herberti* Drivas & Jay, 1990 (*MNHN-IM-2000-35903*), 11 specimens of *Lamellaria* spp. (ZMBN) from Norway, four of which were collected near the type locality of *Lamellaria latens* (O. F. Müller, 1776) (i.e. Bergen), 56 species of *Lamellaria* spp. from the type locality of *Lamellaria perspicua* (Mediterranean Sea) and one specimen of *Marseniopsis* sp. from Argentinian waters, a genus previously considered as endemic to Antarctica.

Overall, the PCR success rate increased dramatically (80–100 vs. 30–50%) in those specimens for which a piece of tissue was excised from the body and fixed and preserved separately, as opposed to specimens that were preserved whole in ethanol. This might be attributable to the high volume of water in the tissues of velutinids causing dilution of the alcohol, and thus reducing the quality of DNA fixation. However, considering the heterogeneity of the dataset in terms of collection and fixation methods, dates and the size of specimens, many additional factors could have affected the PCR success.

SPECIES DELIMITATION

The ten best partitions found by ASAP divided the dataset into 66–91 hypothetical species. The best partition according to ASAP score divided the dataset into 88 hypothetical species [$P = 4.05 \times 10^{-1}$, rank = 13; W (Relative Barcode Gap Width) = 1.82×10^{-4}, rank = 6; threshold distance = 1.98%] and the second best into 81 ($P = 3.19 \times 10^{-1}$, rank = 11; $W = 1.56 \times 10^{-4}$, rank = 9; threshold distance = 3.08%; Supporting Information, Fig. S1). All but seven of the hypothetical species identified by ASAP, in both the first- and the second-best partitions, corresponded to monophyletic groups supported in the ML and BI phylogenetic reconstructions (PP = 0.99–1, Ufb = 97–100). The clades that were not fully supported or that were not retrieved congruently by the two best ASAP partitions are listed below (proceeding from the top to the bottom of the tree). For practical reasons, the 12 main phylogenetic clades (corresponding to genera) were

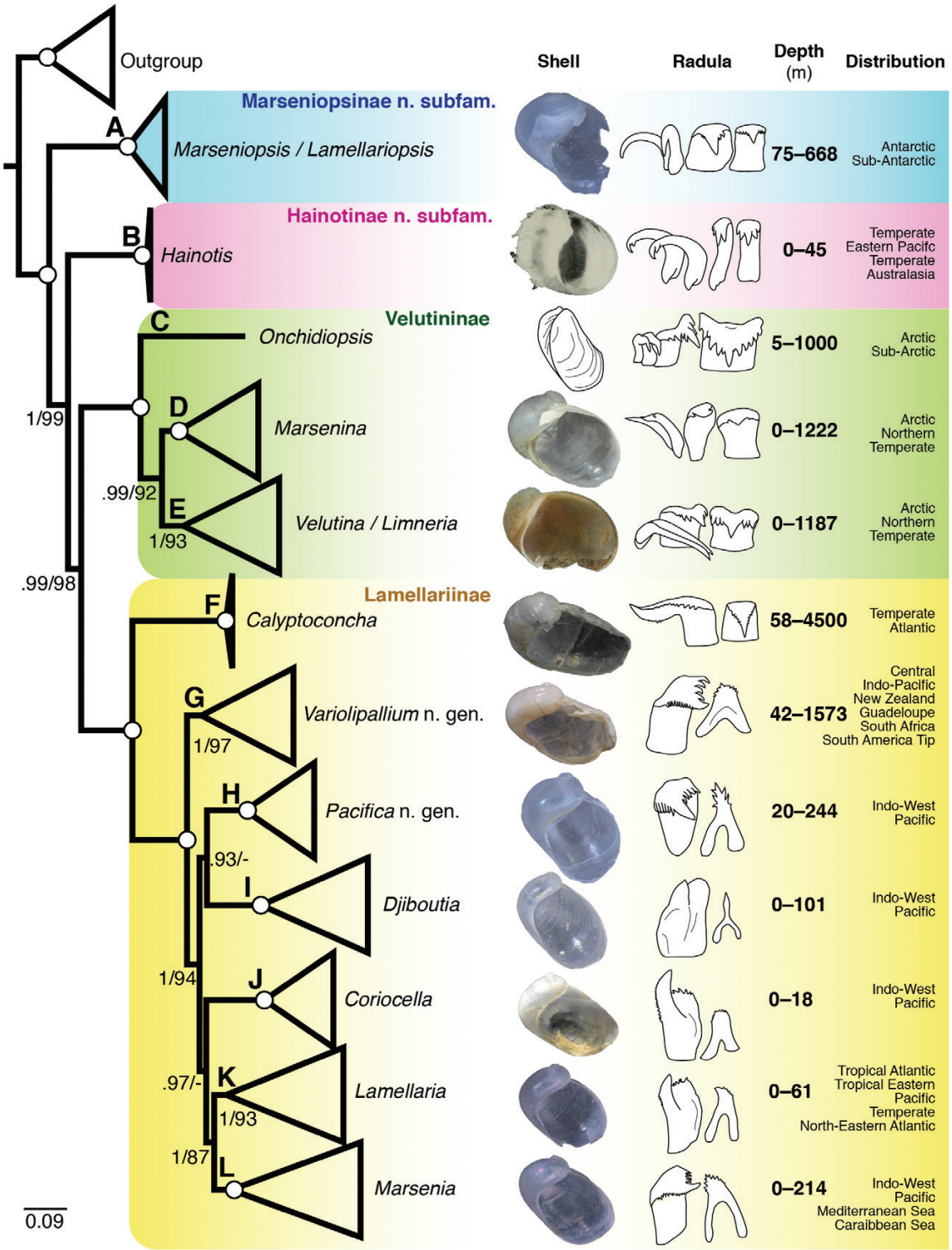

Figure 2. Phylogenetic relationships of the family Velutinidae (Bayesian tree based on the combined dataset), with clades (A–L) collapsed by genera. Numbers at nodes indicate branch support values [posterior probability (PP) and ultrafast bootstrap (UFb) values, respectively]; support values are shown only when at least one of them is ≥ 80%; white circles at nodes indicate maximum support (PP = 1, Ufb = 100). On the right side of the tree, for each genus is reported a representative photograph of the shell, a schematic representation of the radula, the depth range (in metres) and the geographical distribution.

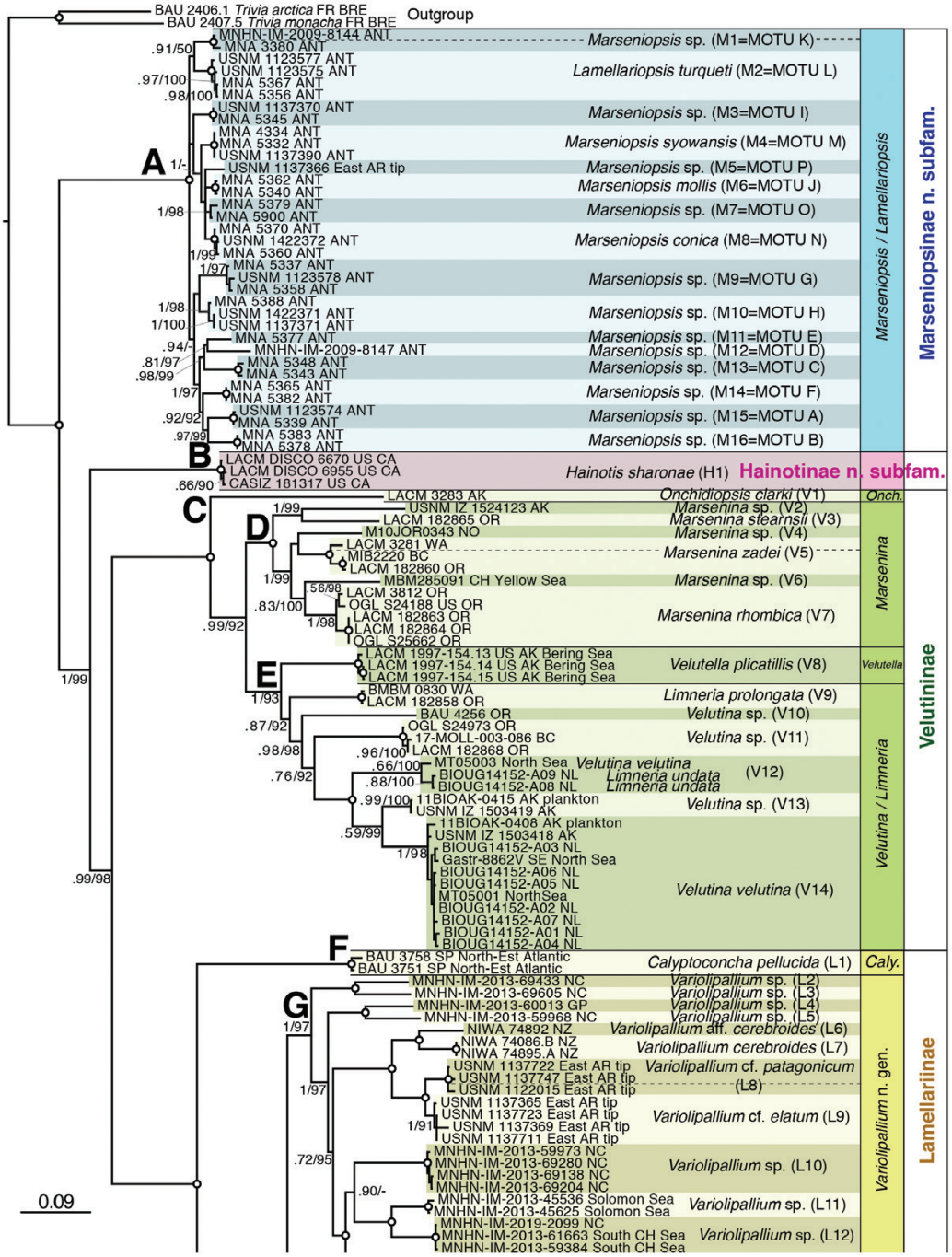

Figure 3. Phylogenetic relationships of the family Velutinidae (Bayesian tree based on the combined dataset) showing clades A–L expanded. Numbers at nodes indicate branch support values [posterior probability (PP) and ultrafast bootstrap (UFb) values, respectively]; support values are shown only when at least one of them is ≥ 80%; white circles at nodes indicate maximum support (PP = 1, Ufb = 100). Boxes indicate hypothetical species; dashed lines indicate possible alternative species partitions. Coloured boxes on the right indicate genera, and white boxes indicate subfamilies. Letters at the end of sample codes broadly indicate the area of origin: AK, Alaska; ANT, Antarctica; AR, Argentina; BC, British Columbia; BRE, Bretagne; CA, California; CH, China; COR, Corse; CR, Costa Rica; FL, Florida; GF, French Guiana; GP, Guadeloupe; HI, Hawaii; IT, Italy; MG, Madagascar; MQ, Martinique; MX, Mexico; MZ, Mozambique; NC, New Caledonia; NL, Newfoundland; NO, Norway; OR, Oregon; PA, Panama; PF, French Polynesia; PG, Papua New Guinea; PH, Philippines; QLS, Queensland; RE, Reunion; SA, Saudi Arabia; SP, Spain; TAS, Tasmania; TW, Taiwan; VU, Vanuatu; WA, Washington State; ZNZ, Zanzibar.

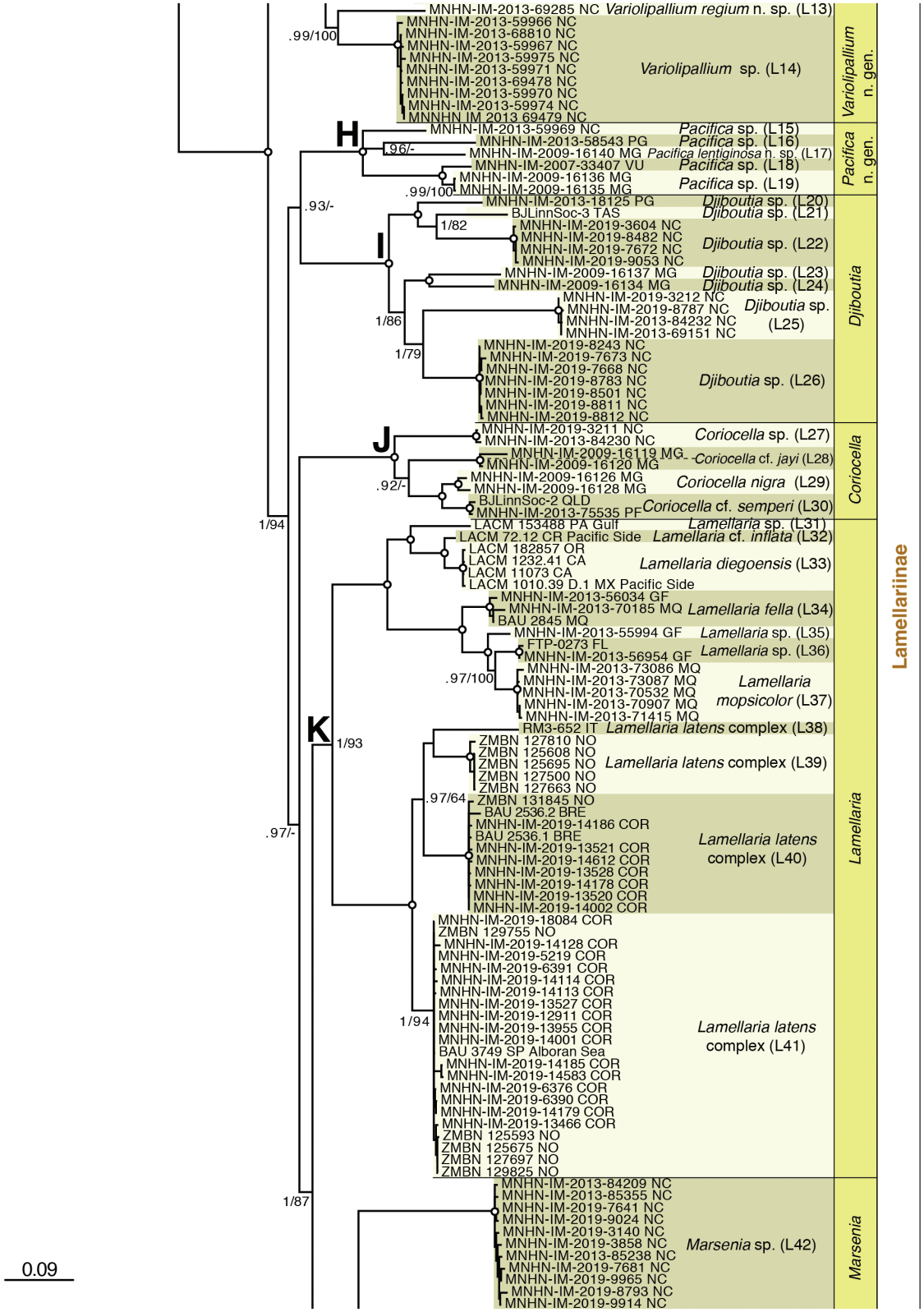

Figure 3. Continued

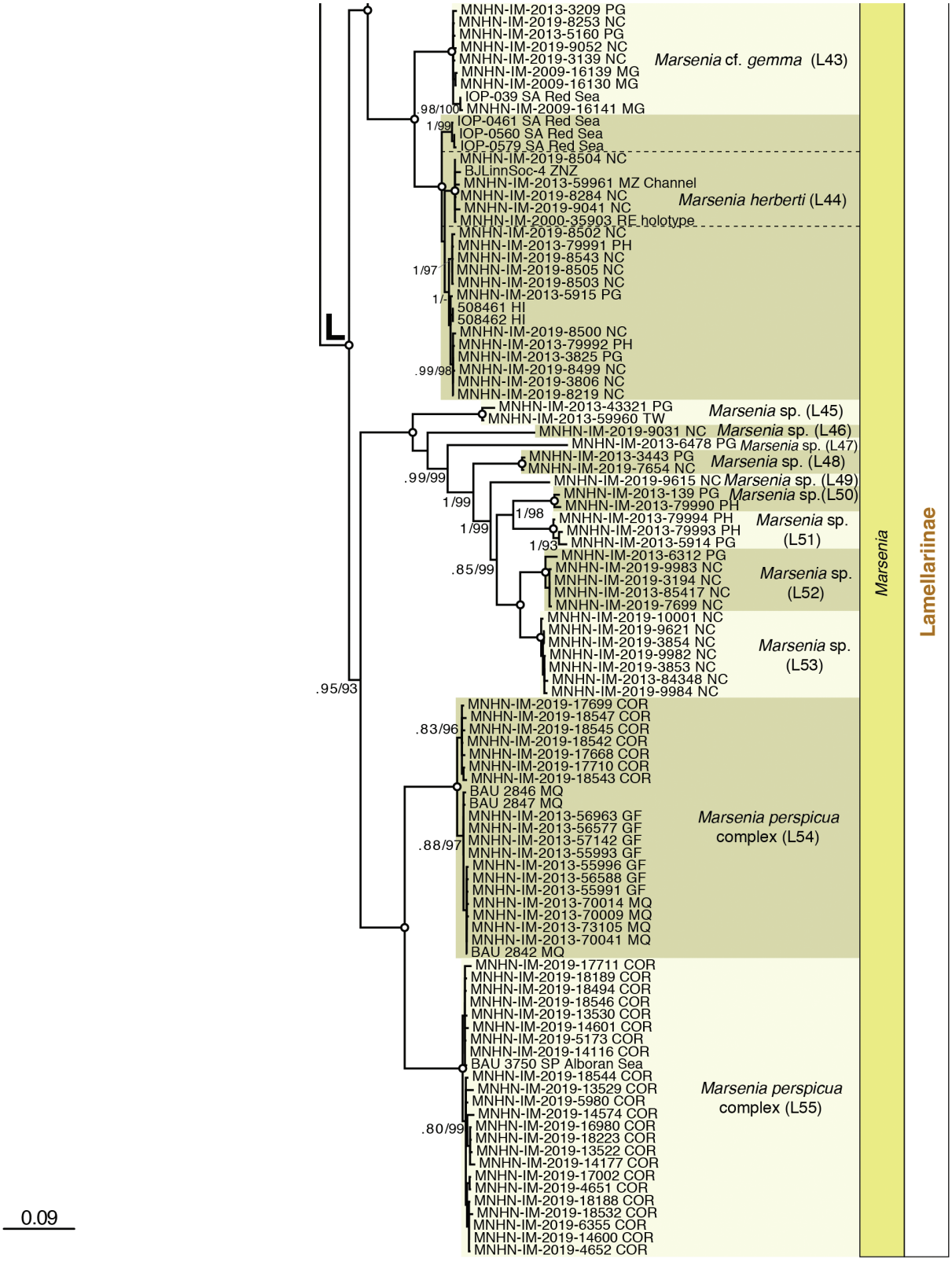

Figure 3. Continued

labelled A–L (Figs 2, 3), and the hypothetical species were numbered as the first letter of the subfamily plus a number (e.g. 'V1' = first hypothetical species of the subfamily Velutininae) (Fig. 3). For hypothetical species of the *Marseniopsis*/*Lamellariopsis* clade (A), the labelling used by Fassio *et al.* (2019) [Molecular Operational Taxonomic Unit (MOTU) A–P] is also reported.

In the *Marseniopsis*/*Lamellariopsis* clade (A), the first partition recognized two specimens, both belonging to M1 (= MOTU K), previously identified by Fassio *et al.* (2019) as distinct species (1.99% of genetic distance). The second partition considered *Marseniopsis mollis* (M6 = MOTU J) and M7 (= MOTU O) as belonging to the same species (0.66–4.58% of *COI* genetic intraspecific distance). However, a monophyletic M6 + M7 clade was not present in any of the phylogenetic trees.

The first partition divided clade V5 (*Marsenina zadei* Behrens *et al.*, 2014) into two species, sympatric in the south of Vancouver Island (interspecific genetic distance = 3.01–3.18%; sp. 1: LACM 3281, Port Townsend, WA, USA, 15 m; sp. 2: MIB2220, Little Beach, Vancouver Island, Canada, and LACM 182860, Brookings, OR, USA, intertidal); whereas the second partition considered them as a single species.

Clade V12, including one sequence from GenBank labelled as *Velutina velutina* and two as *Limneria undata* (T. Brown, 1839), was monophyletic only in the ML analysis (PP = 0.66, Ufb = 100).

Clade L8 [*Variolipallium* cf. *patagonicum* (E. A. Smith, 1881)] was considered a single hypothetical species by the second partition, but it was split into two species by the first. The first partition considered specimens USNM 1137747 and USNM 1122015 (3.07% of genetic distance; collected at ~70 km distance; depth 119 and 120 m, respectively) as belonging to two different species (present only in the ML tree, UfB = 99). The possibility that the only other specimen included in this clade, USNM 1137722, belongs to a fourth species was not evaluated by ASAP because of the lack of a *COI* sequence.

The monophyly of clade L9 [*Variolipallium* cf. *elatum* (Strebel, 1906)] was supported by the BI analysis only (PP = 1, Ufb = 91). The first partition split the two specimens of clade L28 from southern Madagascar (*Coriocella* cf. *jayi* Wellens, 1996) into two sympatric species (2.5% of genetic distance), whereas the second partition retrieved them as a single species.

Clade L44 (*Coriocella herberti*) was divided by the first partition into three hypothetical species, corresponding to three reciprocally monophyletic clades (interspecific genetic distance = 2.00–3.54%): one found only in the Red Sea (PP = 1, UfB = 99), one in the western Indian Ocean islands (Zanzibar, Madagascar and Reunion) and in New Caledonia (PP = 1, UfB = 100), and the last one in the Philippines, Papua New Guinea, New Caledonia and Hawaii (PP = 1). The second partition considered L44 as a single species. In addition, it is worth noting that all three *COI* sequences downloaded from GenBank and obtained from autonomous reef monitoring structures (ARMS) deployed in the Red Sea (also those labelled 'Paguridae' or 'Gastropoda', OP0461, OP0560 and OP0579) unequivocally belong to velutinid species. Lastly, clade L41 (*Lamellaria latens* complex) was supported by the Bayesian analysis only (PP = 1, Ufb = 94).

Of the 36 specimens not included in the ASAP analysis [because their *COI* sequences were short (13 specimens) or absent (23 specimens)], 31 belonged to phylogenetic clades already identified as hypothetical species, but five represented independent phylogenetic lineages, probably corresponding to as many additional species: LACM 3283 (V1) *Onchidiopsis clarki* Behrens *et al.*, 2014, MNHN-IM-2013-60013 (L4) *Lamellaria* sp. from Guadeloupe, LACM 153488 (L31) *Lamellaria* sp. from the Gulf of Panama, LACM 72.12 (L32) *Lamellaria* cf. *inflata* from the Pacific coast of Costa Rica and RM3-652 (L38) from the central Tyrrhenian Sea (belonging to the *Lamellaria latens* species complex).

Accepting the most conservative ASAP partition and integrating it with information from the phylogenetic analysis and *COI* genetic distances, we identified 86 candidate species divided as follows: 16 species in the *Marseniopsis*/*Lamellariopsis* clade, one in the *Hainotis sharonae* lineage, 14 in Velutininae and 55 in Lamellariinae (Fig. 3). Based on morphological characters (Figs 4–11), for 28 of these candidate species it was possible to assign a species name.

Phylogenetic reconstruction

Comparison of the major nodes among all trees, both for single genes and combined, revealed no inconsistencies (i.e. alternative relationships subtended by strongly supported nodes in distinct trees). Phylogenetic analyses of the combined dataset strongly supported (PP = 1, Ufb = 100) the reciprocal monophyly of four major evolutionary lineages: an Antarctic and sub-Antarctic clade ('A') including the genera *Marseniopsis* and *Lamellariopsis*, a clade ('B') including only *Hainotis sharonae*, a clade including the genera belonging to subfamily Velutininae and a fourth clade including the genera belonging to subfamily Lamellariinae (Figs 2, 3; Supporting Information, Figs S2–S9).

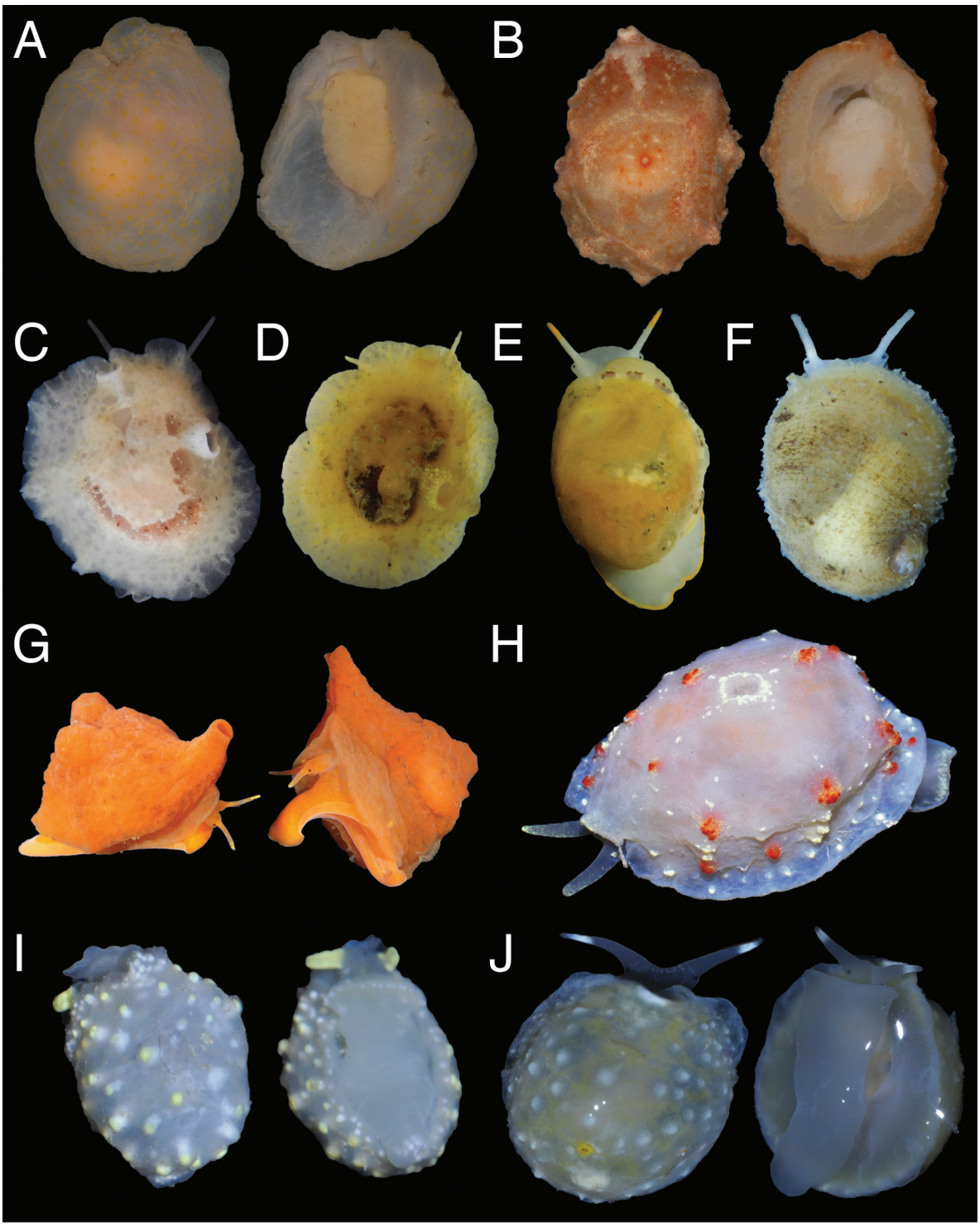

Figure 4. A, *Marseniopsis* sp. (M9), MNA 5376. B, *Marseniopsis conica*, MNA 5361. C, *Marsenina zadei*, LACM 182861. D, *Marsenina rhombica*, LACM 182862. E, *Limneria prolongata*, LACM 182858. F, *Velutina* sp., LACM 182869. G, *Hainotis sharonae*. H, *Variolipallium regium* sp. nov., *MNHN-IM-2013-69285*, holotype. I, *Variolipallium* sp. (L3), MNHN-IM-2013-69605. J, *Variolipallium* sp. (L10), MNHN-IM-2013-69280. Photograph credits: A, B, MNA, Stefano Schiaparelli; C–F, Nancy Treneman; G, iNaturalist, Robin Gwen Agarwal; H–J, MNHN, Philippe Maestrati. For the sequenced specimens, the corresponding species code (see Fig. 3) is reported in parentheses.

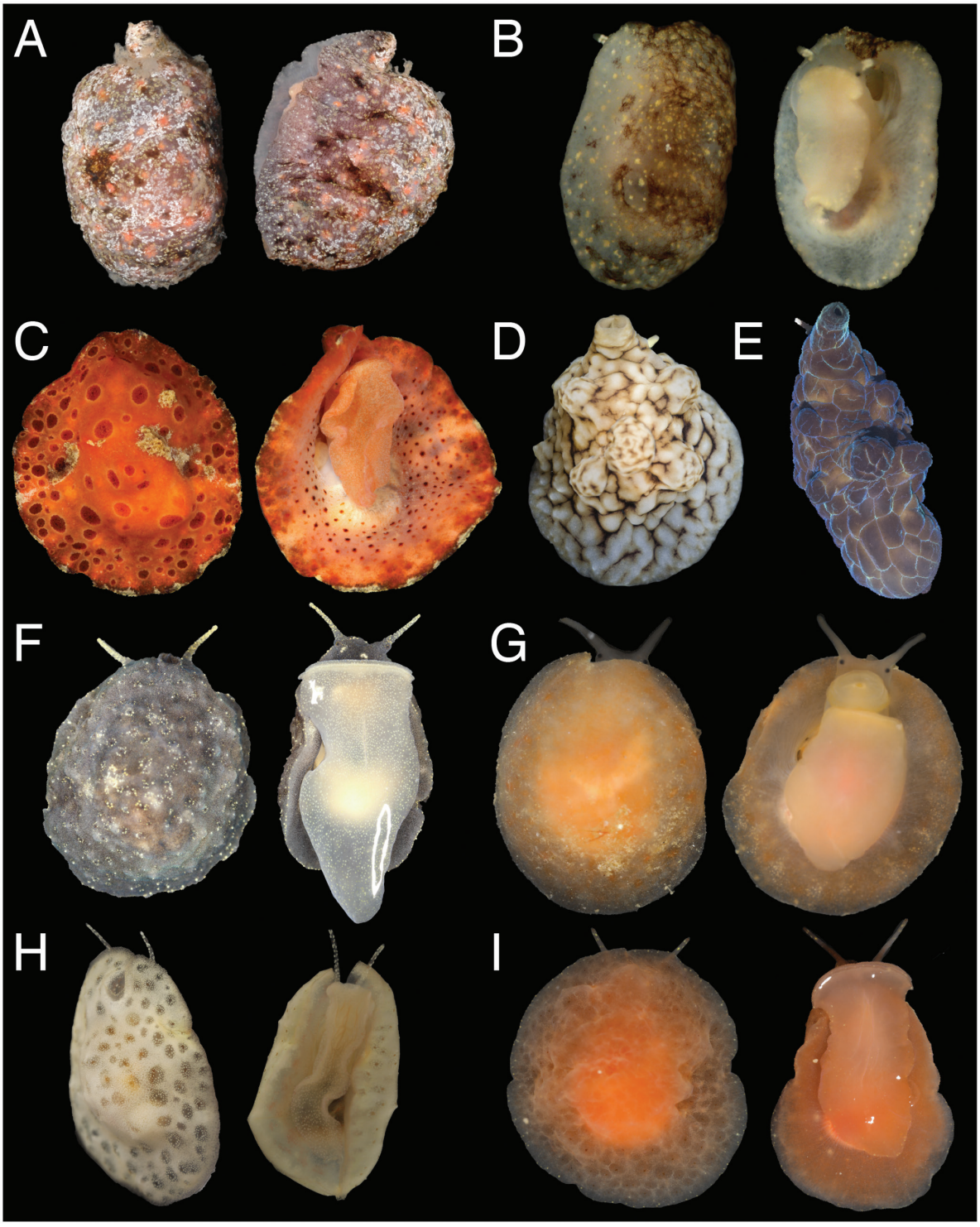

Figure 5. A, *Pacifica lentiginosa* sp. nov., *MNHN-IM-2009-16140*, holotype. B, *Pacifica* sp. (L18), MNHN-IM-2007-33407. C, *Djiboutia* sp. (L22), MNHN-IM-2019-9053. D, *Coriocella* sp., UF-IZ-523481. E, *Coriocella* sp., MNHN-IM-2019-26097. F, *Lamellaria mopsicolor*, MNHN-IM-2013-73086. G, *Lamellaria latens* complex (L41), MNHN-IM-2019-6391. H, *Marsenia herberti*, MNHN-IM-2019-8219. I, *Marsenia perspicua* complex (L55), MNHN-IM-2019-13522. Photograph credits: A–C, F, MNHN, Philippe Maestrati; D, Florida Museum of Natural History—Invertebrate Zoology, Gustav Paulay; E, MNHN, Giulia Fassio; G, I, MNHN, Gilles Devauchelle; H, MNHN, Laurent Charles. For the sequenced specimens, the corresponding clade code (see Fig. 3) is reported in parentheses.

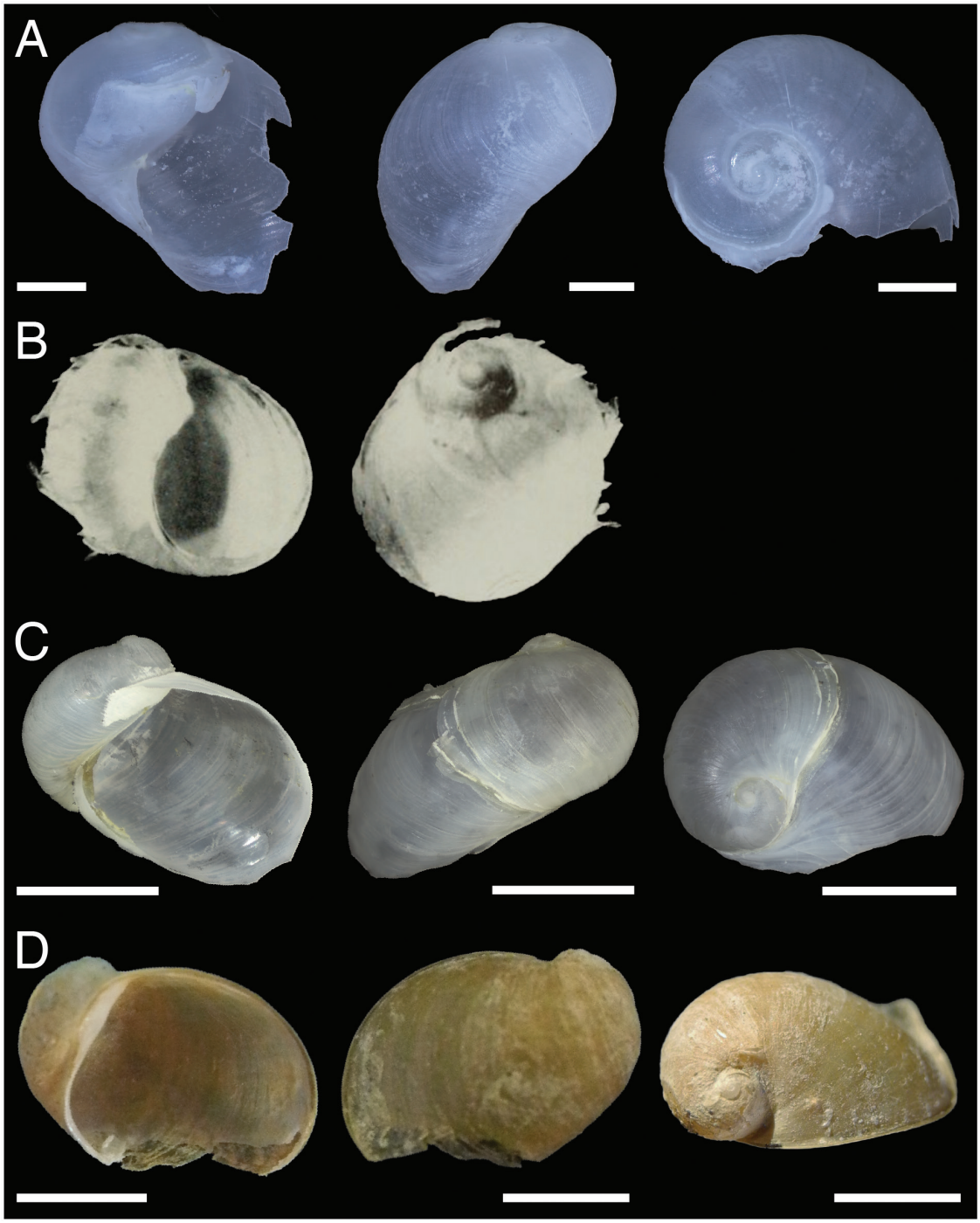

Figure 6. Velutinidae shells. A, *Marseniopsis conica*, BAS 03-764. B, *Hainotis sharonae*, *LACM 1059*, holotype (after Willet, 1939: fig. 1 and 1a). C, *Marsenina rhombica*, BAU 4229. D, *Limneria prolongata*, BAU 4228. Scale bars: A, 1 mm; C, D, 5 mm; B, shell maximum diameter = 5.5 mm, shell height 7.4 mm.

The *Marseniopsis*/*Lamellariopsis* clade was identified as sister to the rest of the family (PP = 1, Ufb = 100) and the *Hainotis* clade as sister (PP = 1, Ufb = 99) to the Velutininae + Lamellariinae clade (PP = 0.99, Ufb = 98). Most of the phylogenetic relationships in the *Marseniopsis*/*Lamellariopsis* clade were not resolved. Instead, *Onchidiopsis* ('C') was confidently identified as sister to the rest of subfamily Velutininae (PP = 1, Ufb = 100). Two other subclades were recovered for this subfamily: one ('D')

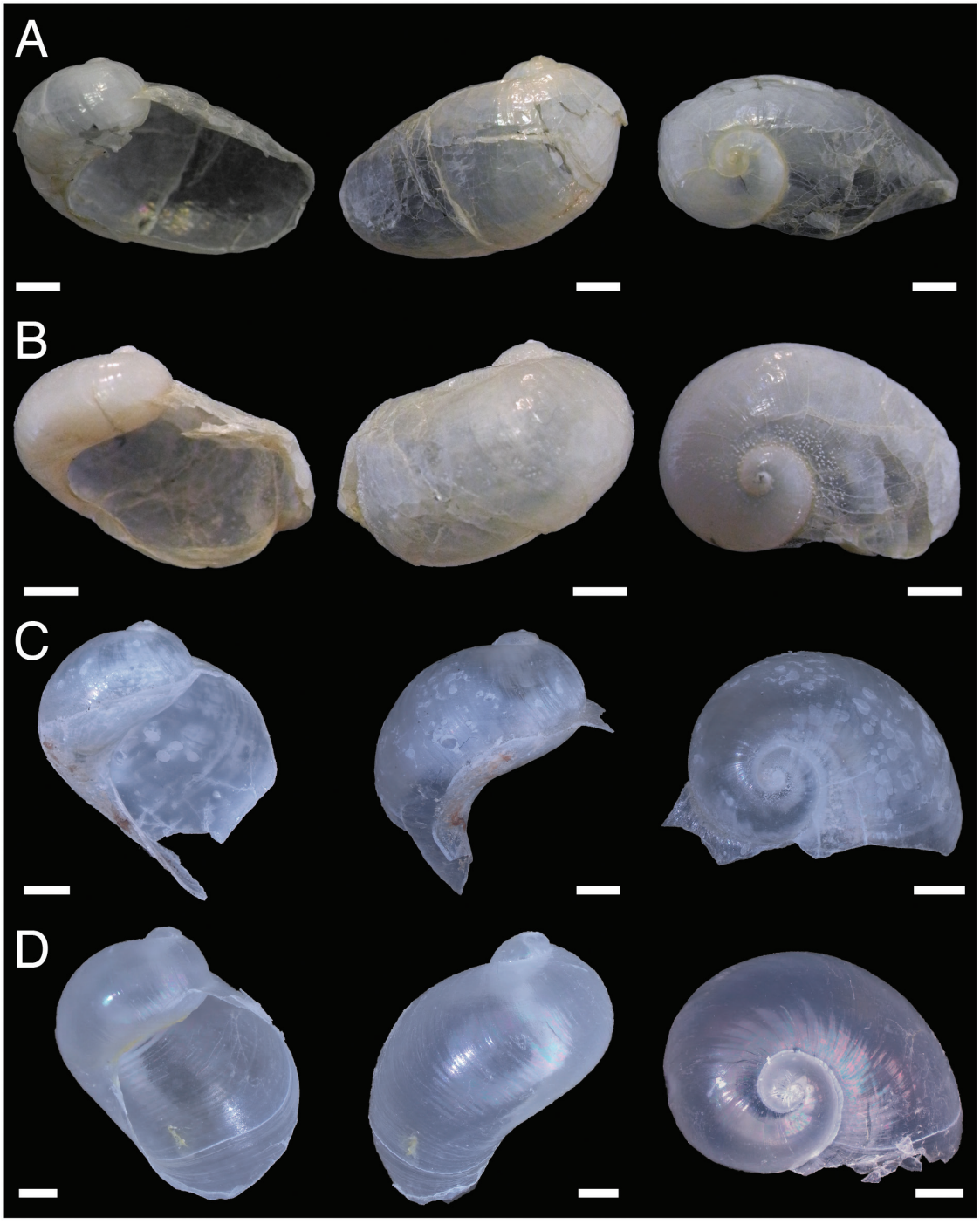

Figure 7. Velutinidae shells. A, *Calyptoconcha pellucida*, BAU 3758. B, *Variolipallium cerebroides*, NIWA 74086.A. C, *Pacifica lentiginosa* sp. nov., *MNHN-IM-2009-16140*, holotype. D, *Pacifica* sp. (L16), MNHN-IM-2013-58543. Scale bars: A, B, 5 mm; C, D, 1 mm. For the sequenced specimens, the corresponding species code (see Fig. 3) is reported in parentheses.

corresponding to the genus *Marsenina* and including a published sequence from Norway (M10JOR0343) erroneously identified as '*Lamellaria latens*' (PP = 1, Ufb = 100) and one ('E') comprising the genera *Limneria*, *Velutella* and *Velutina* (PP = 1, Ufb = 93).

Within subfamily Lamellariinae, seven major lineages were recovered as reciprocally monophyletic: the genus *Calyptoconcha* ('F'), which is sister to the rest of Lamllearíinae (PP = 1, Ufb = 100), and clades 'G' (PP = 1, Ufb = 97), 'H' (PP = 1, Ufb = 100), 'I' (*Djiboutia*,

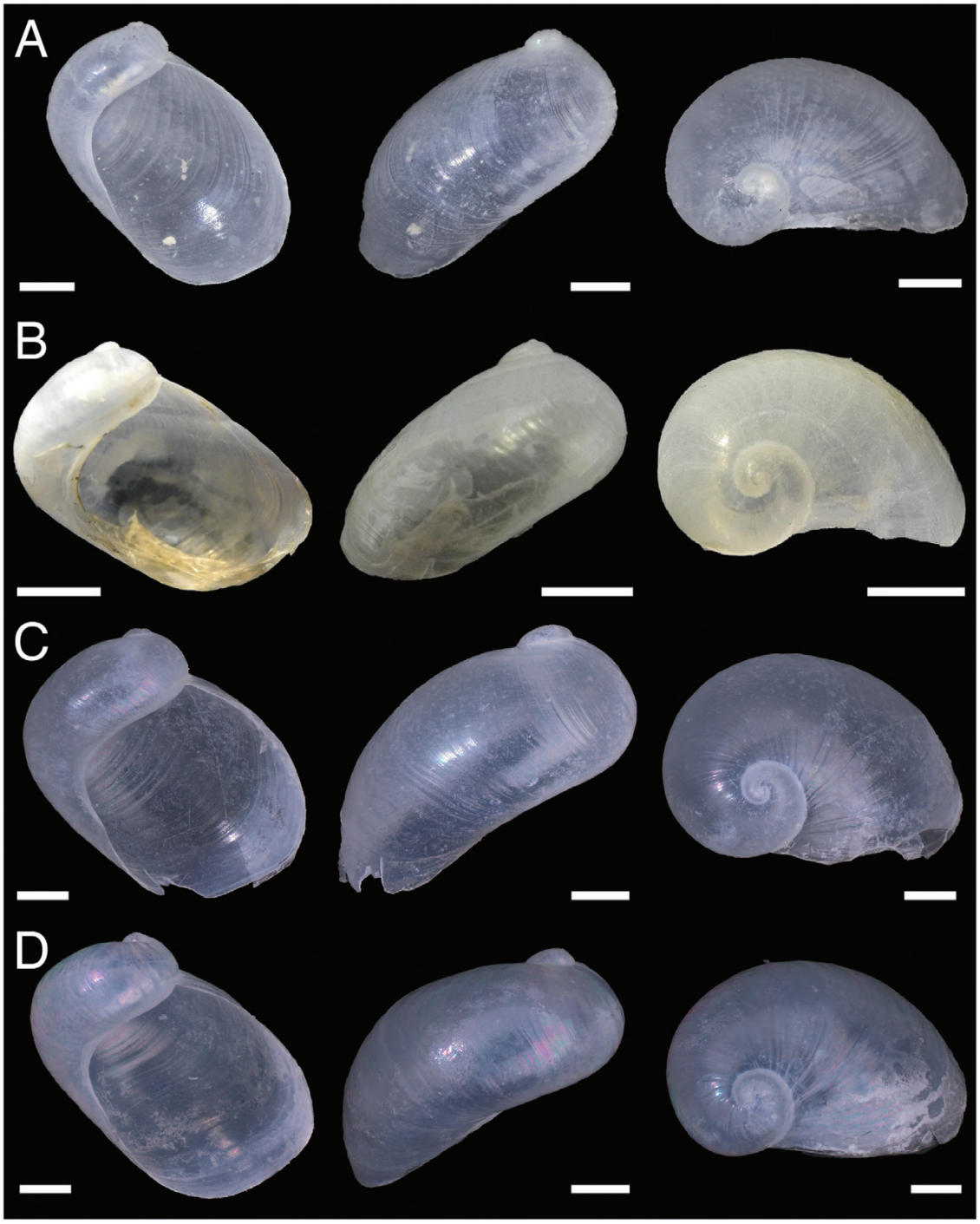

Figure 8. Velutinidae shells. A, *Djiboutia* sp. (L26), MNHN-IM-2019-7668. B, *Coriocella* sp. (L27), MNHN-IM-2013-84230. C, *Lamellaria latens* complex (L41), MNHN-IM-2019-14179. D, *Marsenia perspicua* complex (L55), MNHN-IM-2019-14574. Scale bars: A, C, D, 1 mm; B, 5 mm. For the sequenced specimens, the corresponding species code (see Fig. 3) is reported in parentheses.

PP = 1, Ufb = 100), 'J' (*Coriocella*, PP = 1 Ufb = 100), 'K' (*Lamellaria*, PP = 1, Ufb = 93) and 'L' (*Marsenia*, PP = 1, Ufb = 100). Bayesian inference reconstructions identified clade 'G' as sister to all the others (PP = 1, Ufb = 94). All the internal nodes between the clades listed above (except the one joining 'H' and 'I') were statistically supported in the BI analysis, but not by ML.

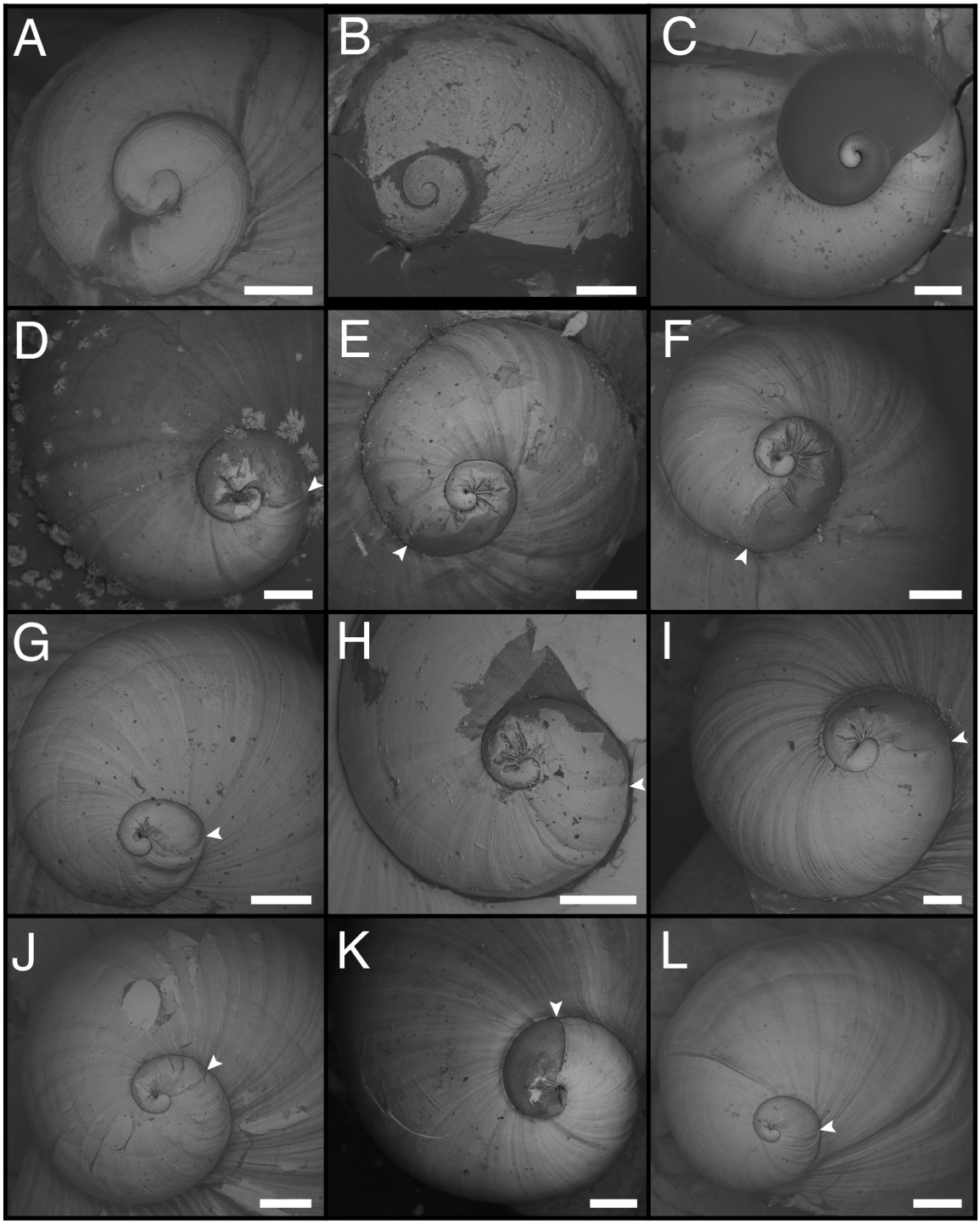

Figure 9. Velutinidae protoconchs. A, *Marseniopsis conica*, BAS 03-764. B, *Marsenina rhombica*, BAU 4229. C, *Calyptoconcha pellucida*, BAU 3758. D, *Variolipallium cerebroides*, NIWA 74086.A. E, *Pacifica lentiginosa* sp. nov., *MNHN-IM-2009-16140*, holotype. F, *Pacifica* sp. (L16), MNHN-IM-2013-58543. G, *Djiboutia* sp. (L22), MNHN-IM-2019-9053. H, *Coriocella* sp. (L27), MNHN-IM-2013-84230. I, *Lamellaria latens* complex (L41), MNHN-IM-2019-14179. J, *Lamellaria mopsicolor*, MNHN-IM-2013-73086. K, *Marsenia perspicua* complex (L55), MNHN-IM-2019-14574. L, *Marsenia* sp. (L42), MNHN-IM-2019-7641. Scale bars: A–L, 500 µm. For the sequenced specimens, the corresponding species code (see Fig. 3) is reported in parentheses. Arrows indicate protoconch I – protoconch II boundary.

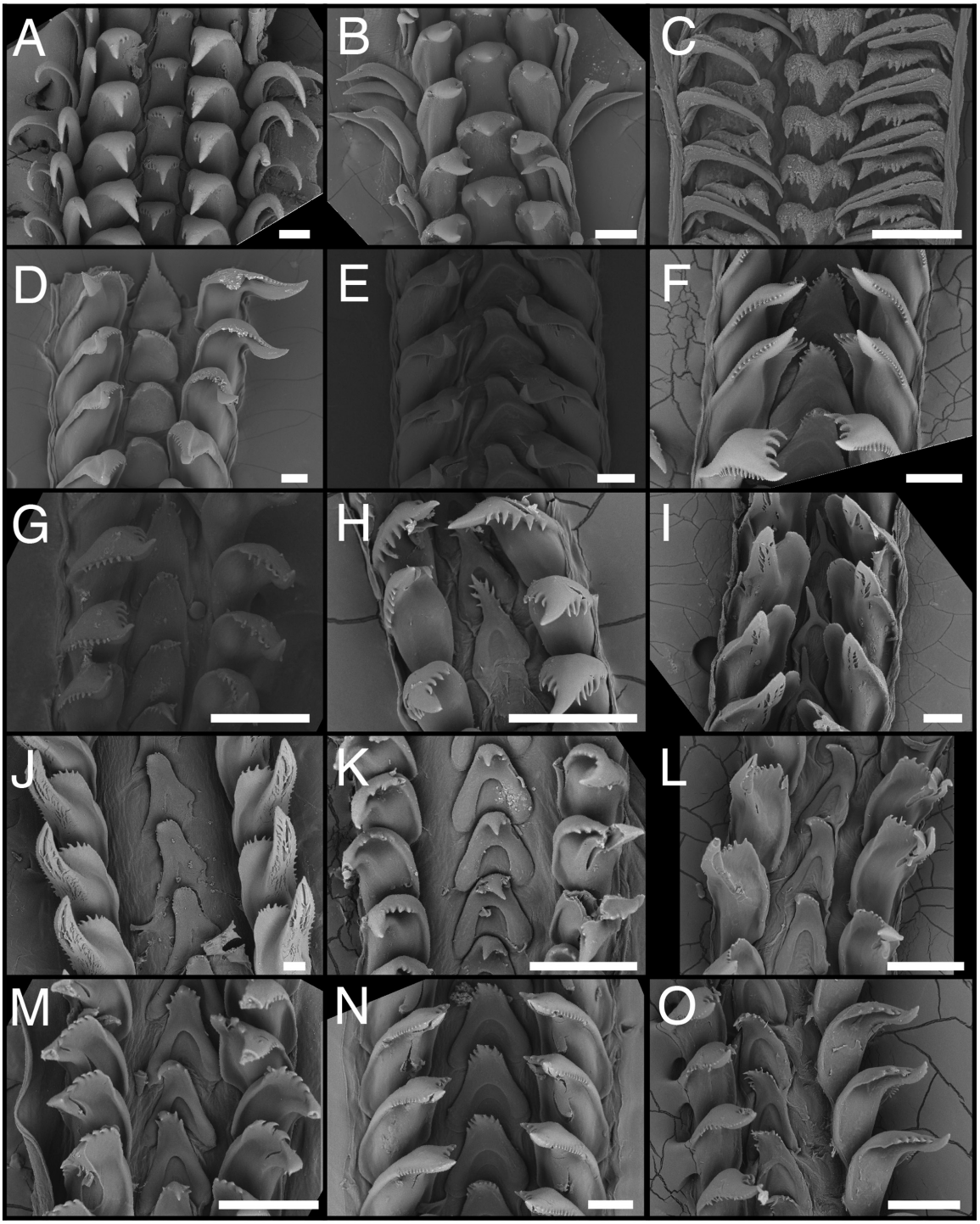

Figure 10. Velutinidae radulae. A, *Marseniopsis mollis*, CE 6137. B, *Marsenina rhombica*, BAU 4229. C, *Velutina* cf. *coriacea*, LACM 182870. D, *Calyptoconcha pellucida*, BAU 3751. E, *Variolipallium regium* sp. nov., *MNHN-IM-2013-69285*, holotype. F, *Variolipallium* sp. (L10), MNHN-IM-2013-69280. G, *Pacifica lentiginosa* sp. nov., *MNHN-IM-2009-16140*, holotype. H, *Pacifica* sp. (L15), MNHN-IM-2013-59969. I, *Djiboutia* sp. (L22), MNHN-IM-2019-9053. J, *Coriocella* sp. (L27), MNHN-IM-2013-84230. K, *Lamellaria mopsicolor*, MNHN-IM-2013-73086. L, *Lamellaria latens* complex (L41), MNHN-IM-2019-14113. M, *Marsenia herberti*, MNHN-IM-2019-8503. N, *Marsenia* sp. (L45), MNHN-IM-2013-59960. O, *Marsenia perspicua* complex (L55), MNHN-IM-2019-5980. Scale bars: A–O, 100 µm. For the sequenced specimens, the corresponding species code (see Fig. 3) is reported in parentheses.

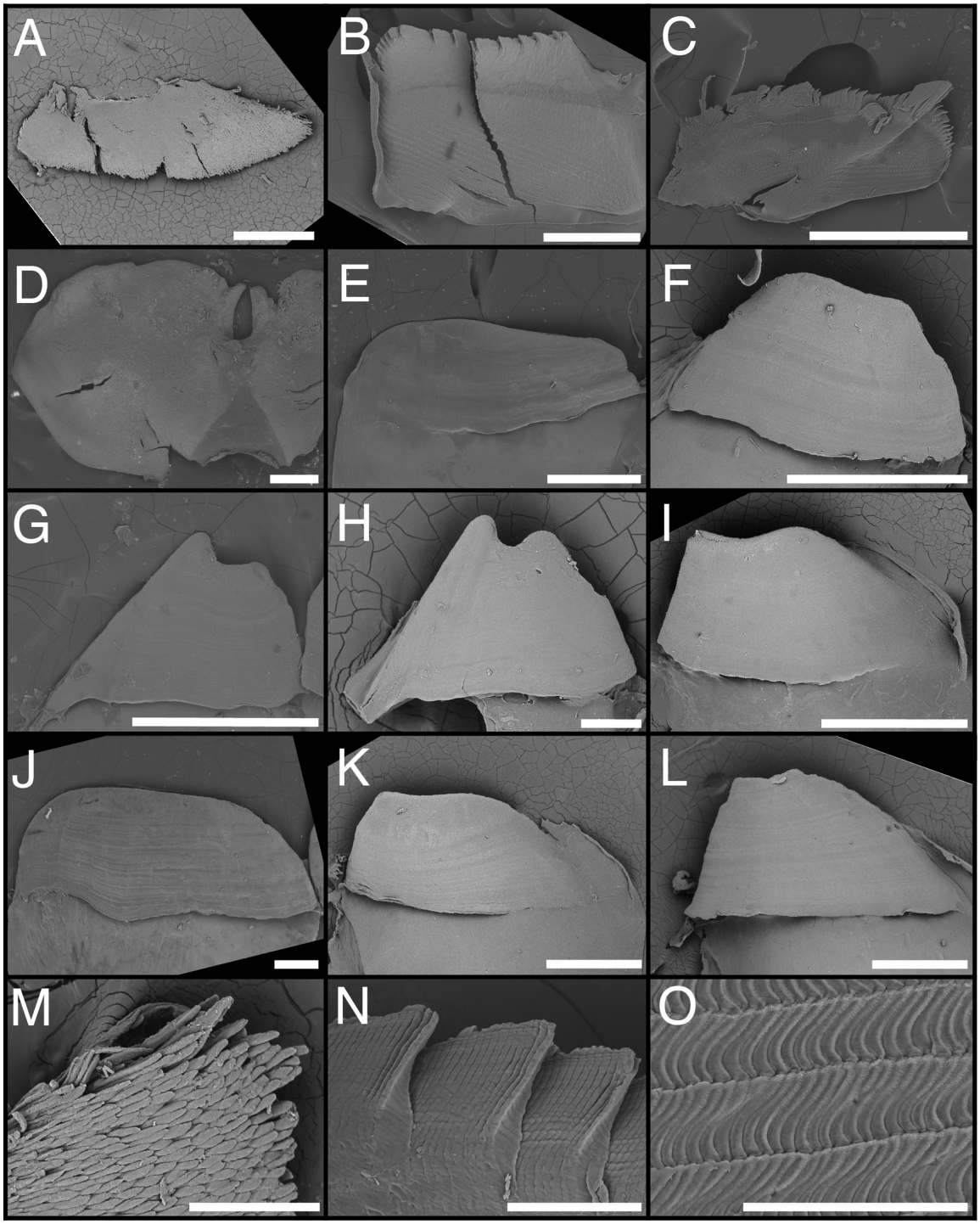

Figure 11. Velutinidae jaws. A, M, *Marseniopsis mollis*, CE 6152. B, N, O, *Marsenina rhombica*, BAU 2339. C, *Limneria prolongata*, BAU 4228. D, *Calyptoconcha pellucida*, BAU 3758. E, *Variolipallium regium* sp. nov., *MNHN-IM-2013-69285*, holotype. F, *Variolipallium* sp. (L10), MNHN-IM-2013-69280. G, *Pacifica lentiginosa* sp. nov., *MNHN-IM-2009-16140*, holotype. H, *Pacifica* sp. (L19), MNHN-IM-2009-16136. I, *Djiboutia* sp. (L22), MNHN-IM-2019-9053. J, *Coriocella* cf. *jayi* (L28), MNHN-IM-2009-16119. K, *Lamellaria latens* complex (L40), BAU 2536.2. L, *Marsenia* sp. (L45), MNHN-IM-2013-59960. Scale bars: H, M–O, 100 µm; A–G, I–L, 500 µm. For the sequenced specimens, the corresponding species code (see Fig. 3) is reported in parentheses.

DISCUSSION

TAXONOMIC IMPLICATIONS OF THE PHYLOGENETIC ANALYSIS

The phylogenetic analyses conducted on the molecular dataset revealed that relationships in the family Velutinidae are far more complex than historical depictions based on morphological characters. In fact, the pattern emerging from our results, while confirming (with some modifications) the previous recognition of Velutininae and Lamellariinae, indicates the need to attribute subfamily rank to two additional lineages (Figs 2, 3).

The new subfamily Marseniopsinae

The *Marseniopsis*/*Lamellariopsis* lineage includes deep-water species with a vestigial shell completely enclosed by the mantle or presenting a small fissure on the dorsum (*Marseniopsis rhombica*; Fig. 4D). Previously thought to be endemic to the Southern Ocean, our analysis extended the range of this group to Argentinian waters (north of Isla de los Estados), where a single specimen belonging to M5 (= new MOTU P) was collected. This peculiar distribution pattern was observed in other genera with planktotrophic larvae, such as the kleptoparasitic genus *Cryocapulus* Schiaparelli, Bouchet, Fassio & Oliverio, 2020 (Capulidae). *Cryocapulus* includes two species with an echinospira larva and a distribution similar to that of the *Marseniopsis*/*Lamellariopsis* clade: *Cryocapulus subcompressus* (Pelseneer, 1903), endemic to the Southern Ocean, and *Cryocapulus compressus* (E. A. Smith, 1891), in South America from 43°S southwards on the Pacific side and from 28°S southwards on the Atlantic side (Schiaparelli *et al.*, 2000; Cárdenas *et al.*, 2008; Fassio *et al.*, 2021). The species included in the *Marseniopsis*/*Lamellariopsis* clade present two protoconch types that differ mainly in the nucleus size: one is smaller and similar in size to that reported for the rest of the family, the other is larger, possibly suggesting a shortening of the larval phase (Fassio *et al.*, 2019). Given the recovered phylogenetic pattern, the support of diagnostic radular and jaw features, the distribution range and the genetic divergence from the other velutinid lineages, we recognize this clade as a new subfamily Marseniopsinae, described below (see Systematics section).

The new subfamily Hainotinae

The monotypic *Hainotis* lineage is currently included in subfamily Lamellariinae, with which it shares the same radular formula but nevertheless has different tooth shapes. However, it emerged as a distinct lineage in our phylogenetic analyses. The genus *Hainotis* is present along the coast of California and has a peculiar polygonal dorsal mantle that completely encloses the shell (Fig. 4G). Its phylogenetic position and the unique mantle shape support the placement of this genus in a new subfamily, described below (see Systematics section). Based on morphological characters, in particular, the shape of the radula and jaws, the genus *Mysticoncha* J. K. Allan, 1936, from temperate South Australia, Victoria and New Zealand, is also included in this new subfamily.

The rest of the velutinids match features of the two traditionally recognized subfamilies: Velutininae and Lamellariinae.

Subfamily Velutininae

Velutininae are distributed in all Arctic and temperate areas. They have the same radular formula as Marseniopsinae and Hainotinae (2:1:1:1:2), but with a larger base on the lateral and central teeth. In this group, the jaws have a characteristic appearance, being composed of scale-like elements (as in Marseniopsinae) presenting a denticulation on the masticatory side (Fig. 11A, M). Velutininae were thought to include all velutinid species with a shell completely or partly exposed (some with a small fissure in the centre of the dorsum). However, we found at least nine additional species, belonging to two new genera in subfamily Lamellariinae and one in Marseniopsinae, that possess a small fissure on the dorsal mantle, showing that this morphological character is not diagnostic at the subfamily level.

Subfamily Lamellariinae

The subfamily Lamellariinae is by far the largest in terms of the number of genera and species. It can be found from shallow to deep sea, in all tropical areas and in the temperate northern Atlantic. Many of the taxa included in this subfamily, even if phylogenetically distant, can have overlapping morphologies, making them very hard to distinguish without a genetic analysis. Traditionally, lamellariine taxonomy is based on a short list of morphological characters, some of which were confirmed in our molecular results to be diagnostic at the genus level (e.g. shape of the radular teeth). The jaws, shell and protoconch can be useful additional characters for those genera showing peculiar shapes but are often similar across the whole subfamily and therefore hard to use alone as diagnostic characters. Regarding shell shape, only macro-differences [such as high vs. low spire, well calcified vs. less calcified (here termed as membranaceus)] are diagnostic. Fretter & Graham (1962: 319–322) described differences between the

shells of *Lamellaria latens* and '*Lamellaria*' *perspicua*, but in fact, when several specimens, from both sexes and of different sizes, are observed and compared, many of these alleged morphological differences turn out to represent a gradient of shapes overlapping between different species (e.g. Fig. 8C, D). Bergh (1887) had suggested using the conformation of the vas deferens, forming either a loop or several folds in the haemocoel (between the body wall and the base of the penis), as a genus-level diagnostic character. Simone (2004) considered this character as 'additive' because of its ontogeny, because a clearly distinguishable loop was visible only in mature males. Our results suggest that molecular congeners can present different states of this character, and even at the species level its reliability is questionable.

Within the subfamily Lamellariinae, diagnosed by a synapomorphic radula lacking marginal teeth (formula 0:1:1:1:0), we recognize the following seven phylogenetic lineages consistent with genus-level taxonomic ranking: *Calyptoconcha* Bouchet & Warén, 1993 ('F'), *Variolipallium* Fassio, Bouchet & Oliverio ('G'), *Pacifica* Fassio, Bouchet & Oliverio ('H'), *Djiboutia* Vayssière, 1912 ('I'), *Coriocella* ('J'), *Lamellaria* ('K') and *Marsenia* Oken, 1823 ('L'); plus *Marseniella*, not present in our molecular dataset.

Calyptoconcha

The *Calyptoconcha* lineage is represented in the tree by two specimens of *Calyptoconcha pellucida* (A. E. Verrill, 1880) from the Bay of Biscay. This genus can be diagnosed confidently by three characters: the shape of the rachidian tooth, not bifurcated at the base (Fig. 10D); the shape of the jaws, presenting a small vertical protrusion in the interior side; and the appearance of the larval shell, which lacks subsutural axial folds on protoconch I and possesses a smaller nucleus compared with other lamellariines (54–75 µm; Fig. 9C). Specimens belonging to this genus are also comparatively large (≤ 4 cm in length) with respect to other lamellariines and can occur at greater depths (≤ 4500 m). Owing to the peculiar and unique characteristics of the radula and jaws, this genus is easy to identify, and we can attribute two additional species to it: *Marsenia capensis* Bergh, 1907 (South Africa, Cape Point) and *Lamellaria branca* Simone, 2004 (Brazil, São Paulo state, off Ubatuba).

The new genus Variolipallium

An additional genus ('G'), sister to all remaining lamellariines, is widely distributed in tropical and southern temperate areas, from offshore to deep waters (42–1573 m deep). This genus is characterized by a weakly calcified and high-spired shell, like *Calyptoconcha* and *Marseniopsis*, combined with a rachidian tooth with a bifurcated base. The external morphology is variable, ranging from a wrinkled mantle resembling the convolutions of a brain, as in *Lamellaria cerebroides* Hutton, 1882, to a completely smooth mantle. This previously unrecognized lineage here described as new (see the Systematics section below) includes at least eight species that have a small fissure in the dorsal mantle (see Fig. 4H, J). The type species has a remarkable mantle coloration, with a light background studded with dark orange and white spots, and an octagonal shape (Fig. 4H).

Other genera of the subfamily Lamellariinae share a rachidian tooth with bifurcated base, like an inverted 'V', and can be divided into two major lineages: one including two sister genera, *Pacifica* Fassio, Bouchet & Oliverio and *Djiboutia*, and the other including the genus *Coriocella* as sister to the remaining two, *Lamellaria* and *Marsenia*.

The new genus Pacifica

The clade corresponding to the new genus *Pacifica* includes a small number of undescribed species, and the type species (*Pacifica lentiginosa*) lives in South Madagascar. This genus is characterized by the presence of several long denticles on the rachidian and lateral teeth and by jaws that are not elongated, with an external protrusion on the upper side (Fig. 11G, H). This genus is restricted to the Indo-West Pacific and includes one of the species described by Bergh (1886b) from the Philippines, *Marsenia indecora* Bergh, 1886.

Djiboutia

Djiboutia was established by Vayssière (1912) for *Djiboutia verrucosa* Vayssière, 1912 from the Gulf of Tadjoura (Djibouti). The diagnostic character of this genus is the unique shape of the rachidian tooth: bifurcated base, smooth and slender (Fig. 10I). Although our molecular dataset lacks specimens from the type locality of *D. verrucosa*, we confidently identify this clade by its peculiar rachidian tooth and show that its range extends at least from Madagascar to New Caledonia. Two additional species, *Lamellaria australis* Basedow, 1905 and *Marsenia sibogae* Bergh, 1908, are allocated to *Djiboutia* based on the same diagnostic character.

Coriocella

The *Coriocella* lineage was the easiest to identify confidently, based on the characteristic shape of the dorsal mantle, with two to six large warts (Fig. 5D, E). However, given that alcohol fixation can prevent easy detection of these warts, additional useful characters can be the calcified shell and the relatively large size

(≤ 8.5 cm in length). The diversity of this genus was documented by Wellens (1991, 1995, 1998, 1999), who also proposed diagnostic keys. Two specimens present in our dataset and collected in Madagascar (MNHN-IM-2009-16126 and MNHN-IM-2009-16128) were identified as belonging to the type species, *Coriocella nigra* Blainville, 1824.

Lamellaria

The type species of the genus *Lamellaria* is *Lamellaria tentaculata* Montagu, 1816, (type locality: south-west of the British Isles) by subsequent designation of Wenz (1940). *Lamellaria tentaculata* is generally treated as a synonym of *Bulla latens* O. F. Müller, 1776 (type locality: around Bergen). Given that clade 'K' includes specimens belonging to *Lamellaria latens*, we propose here a restricted concept of the genus *Lamellaria* Montagu, 1816, corresponding to clade 'K', including Mediterranean, north-eastern Atlantic, Caribbean and tropical eastern Pacific species. *Lamellaria* can be diagnosed by the radular morphology, specifically the presence of denticles restricted to the left side of the rachidian tooth cusp (Fig. 10K, L). Owing to the high level of variability of shell morphology and mantle coloration, this genus name, in addition to *Marsenia* (currently regarded as a synonym of *Lamellaria*), has been used historically for a vast array of species that our phylogenetic analyses demonstrated to belong to distinct lineages. It is likely that the same issue hampered the identification of the multiple species that have been grouped so far under the name *Lamellaria latens*. Our molecular species delimitation approach revealed that *Lamellaria latens* is a complex of at least four species with overlapping shell morphologies. Given that two of these cryptic species are present at the type locality in Norway (Fig. 3: clades L39 and L41), the allocation of the name *Lamellaria latens* is not straightforward. We also included *Coriocella fella* Er. Marcus & Ev. Marcus, 1970 in the genus *Lamellaria*, based on its characteristic rachidian tooth, unilaterally denticulated, and the general shape of the shell and absence of the typical mantle dorsal warts of *Coriocella*.

Marsenia

The last clade ('L'; Fig. 2) is diagnosed by the presence of lateral teeth with a single external cusp with small denticles and a rachidian tooth with bifurcated base. This radula is similar to that of the new genus *Pacifica* except for the smaller size of the denticles on the lateral teeth (Fig. 10M–O). This lineage includes several species, two of which are cryptic and ascribable to *Helix perspicua* Linnaeus, 1758: one is amphi-Atlantic (present in the Mediterranean and the Caribbean), while the other is restricted to the Mediterranean.

Helix perspicua (type locality: Mediterranean Sea) is currently considered a synonym of *Bulla haliotidea* Montagu, 1803, the type species of the genus *Marsenia* (currently regarded as a synonym of *Lamellaria*), the name that we propose to use for this lineage. This genus also includes, among others, *Coriocella herberti* Drivas & Jay, 1990 (for which the holotype was sequenced; Fig. 3: clade L44) and a clade that might represent *Marsenia gemma* Bergh, 1875 (Fig. 3; clade L43). For two species included in this genus, *Marsenia perspicua* complex L55 and *Marsenia* sp. L45, specimens with a shell not completely exposed were observed. Owing to the high level of variability of shell morphology and mantle coloration, this genus name, in addition to the name *Lamellaria*, has been used historically for a vast array of species that our phylogenetic analyses demonstrated to belong to at least four distinct lineages (*Variolipallium*, *Lamellaria*, *Marsenia* and *Pacifica*).

Marseniella

Lastly, we include in the subfamily Lamellarinae the monotypic genus *Marseniella* Bergh, 1886, type species *Marseniella borealis* Bergh, 1886 (type locality: Florø, north of Bergen, Norway), based on its radular formula (0:1:1:1:0) and the shape of the rachidian tooth, which presents a bifurcated base. *Marseniella* is also characterized by a shell that is peculiar in consistency and shape; it is only partly calcified, similar to that of *Onchidiopsis* (Velutininae), flatter than *Lamellaria*/*Marsenia*, with a broad last whorl detached from the spire (Bergh, 1887: pl. X figs 1, 2). No specimen in our molecular dataset has a morphology matching these characters.

Based on these observations, we here propose a revised classification of the family Velutinidae (for a synopsis of the most useful characters and information for diagnosis of subfamilies and genera, see Table 2).

SYSTEMATICS

Superfamily Velutinoidea Gray, 1840

Family Velutinidae Gray, 1840

Velutinidae Gray, 1840: 90; type genus *Velutina* J. Fleming, 1820.

Included subfamilies: Hainotinae Fassio, Bouchet, Schiaparelli & Oliverio subfam. nov., Lamellariinae d'Orbigny, 1841, Marseniopsinae Fassio, Bouchet, Schiaparelli & Oliverio subfam. nov., Velutininae Gray, 1840.

Description: Small to medium size for the superfamily, 0.5–11.5 cm total length. Shell exposed to completely

Table 2. Synopsis of the most useful characters and information for diagnosis of subfamilies and genera

Character	Marseniopsinae	Hainotinae	Velutininae	Lamellariinae	*Calyptoconcha*	*Variolipallium*	*Pacifica*	*Djiboutia*	*Coriocella*	*Lamellaria*	*Marsenia*	*Marseniella*
External morphology												
Shape	Flat or dome shaped; outline rounded or polygonal	Dome shaped; outline rounded or polygonal	Flat or dome shaped; outline rounded	Flat or dome shaped; outline rounded or polygonal	Flat or dome shaped; outline rounded	Flat or dome shaped; outline rounded or polygonal	Flat or dome shaped; outline rounded	Flat or dome shaped; outline rounded	Dome shaped; outline rounded, two to six warts	Flat or dome shaped; outline rounded, rounded	Flat or dome shaped; outline rounded	Flat; outline rounded
Size (cm)	0.5–11.5	0.5–5.0	0.5–11.0	0.5–10.0	1–4	0.5–3.0	0.5–1.0	0.5-3.3	1.5–8.5	0.3–1.1	0.3–10	2.2
Mantle	Fused or dorsal fissure	Fused	Fused or not fused	Fused or dorsal fissure	Fused	Fused or dorsal fissure	Fused	Fused	Fused	Fused	Fused or dorsal fissure	Fused
Shell												
Shape	Ear shaped	Ear shaped	Ear, shield or cap shaped	Ear shaped	Ear shaped	Ear shaped	Ear shaped	Ear shaped	Ear shaped	Ear shaped	Ear shaped	Ear shaped, last whorl detached from spire
Spire	High	High	Low or high	Low or high	High	High	Low	Low	Low	Low	Low or high	Low
Thickness	Very thin	Thin or very thin	Moderately thin or thin	Thin or very thin	Very thin	Very thin	Very thin	Thin or very thin	Thin	Thin	Thin	Thin
Texture	Weak to membranaceous	Weak	Strong to weak	Strong to membranaceus	Weak to membranaceous	Weak to membranaceous	Weak	Weak	Strong to moderate	Weak	Weak	Membranaceous
Periostracum	Thin to not visible	Thin to moderately developed, hairy	Moderately or well developed, occasionally hairy	Thin to not visible	Not visible	Not visible	Not visible	Not visible	Thin	Not visible	Not visible	?
Nucleous	With or without granular sculpture	?	With or without granular sculpture	Subsutural axial folds	Smooth	Subsutural axial folds	Subsutural axial folds	Subsutural axial folds	Subsutural axial folds	Subsutural axial folds	Subsutural axial folds	?

Table 2. Continued

Character	Marseniopsinae	Hainotinae	Velutininae	Lamellariinae	*Calyptoconcha*	*Variolipallium*	*Pacifica*	*Djiboutia*	*Coriocella*	*Lamellaria*	*Marsenia*	*Marseniella*
Radula												
Formula	2:1:1:1:2	2:1:1:1:2	2:1:1:1:2	0:1:1:1:0	0:1:1:1:0	0:1:1:1:0	0:1:1:1:0	0:1:1:1:0	0:1:1:1:0	0:1:1:1:0	0:1:1:1:0	0:1:1:1:0
Rachidian	Elongated.Base rectangular. Cusp, three to four small to pronounced denticles, each side	Elongated. Base rectangular. Cusp, two denticles each side	Squared. Base broad. Cusp with or without one to six pronounced denticles each side	Elongated. Base with or without bifurcation. Cusp with or without several denticles	Elongated.Base squared. Cusp, several small denticles	Elongated. Base bifurcated.Cusp, few to several very small to pronounced denticles	Elongated. Base bifurcated. Cusp, three or four long denticles each side	Elongated. Base bifurcated.Cusp smooth, slim	Elongated. Base bifurcated. Cusp, several small denticles	Elongated. Base bifurcated.Cusp, few to several small denticles, right side	Elongated. Base bifurcated. Cusp, several denticles	Elongated. Base bifurcated. Cusp, several denticles
Lateral	Elongated.Cusp triangular, external.Denticles: two or three small to pronounced, internal; one or two small to large, external	Elongated. Cusp external.Denticles: one internal; two external.	Squared or elongated. Cusp triangular, internal or external. Denticles: one to six, both sides	Elongated.Cusp external, with or without bold, with or without internal truncated projection.Denticles: with or without both or internal side	Elongated. Cusp triangular external. Denticles: several small, both sides	Elongated. Cusp triangular external. Denticles: few to several, very small to pronounced, both sides or internal side	Elongated. Cusp triangular external. Denticles: four to seven, long, both sides	Elongated. Cusp bold, smooth, external. Truncated projection internal, smooth	Elongated. Cusp bold, external, triangular. Denticles: small, external. Truncated projection, internal, small denticles, distal side	Elongated. Cusp bold, external, smooth. Truncated projection internal, several small denticles, distal side	Elongated. Cusp triangular, external. Denticles: several, both sides	Elongated. Cusp triangular, external. Denticles: several, both sides
Marginal	Narrow, smooth	Narrow, one small denticle, internal side	Narrow, with or without one small denticle, internal side	–	–	–	–	–	–	–	–	–
Jaws												
Shape	Elongated	Elongated. Denticles	Short to elongated. Denticles	Short to elongated	Short.Small, vertical, central protrusion	Short to elongated	Short.External, upper side protrusion	Short	Elongated	Short to elongated	Short to elongated	Short

Table 2. Continued

Character	Marseniopsinae	Hainotinae	Velutininae	Lamellarinae	*Calyptoconcha*	*Variolipallium*	*Pacifica*	*Djiboutia*	*Coriocella*	*Lamellaria*	*Marsenia*	*Marseniella*
Composition	Scale-like elements	?	Scale-like elements	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform	Uniform
Geographical distribution	Southern Ocean, southern Argentinian waters	North-eastern Pacific, South Australia, New Zealand	Arctic, worldwide temperate regions	Worldwide temperate, tropical regions	Northern temperate Atlantic, Alboran Sea, South Africa, Brazil, Uruguay	Tropical West Pacific, New Zealand, Caribbean, tip of South America, South Africa	Indo-West Pacific	Indo-West Pacific	Indo-West Pacific	Tropical and Temperate eastern Pacific, Tropical Atlantic, north-eastern Atlantic, Mediterranean Sea, North Sea	Indo-West Pacific, Mediterranean Sea, Caribbean Sea	Norway
Depth (m)	75–668	0–45	0–1200	0–4500	58–4500	42–1573	20–244	0–101	0–18	0–61	0–214	?

enclosed by the mantle, thin to very thin, from strongly calcified to membranaceus; ear, shield or cap shaped, low to high spired, with expanded aperture; smooth or weakly sculptured by axial growth lines. Periostracum from thick and hairy to not visible.

Protoconch of 0.76–2.10 whorls; protoconch I of 0.25–1.20 whorls, smooth or with microgranules, with or without subsutural axial folds, nucleus diameter 54–875 µm; protoconch II with or without marked axial ribs or growth lines; protoconch–teleoconch boundary not always distinct.

Echinospira planktotrophic larva with double larval shell: the outer periostracal planispiral, smooth and rounded or strongly carinate, the inner helicoid.

Mantle flat (Fig. 4C) or dome shaped (Fig. 4A), outline from above rounded (Fig. 4J) or polygonal (Fig. 4B, H); thick or thin, with or without dorsal warts or tubercles; with or without anterior (inhalant) and right lateral (exhalant) siphon folds; texture smooth, wrinkled, jelly-like or velvet-like; colour highly variable, almost transparent to white, grey, beige, yellow, orange, red, violet, blue, dark green, brown, black, often patterned.

Penis to the right of the right cephalic tentacle; with or without a lateral subterminal papilla; with or without tip of the seminal duct protruding from the penis tip. Vas deferens with or without a free loop in haemocoel.

Radula taenioglossate (with formula 2:1:1:1:2) or reduced taenioglossate (if lacking marginal teeth, formula 0:1:1:1:0); rachidian tooth base rectangular (broad or elongated) or bifurcated (inverted V-shape), rachidian cusp with or without several external denticles; lateral teeth broad or elongated, with a pointed, triangular, internal or external cusp or one external cusp plus one truncated projection, with or without denticles; marginals, when present, narrow, with or without denticles.

Jaws of variable shape, short to elongated; homogeneous or composed of scale-like elements; with or without uniform masticatory denticles.

Distribution: Worldwide, from shallow to abyssal waters (0–4500 m).

Remarks: Velutinids differ from the other two velutinoidean families (Triviidae and Eratoidae) chiefly in their thin to very thin, helicoid shell, with expanded aperture (vs. solid, cowry-like, with narrow aperture in triviids and eratoids) and the planispiral outer layer of the echinospira larval shell (vs. helicoid in triviids and eratoids). Also, the siphon is proportionally shorter in velutinids than in triviids and eratoids.

Many velutinid species are reported to live and feed on ascidians (Wilson, 1998), and the colour and texture of the dorsal mantle can mimic the ascidian host. Both hermaphroditic and gonochoristic species are reported

(Wilson, 1998). Egg capsules are flask shaped (Diehl, 1956; Fretter & Graham, 1962) and are laid in holes in the tunic of the ascidians (Peck *et al.*, 2006; Fassio *et al.*, 2019).

MARSENIOPSINAE FASSIO, BOUCHET, SCHIAPARELLI & OLIVERIO SUBFAM. NOV.

(FIGS 2, 3, 4A, B, 6A, 9A, 10A, 11A, M)

Zoobank registration: urn:lsid:zoobank.org:act:0FF5505F-49D2-4814-8E81-CA559340917E

Type genus: Marseniopsis Bergh, 1866.

Included genera: Marseniopsis Bergh, 1866, *Lamellariopsis* Vayssière, 1906 (probably a synonym of *Marseniopsis* Bergh, 1866).

Description: Body of small to medium size for the family, 0.5–11.5 cm total length. Shell very thin, weakly calcified to membranaceus; ear shaped, high spired, with expanded aperture; smooth or weakly sculptured by axial growth lines; enclosed by the mantle. Periostracum thin to not visible.

Protoconch of 0.76–1.9.0 whorls; protoconch I of 0.25–0.73 whorls, with or without granular sculpture, nucleus diameter 150–875 µm; protoconch II with or without marked longitudinal ribs; protoconch–teleoconch boundary not always distinct.

Mantle flat or dome shaped, outline rounded or polygonal; often thick, but sometimes thin, with or without warts; with anterior siphonal fold; texture smooth to wrinkled or jelly-like; colour highly variable, almost transparent to white, grey, beige, yellow, orange, red or brown, frequently patterned with dots and/or polygonal lines.

Penis to the right of the right cephalic tentacle; with or without a lateral subterminal papilla. Vas deferens with a free loop in haemocoel.

Radula taenioglossate, formula 2:1:1:1:2; rachidian tooth elongated, with rectangular base, elongated; rachidian cusp with three or four small to pronounced external denticles on each side; lateral teeth elongated, with pointed triangular external cusp, with two or three small to pronounced denticles on the internal side and one or two small to large denticles on the external side; marginals narrow, without denticles.

Jaws elongated, composed of scale-like elements.

Distribution: Southern Ocean and south Argentinian waters; 75–668 m deep.

Remarks: Fassio *et al.* (2019) suggested that the radiation of velutinids in Antarctica might represent a lineage worthy of taxonomic recognition at subfamily level. This is here confirmed, and the geographical range is now extended outside the Southern Ocean to Argentina, with the record of M5 (= new MOTU P) from north of Isla de los Estados (USNM 1137366, 54°27′19.1″S, 63°52′39.4″W, 108 m depth). Marseniopsinae can be diagnosed by the radular formula combined with the elongated shape of the rachidian tooth with a rectangular base, and by an ear-shaped shell, not well calcified, with a high spire.

Lamellariopsis is probably a synonym of *Marseniopsis*, but the genetic analysis of type or topotypical material is needed to check it. Two types of protoconchs, potentially indicating a difference in the length of the larval phase, have been described for this subfamily (see Fassio *et al.*, 2019).

HAINOTINAE FASSIO, BOUCHET, SCHIAPARELLI & OLIVERIO SUBFAM. NOV.

(FIGS 2, 3, 4G, 6B)

Zoobank registration: urn:lsid:zoobank.org:act:A356DC93-B469-4DC0-B075-ED51CAEBDAA4

Type genus: Hainotis F. Riedel, 2000.

Included genera: Hainotis F. Riedel, 2000, *Mysticoncha* J. K. Allan, 1936.

Description: Body of small to medium size, 0.5–5.0 cm total length. Shell thin to very thin, weakly calcified, ear shaped, high spire, with expanded aperture, smooth, with or without growth lines, completely enclosed by the mantle. Periostracum thin to moderately developed and hairy.

Protoconch of 1.7–2.1 whorls; protoconch I of 0.6 whorls, smooth or with weak growth striations, nucleus diameter 86 µm; protoconch–teleoconch boundary not always distinct.

Mantle dome shaped, outline rounded or polygonal (low ridges dividing the mantle into six areas, from a raised hexagonal area at the centre of the dorsum); thin to thick; with anterior elongated siphonal fold; colour highly variable, almost transparent to white, grey, beige, yellow, orange, red, violet, brown or black, frequently patterned with dots and/or polygonal shape lines.

Penis and vas deferens unknown.

Radula taenioglossate, formula 2:1:1:1:2; rachidian tooth elongated, with rectangular base; rachidian cusp with two external denticles on each side; lateral teeth elongated, with a pointed external cusp, with one denticle on the internal side and two on the external side; marginals narrow, with one small denticle on the internal side.

Jaws elongated, with masticatory denticles.

Distribution: North-eastern Pacific (from Oregon to northern Mexico), South Australia, New Zealand; 0–45 m deep.

Remarks: This subfamily is represented in the phylogenetic tree only by specimens of *Hainotis sharonae* described from the coast of California (type locality: Anaheim Bay, Orange County, CA, USA; Willett, 1939). This lineage is diagnosed by its shell with a higher spire, a radular formula of 2:1:1:1:2 with elongated central and lateral teeth, and an elongated anterior siphonal fold.

Pending further molecular analysis, we suggest also including the genus *Mysticoncha* in this subfamily because its radular formula and shape, shell shape, siphon shape and temperate distribution (South Australia, Victoria and New Zealand) are consistent with those of the type genus, *Hainotis*.

VELUTININAE GRAY, 1840

(FIGS 2, 3, 4C–F, 6C, D, 9B, 10B, C, 11B, C, N, O)

Velutininae Gray, 1840: 90; type genus *Velutina* J. Fleming, 1820.
Marseninidae Odhner, 1913: 9 [as Marsenininae]; type genus *Marsenina* Gray, 1850.
Sacculidae Thiele, 1929: 266; type genus *Sacculus* Hirase, 1927 [permanently invalid, being the type genus a junior homonym of *Sacculus* Grosse, 1851 (Rotifera)].
Pseudosacculidae Kuroda, 1933: 186 [replacement name for Sacculidae Thiele]; type genus *Pseudosacculus* Hirase, 1928.
Capulacmaeidae Golikov & Gulbin, 1990: 108 [as Capulacmaeinae]; type genus *Capulacmaea* M. Sars, 1859.

Included genera: *Cartilagovelutina* Golikov & Gulbin, 1990, *Ciliatovelutina* Golikov & Gulbin, 1990, *Cilifera* Golikov & Gulbin, 1990, *Limneria* H. Adams & A. Adams, 1851, *Marsenina* Gray, 1850, *Onchidiopsis* Bergh, 1853, *Piliscus* Lovén, 1859, *Pseudosacculus* Hirase, 1928, *Pseudotorellia* Warén, 1989, *Torellivelutina* J. H. McLean, 2000, *Velutina* J. Fleming, 1820.

Description: Body of small to medium size for the family, 0.5–11.0 cm total length. Shell moderately thin to thick, weakly to strongly calcified; ear, shield or cap shaped, low to high spire, with expanded aperture; smooth or weakly sculptured by axial growth lines; exposed or completely enclosed by the mantle. Periostracum moderately or well developed, occasionally hairy.

Protoconch of 1.1–2.0 whorls; protoconch I of 0.50–0.64 whorls, nucleus diameter 125–186 µm, smooth or with microgranules; protoconch–teleoconch boundary not always visible.

Mantle flat or dome shaped, outline rounded; thick or thin, with or without dorsal tubercles; with or without anterior and right lateral siphonal folds; texture smooth, wrinkled or jelly-like; colour highly variable, almost transparent to white, grey, beige, yellow, orange, brown, often patterned.

Penis to the right of the right cephalic tentacle, with tip of the seminal duct protruding from the penis tip. Vas deferens without a free loop in haemocoel.

Radula taenioglossate, formula 2:1:1:1:2, rachidian tooth squared, with broad base, rachidian cusp with or without one to six pronounced external denticles; lateral teeth squared or elongated, with a pointed triangular internal or external cusp, with or without one to six denticles on both sides; marginals narrow, with or without one small denticle on the internal side.

Jaws short to elongated, composed of scale-like elements, with denticles on the masticatory margin.

Distribution: Arctic and temperate regions worldwide, 0–1200 m deep.

Remarks: Velutinines can be diagnosed by their squared rachidian tooth with a broad base, and the jaws composed of scale-like elements, with denticles. Their shells can range from strongly calcified and completely exposed (e.g. *Velutina*) to almost without calcification and completely enveloped by the mantle (e.g. *Onchidiopsis*). Some genera (e.g. *Velutina* and *Limneria*) also have a hairy periostracum. In addition to the anterior inhalant siphon, an exhalant siphon is made by a right lateral mantle fold in some genera (e.g. *Marsenina* and *Onchidiopsis*). Before the present study, six genera (two of them with subgenera; see Gulbin & Golikov, 1997) were classified in this subfamily. However, the present molecular phylogeny suggests that *Limneria* and *Velutina* might be synonyms. In addition, pending molecular analysis of the type material, we propose to place *Pseudosacculus* in this subfamily, based on the description of the only included species, *Pseudosacculus okai* (Hirase, 1927). The radular formula (2:1:1:1:2) and morphology (Hirase, 1927: 125, fig. 8) and the presence of a small dorsal aperture in the mantle are congruent with this placement. It should be noted that Pelseneer (1935) suggested that *Pseudosacculus okai* might be classifiable in *Marsenina*, which would make *Pseudosacculus* a junior synonym.

LAMELLARIINAE D'ORBIGNY, 1841

(FIGS 2, 3, 4H–J, 5A–I, 7A–D, 8A–D, 9C–L, 10D–L, 11D–L)

Lamellariinae d'Orbigny, 1841: 200; type genus *Lamellaria* Montagu, 1816.
Coriocellidae Troschel, 1848: 545; type genus *Coriocella* Blainville, 1824.
Lamellariidae d'Orbigny, 1841: 200; type genus *Lamellaria* Montagu, 1816.
Marseniidae Leach in Gray, 1842: 268 [as Marseniadae]; type genus *Marsenia* Oken, 1823.

Included genera: *Calyptoconcha* Bouchet & Warén, 1993, *Coriocella* Blainville, 1824, *Djiboutia* Vayssière, 1912, *Lamellaria* Montagu, 1816, *Marseniella* Bergh, 1886, *Marsenia* Oken, 1823, *Pacifica* Fassio, Bouchet & Oliverio gen. nov., *Variolipallium* Fassio, Bouchet & Oliverio gen. nov.

Description: Body of small to medium size for the family, 0.5–10.0 cm total length. Shell thin to very thin, from strongly calcified to membranaceus; ear shaped, low to high spire, with expanded aperture; smooth or weakly sculptured by axial growth lines; completely enclosed by the mantle or with a small dorsal fissure. Periostracum thin to not visible.

Protoconch of one to two whorls; protoconch I of 0.46–1.20 whorls, smooth, with subsutural axial folds, nucleus diameter 54–250 µm; protoconch II with or without axial growth lines; protoconch–teleoconch boundary not always distinct.

Mantle flat or dome shaped, outline rounded or polygonal; thick or thin, with or without dorsal warts or tubercles; with anterior siphon fold; texture smooth, wrinkled, jelly- or velvet-like; colour highly variable, almost transparent to white, grey, beige, yellow, orange, red, violet, blue, dark green, brown or black, often patterned with dots, lines or irregular colour patches.

Penis to the right of the right cephalic tentacle, with or without a lateral subterminal papilla. Vas deferens with or without a free loop or, less frequently, several folds in the haemocoel.

Radula reduced taenioglossate, formula 0:1:1:1:0; rachidian tooth base bifurcated or rectangular; rachidian cusp with or without several external denticles; lateral teeth elongated, with a single external pointed cusp, or composed of an external, pointed and bold cusp plus a internal truncated projection; in both cases with or without several denticles.

Jaws homogeneous, short to elongated.

Distribution: Temperate and tropical regions worldwide; 0–4500 m deep.

Remarks: Lamellariines are diagnosed by their reduced taenioglossate radula lacking marginals (formula 0:1:1:1:0), a mantle completely enclosing the shell in most species (the only exception so far being *Variolipallium regium*) and an anterior siphon.

The name *Echinospira* was introduced by Krohn, 1853 for *Echinospira diaphana* Krohn, 1853, based on a (velutinid?) larva collected in the plankton of the Messina Strait (Italy). Based on the original description, we have no clues confidently to identify this animal, which might be one of the cryptic species in either of the two genera (*Lamellaria* and *Marsenia*) present in the Central Mediterranean.

Within the examined material, we have recognized the following six lineages that merit recognition at genus level.

CALYPTOCONCHA BOUCHET & WARÉN, 1993

(FIGS 2, 3, 7A, 9C, 10D, 11D)

Calyptoconcha Bouchet & Warén, 1993: 742. Type species *Lamellaria pellucida* A. E. Verrill, 1880, by original designation.

Included species: *Calyptoconcha branca* (Simone, 2004) **comb. nov.**, *Calyptoconcha capensis* (Bergh, 1907) **comb. nov.**, *Calyptoconcha pellucida* (A. E. Verrill, 1880).

Description: Body of small to medium size for the subfamily, 1–4 cm total length. Shell very thin, weakly calcified to membranaceus; ear shaped, high spired with expanded aperture; smooth or weakly sculptured by axial growth lines; completely enclosed by the mantle. Periostracum not visible.

Protoconch of 1.77–1.80 whorls; protoconch I of 0.58–1.00 whorls, smooth, nucleus diameter 54–75 µm; protoconch II with axial growth lines; protoconch–teleoconch boundary not always distinct.

Mantle flat or dome shaped, outline rounded; thick to very thick, with anterior and right lateral siphon folds; texture smooth or wrinkled; colour variability unknown.

Penis to the right of the right cephalic tentacle, with a subterminal lateral papilla. Vas deferens with a free loop in haemocoel.

Radula reduced taenioglossate, formula 0:1:1:1:0; rachidian tooth base squared; rachidian cusp with several small external denticles; lateral teeth elongated, triangular with a single external pointed cusp, with several small denticles on both sides.

Jaws homogeneous, short, with a small vertical protrusion in the centre.

Distribution: Northern temperate Atlantic, Alboran Sea, South Africa, Brazil, Uruguay; 58–4500 m deep.

Remarks: The genus *Calyptoconcha* can be distinguished by the combination of a reduced

taenioglossate radula (formula 0:1:1:1:0), a rachidian tooth with a squared base, and a non-calcified internal vestigial shell (often broken in dredged specimens and difficult to remove from the body) with a comparatively higher spire. The protoconch is also different from the rest of the subfamily in having a small diameter of the nucleus, a small diameter of the first whorl and lacking subsutural axial folds on protoconch I. The jaws show a diagnostic small vertical protrusion in the centre.

Based on the radular formula, the shape of the rachidian tooth and composition of the shell, we include in this genus the South African *Marsenia capensis* (Cape Point, 239–1463 m). We also suggest including *Lamellaria branca* (type locality: Brazil, off Sao Paulo state, in 78 m) based on its radula and shell shape, although the shell seems to be calcified compared with the other two congeners, which might be related to its shallower water habitat.

VARIOLIPALLIUM FASSIO, BOUCHET & OLIVERIO GEN. NOV.

(FIGS 2, 3, 4H–J, 7B, 9D, 10E, F, 11E, F)

Zoobank registration: urn:lsid:zoobank.org:act:170D2A4B-E62D-4612-9737-FFC39B639EFA

Type species: Variolipallium regium Fassio, Bouchet & Oliverio sp. nov.

Included species: Variolipallium cerebroides (Hutton, 1882) **comb. nov.**, *Variolipallium elatum* (Strebel, 1906) **comb. nov.**, *Variolipallium leptoconcha* (Bergh, 1907) **comb. nov.**, *Variolipallium nodosum* (Ev. Marcus, 1987) **comb. nov.**, *Variolipallium patagonicum* (E. A. Smith, 1881) **comb. nov.** and *Variolipallium regium* Fassio, Bouchet, Oliverio sp. nov.

Description: Body of small to medium size for the subfamily, 0.5–3.0 cm total length. Shell very thin, weakly calcified to membranaceus; ear shaped, high spired, with expanded aperture; smooth or weakly sculptured by axial growth lines; completely enclosed by the mantle or presenting a small dorsal fissure. Periostracum not visible.

Protoconch of 1.24–1.70 whorls; protoconch I of 0.48–1.20 whorls, nucleus diameter 100–150 µm, smooth, with subsutural axial folds; protoconch II with axial growth lines; protoconch–teleoconch boundary not always distinct.

Mantle flat or dome shaped, outline rounded or polygonal; thick to thin, often with a few to several dorsal tubercles; with anterior siphon fold; texture smooth to wrinkled (resembling the convolutions of a brain); colour variable, almost transparent to white, grey, yellow, orange to red, pink to violet, light blue, brown, dark green, occasionally patterned with spots. Cephalic tentacle tips can be white, lime yellow or almost transparent.

Penis to the right of the right cephalic tentacle, with or without a lateral subterminal papilla. Vas deferens without a free loop in haemocoel.

Radula reduced taenioglossate, formula 0:1:1:1:0; rachidian tooth base bifurcated; rachidian cusp with few to several, very small to pronounced external denticles; lateral teeth elongated, with a pointed triangular external cusp, with few to several, very small to pronounced denticles on both sides or only on the internal side.

Jaws homogeneous, short to elongated.

Distribution: Tropical West Pacific (South China Sea, Papua New Guinea, New Caledonia), New Zealand; Caribbean; tip of South America (Chile, Argentina, Falkland Islands), South Africa; 42–1573 m deep.

Etymology: From *Variola*, the Latin name for smallpox, and *pallium*, meaning 'mantle', referring to the coloured small tubercles on the mantle of the type species and other members of the group. Gender neuter.

Remarks: Variolipallium can be diagnosed by a membranaceous to weakly calcified shell with high spire (similar to that of *Calyptoconcha* and *Marseniopsis*) and a bifurcated rachidian tooth (like *Lamellaria*, *Marsenia*, etc.), although in *Variolipallium* the 'V'-shaped base of the rachidian tooth can be comparatively less marked.

All the species included in this genus have been found at depths > 95 m.

The dorsal appearance of the mantle varies from wrinkled, with several tubercles (resembling the convolutions of a brain), to rather smooth and studded with fewer small tubercles of different colour, to completely smooth. Several species (*Variolipallium cerebroides*, *Variolipallium* cf. *patagonicum*, *Variolipallium* cf. *elatum*, *Variolipallium* sp. L10, *Variolipallium* sp. L11, *Variolipallium* sp. L12, *Variolipallium* sp. L14 and *Variolipallium regium*) include specimens with a small to very small dorsal mantle fissure, occasionally marked by a small black spot (visible also in preserved specimens).

Lamellaria patagonica E. A. Smith, 1881 (type locality: Trinidad Channel, Chile, in 54 m) and *Lamellaria elata* Strebel, 1906 (type locality: Puerto Condor, Chile) belong to this genus based on their fragile and high-spired shells, smooth mantle and radular formula and shape. *Variolipallium patagonicum* and *Variolipallium elatum* can be distinguished by a more rapidly expanding first whorl in the former and, consequently, a higher shell in the latter, also resulting

in a flatter body in *Variolipallium patagonicum* and a more globose one in *Variolipallium elatum*.

Lamellaria ampla Strebel, 1906 (Ushuaia, Argentina) might also belong here (based on shell shape and shell consistency), but further analysis of the type material is necessary, because the radula, in particular, is not described in the original description. However, the general description, in particular the jelly-like mantle, wrinkled, grey with darker spots, would also be compatible with a position in Marseniopsinae.

Lamellaria leptoconcha (South Africa, Cape Point, in 1097–1280 m) is included in *Variolipallium* based on the membranaceus texture of the shell and the shape of the rachidian tooth. Bergh (1907: pl. IX, fig. 18) sketched a rachidian tooth with a not marked but visible 'V'-shaped base (similar to our SEM photographs; Fig. 10E, F), and in the description underlined that the difference between this species and *Marsenia leptolemma* (= *Calyptoconcha pellucida*) was the shape of the rachidian tooth (that in *Calyptoconcha* indeed has a squared base).

Lamellaria cerebroides (Auckland, New Zealand) is included in *Variolipallium* based on the radular formula and shape, and the wrinkled dorsum appearance. *Lamellaria verrucosa* (= *Lamellaria nodosa*) (Auckland Islands) is also included in this genus based on the membranaceus texture of the shell, the rugose appearance of the dorsum, and the radular formula and shape. Odhner (1924) described it as being similar to *Marseniopsis mollis*, but the radular formula of *Lamellaria verrucosa* clearly indicates that it belongs to the subfamily Lamellariinae.

The original description of *Lamellaria ophione* Gray, 1850 is general (fitting most lamellariine genera) and does not report any information regarding diagnostic characters. However, considering the type locality (Auckland, New Zealand), there is a chance that this species also belongs to this genus, because this is the only lamellarine genus recorded in this area so far.

VARIOLIPALLIUM REGIUM FASSIO, BOUCHET & OLIVERIO **SP. NOV.**

(FIGS 2, 3, 4H, 10E, 11E)

Zoobank registration: urn:lsid:zoobank.org:act:F6A02278-42DC-42FB-843B-5C0B1E78C254

Type material: Holotype: *MNHN-IM-2013-69285*, male.

Type locality: New Caledonia, south-west Ile des Pins, KANACONO st. DW4713, 22°47′S, 167°24′E, 356–380 m.

Description: Body of medium size for the genus, 3 cm total length. Shell very thin, weakly calcified; ear shaped, high spire, with expanded aperture; smooth or weakly sculptured by axial growth lines; not completely enclosed by the mantle, with a little fissure hole present at the top of the dorsal mantle. Periostracum not visible.

Protoconch number of whorls unknown; nucleus diameter 150 µm; protoconch I with 1.1 whorls, smooth, with subsutural axial folds; protoconch II with axial growth lines; protoconch–teleoconch boundary not distinct.

Mantle dome shaped, outline polygonal (with a slight octagonal shape); thin; with anterior siphon folds; texture smooth; dorsal mantle colour light pink, light blue around the boundaries; eight ridges starting from a rhombus-shaped figure at the top (made of white small spots) and reaching the mantle edge, occasionally highlighted by several white or dark orange spots; a little bump approximately halfway on each ridge line, coloured in dark orange; ridges and bumps more visible after alcohol preservation; a little hole in the mantle at the centre of the dorsal rhombus-shaped figure; cephalic tentacles light blue/transparent, studded with little white spots increasing in number toward the tips.

Penis to the right of the right cephalic tentacle; with a lateral subterminal papilla. Vas deferens without a free loop in haemocoel.

Radula reduced taenioglossate, formula 0:1:1:1:0; rachidian tooth base bifurcated; rachidian cusp with few external very small denticles; lateral teeth elongated, with a pointed triangular external cusp, with few denticles on the internal side.

Jaws elongated.

Distribution: So far known only from the type locality (New Caledonia); 356–380 m deep.

Etymology: From the Latin adjective *regius -a -um*, meaning 'regal', referring to the dorsal coloration pattern of the holotype.

Remarks: Deep-water species, with a uniquely coloured dorsal mantle (pale in the background, with colourful white and red/orange spots) and a characteristic octagonal mantle outline. However, owing to the high variability in shell shape and mantle coloration in this family, the most reliable way to identify this species remains by molecular analysis.

PACIFICA FASSIO, BOUCHET & OLIVERIO **GEN. NOV.**

(FIGS 2, 3, 5A, B, 7C, D, 9E, F, 10G, H, 11G, H)

Zoobank registration: urn:lsid:zoobank.org:act:BC75A004-F0A8-40C5-9636-2B3CFDC96EEF

Type species: *Pacifica lentiginosa* Fassio, Bouchet & Oliverio sp. nov.

Included species: *Pacifica indecora* (Bergh, 1886) **comb. nov.**, *Pacifica lentiginosa* Fassio, Bouchet & Oliverio sp. nov.

Description: Body of small size for the subfamily, 0.5–1.0 cm total length. Shell very thin, weakly calcified; ear shaped, low spire, with expanded aperture; smooth or weakly sculptured by axial growth lines; completely enclosed by the mantle. Periostracum not visible.

Protoconch of 1.6–1.8 whorls; nucleus diameter 110–135 µm; protoconch I 1.1–1.2 whorls, smooth, with subsutural axial folds; protoconch II with axial growth lines; protoconch–teleoconch boundary not always distinct.

Mantle flat or dome shaped, outline rounded; thin; with anterior siphon folds; texture smooth; colour almost transparent to white, grey, yellow, orange, pink, violet, brown, patterned with many small and big spots or colour patches.

Penis to the right of the right cephalic tentacle; with a lateral subterminal papilla. Vas deferens with or without a free loop in haemocoel.

Radula reduced taenioglossate, formula 0:1:1:1:0; rachidian tooth base bifurcated; rachidian cusp with three or four external long denticles on each side; lateral teeth elongated, with a pointed triangular external cusp, with four to seven long denticles on each side side.

Jaws short, with an external protrusion on the upper side.

Distribution: Indo-West Pacific (Madagascar, Philippines, Papua New Guinea, New Caledonia, Vanuatu); 20–244 m deep.

Etymology: From the Latin adjective *pacifica*, meaning 'peaceful', as a symbolic quest for peace from the scientific community. Gender feminine.

Remarks: This lineage includes a few Indo-West Pacific species with a peculiar radula (both rachidian and lateral teeth with long denticles) and a unique jaw shape, small and with an external protrusion on the upper side. The two specimens photographed alive showed a dorsal mantle with several coloured spots.

Marsenia indecora Bergh, 1886 (Philippines Sea) belongs to this genus because of its peculiar jaw shape and radular shape. Bergh (1886b) himself regarded this species as remarkably different from all other species he described from the Philippines (that are now included in the genus *Marsenia*).

PACIFICA LENTIGINOSA FASSIO, BOUCHET & OLIVERIO **SP. NOV.**

(FIGS 2, 3, 5A, 7C, 9E, 10G, 11G)

Zoobank registration: urn:lsid:zoobank.org:act:210F01F5-C95D-4F27-A63D-9715015E67EE

Type material: Holotype: *MNHN-IM-2009-16140* (Sud Madagascar, Lavanono West sector, ATIMO VATAE/BP21, 25°23.1–23.2′S, 44°51.4–51.6′E, 20 m deep, female).

Material examined: *MNHN-IM-2009-16140* (Sud Madagascar, Lavanono West sector, ATIMO VATAE/BP21, 25°23.1–23.2′S, 44°51.4–51.6′E, 20 m deep, female).

Description: Body of medium size for the genus, 1 cm total length. Shell very thin, weakly calcified; ear shaped, low spire, with expanded aperture; weakly sculptured by axial growth lines; completely enclosed by the mantle. Periostracum not visible.

Protoconch of 1.6 whorls; nucleus diameter 110 µm; protoconch I 1.2 whorls, smooth, with subsutural axial folds; protoconch II with axial growth lines; protoconch–teleoconch boundary distinct.

Mantle dome shaped, outline rounded; thin; with anterior siphon folds; texture slightly wrinkled; dorsal mantle colour light violet, patterned with several small white and beige spots, fewer bigger orange spots and some brown patches.

Penis unknown; vas deferens unknown.

Radula reduced taenioglossate, formula 0:1:1:1:0; rachidian tooth base bifurcated; rachidian cusp with three external long denticles on each side; lateral teeth elongated, with a pointed triangular external cusp, with four or five long denticles on each side.

Jaws short; with an external protrusion on the upper side.

Distribution: So far known only from the type locality (southern Madagascar), 20 m deep.

Etymology: From the Latin adjective *lentiginosa*, meaning 'freckled', referring to the dorsal coloration of the holotype.

Remarks: This species is known only from shallow waters of southern Madagascar. Owing to the high variability in shell shape and mantle coloration in this family, the most reliable way to identify this species remains by molecular analysis.

DJIBOUTIA VAYSSIÈRE, 1912

(FIGS 2, 3, 5C, 8A, 9E, 10I, 11I)

Djiboutia Vayssière, 1912: 121; type species *Djiboutia verrucosa* Vayssière, 1912 by monotypy.

Included species: *Djiboutia australis* (Basedow, 1905) **comb. nov.**, *Djiboutia sibogae* (Bergh, 1908) **comb. nov.**, *Djiboutia verrucosa* Vayssière, 1912.

Description: Body of small to medium size for the subfamily, 0.5–3.3 cm total length. Shell thin to very thin, weakly calcified; ear shaped, low spire, with expanded aperture; smooth or weakly sculptured by axial growth lines; completely enclosed by the mantle. Periostracum not visible.

Protoconch of 1.30–1.75 whorls; nucleus diameter 120–145 µm; protoconch I 0.75–1.00 whorls, smooth, with subsutural axial folds; protoconch II with axial growth lines; protoconch–teleoconch boundary not always distinct.

Mantle flat or dome shaped, outline rounded; thin; with anterior siphon folds; texture smooth; colour highly variable, almost transparent to white, grey, beige, yellow, orange, red, violet, brown, black, often patterned with dots or patches of colour.

Penis to the right of the right cephalic tentacle; with or without a lateral subterminal papilla. Vas deferens without a free loop in haemocoel.

Radula reduced taenioglossate, formula 0:1:1:1:0; rachidian tooth base bifurcated; rachidian cusp smooth and slim; lateral teeth elongated, composed of a smooth, external, pointed and bold cusp, plus a smooth internal truncated projection.

Jaws short.

Distribution: Indo-West Pacific (Madagascar, Gulf of Tadjoura, Papua New Guinea, Sulawesi, southern Australia and Tasmania, New Caledonia); 0–101 m deep.

Remarks: The key character to recognize this genus is the rachidian tooth (bifurcated, smooth and slim, without denticles) that represents a unique combination in this family. Based on this character and on an overall similar morphology, we suggest that *Lamellaria australis* and *Marsenia sibogae* belong to this genus.

Coriocella Blainville, 1824

(Figs 2, 3, 5D, E, 8B, 9H, 10J, 11J)

Coriocella Blainville, 1824: 259; type species *Coriocella nigra* Blainville, 1824 by monotypy.
Chelinotus Swainson, 1840: 355; type species: *Sigaretus tonganus* Quoy & Gaimard, 1832 by monotypy.
Chelyonotus Herrmannsen, 1846: 221; unnecessary replacement name for *Chelinotus* Swainson.

Included species: *Coriocella hibyae* Wellens, 1991, *Coriocella jayi* Wellens, 1996, *Coriocella nigra* Blainville, 1824, *Coriocella safagae* Wellens, 1999, *Coriocella semperi* (Bergh, 1875), *Coriocella tongana* (Quoy & Gaimard, 1832).

Description: Body of small to medium size for the subfamily, 1.5–8.5 cm. Shell thin, strongly to moderately calcified; ear shaped, low spire, with expanded aperture; smooth or weakly sculptured by axial growth lines; completely enclosed by the mantle. Periostracum thin.

Protoconch of 1.0–1.3 whorls; protoconch I 0.46–1.10 whorls, nucleus diameter 122–150 µm, smooth, with subsutural axial folds; protoconch II with or without axial growth lines; protoconch–teleoconch boundary not always distinct.

Mantle dome shaped, outline rounded; thick, with two to six warts on the dorsum; with anterior siphon folds; smooth, wrinkled, often velvet-like in texture; colour highly variable, beige, yellow, red, violet, blue, dark green, brown, black, often patterned with irregular colour patches or spots.

Penis to the right of the right cephalic tentacle; with tip of the seminal duct protruded from the penis tip. Vas deferens without a free loop in haemocoel.

Radula reduced taenioglossate, with formula 0:1:1:1:0; rachidian tooth base bifurcated; rachidian cusp with several external small denticles; lateral teeth elongated, with one external triangular pointed and bold cusp with small denticles on the external side, plus one truncated projection with small denticles on the distal side.

Jaws elongated.

Distribution: Indo-West Pacific (Madagascar, Reunion, Mauritius, Red Sea, Maldives, Philippines, northern Australia, New Caledonia, French Polynesia, Tonga); 0–18 m deep.

Remarks: *Coriocella* is probably the lamellarine genus that can be recognized best from the external morphology only, thanks to the presence of a variable, species-specific number of warts, well evident on the dorsum of living animals (e.g. three for *Coriocella nigra*; five for *Coriocella safage* Wellens, 1999, *Coriocella hibyae*, *Coriocella semperi* and *Coriocella tongana* (Quoy & Gaimard, 1832); and six for *Coriocella jayi*), and the typical light brown or dark velvet-like coloration. However, the warts can become barely visible and the colour often vanishes once the specimen is preserved in alcohol. The shell shape is hardly distinguishable from the other low-spired lamellariine genera (*Lamellaria*, *Marsenia* and *Djiboutia*). However, most adult specimens of *Coriocella* show a higher level of shell calcification compared with the rest of the subfamily.

Lamellaria Montagu, 1816

(Figs 2, 3, 5F, G, 8C, 9I, J, 10K, L, 11K)

Lamellaria Montagu, 1816: 184; type species *Lamellaria tentaculata* Montagu, 1816 by subsequent

designation of Wenz, 1940: 955 as *Bulla latens* O. F. Muller, 1776.
Cryptocella H. Adams & A. Adams, 1853: 202; type species *Lamellaria tentaculata* Montagu, 1816 by subsequent designation of Kobelt, 1876–1881: 78.

Included species: *Lamellaria diegoensis* Dall, 1885, *Lamellaria fella* (Er. Marcus & Ev. Marcus, 1970) **comb. nov.**, *Lamellaria inflata* (C. B. Adams, 1852), *Lamellaria latens* (O. F. Müller, 1776), *Lamellaria mopsicolor* Ev. Marcus, 1958.

Description: Body of small to medium size for the subfamily, 0.3–1.1 cm total length. Shell thin, weakly calcified; ear shaped, low spire, with expanded aperture; smooth or weakly sculptured by axial growth lines; completely enclosed by the mantle. Periostracum not visible.

Protoconch of 1.1–2.0 whorls; protoconch I 0.56–1.10 whorls, nucleus diameter 125–214 µm, smooth, with subsutural axial folds; protoconch II with or without axial growth lines; protoconch–teleoconch boundary not always distinct.

Mantle flat or dome shaped, outline rounded; thick or thin, rarely with dorsum tubercles; with anterior siphon folds; texture smooth/wrinkled/jelly-like; colour highly variable, almost transparent to white, grey, beige, yellow, orange, red, violet, brown, often patterned with dots or streaks of colour.

Penis to the right of the right cephalic tentacle; with or without a lateral subterminal papilla. Vas deferens with or without a free loop or several folds in the haemocoel.

Radula reduced taenioglossate, with formula 0:1:1:1:0; rachidian tooth base bifurcated; rachidian cusp with few to several small external denticles on the right side only; lateral teeth elongated, composed of an external, pointed and bold cusp without denticles, plus an internal truncated projection, with several small denticles on the distal side.

Jaws short to elongated.

Distribution: Tropical and temperate Eastern Pacific, Tropical Atlantic, north-eastern Atlantic, Mediterranean Sea, North Sea; 0–61 m deep.

Remarks: The genus *Lamellaria* can be distinguished from the others thanks to the rachidian tooth with a bifurcated base and denticles only on the left side of the cusp and the lateral tooth composed of one cusp and one projection. Species of this genus can be divided in two main lineages: one present in the temperate north-eastern Atlantic and one in the central–western Atlantic tropics and in the tropical and temperate eastern Pacific. Our analyses indicate that the type species, *Lamellaria latens*, is part of a monophyletic complex of cryptic species (at least four).

We include in this genus *Coriocella fella*, owing to its characteristic rachidian tooth, unilaterally denticulated, the general shape of the shell and the absence of the typical mantle dorsal warts of *Coriocella*.

Marsenia Oken, 1823

(Figs 2, 3, 5H, I, 8D, 9K, L, 10M–O, 11L)

Marsenia Oken, 1823: columns 458, 460; type species *Bulla haliotoidea* Montagu, 1803 = *Helix perspicua* Linnaeus, 1758 by monotypy.

Included species: *Marsenia herberti* (Drivas & Jay, 1990) **comb. nov.**, *Marsenia perspicua* (Linnaeus, 1758), *Marsenia affinis* Bergh, 1886 [*taxon inquirendum*], *Marsenia cabulana* Bergh, 1886 [*taxon inquirendum*], *Marsenia dubia* Bergh, 1886 [*taxon inquirendum*], *Marseniagemma* Bergh, 1875 [*taxon inquirendum*], *Marsenia isabellina* Bergh, 1875 [*taxon inquirendum*], *Marsenia perspicua* var. *lara* Bergh, 1899 [*taxon inquirendum*].

Description: Body of small to medium size for the subfamily, 0.3–10.0 cm total length. Shell thin, weakly calcified; ear shaped, low to high spire, with expanded aperture; smooth or weakly sculptured by axial growth lines; completely enclosed by the mantle or presenting a small dorsal fissure. Periostracum not visible.

Protoconch of 1.2–1.6 whorls; protoconch I 0.6–0.75 whorls, nucleus diameter 100–250 µm, smooth, with subsutural axial folds; protoconch II with or without axial growth lines; protoconch–teleoconch boundary not always distinct.

Mantle flat or dome shaped, outline rounded; thick or thin, with or without tubercles on dorsum; with anterior siphon folds; texture smooth/wrinkled/jelly-like; colour highly variable, almost transparent to white, grey, beige, yellow, orange, red, violet, brown, often patterned with dots, streaks or patches of colour.

Penis to the right of the right cephalic tentacle; with or without a lateral subterminal papilla. Vas deferens with or without a free loop in haemocoel.

Radula reduced taenioglossate, with formula 0:1:1:1:0; rachidian tooth base bifurcated; rachidian cusp with several external denticles; lateral teeth elongated, with a pointed triangular external cusp, with several denticles on both sides.

Jaws short to elongated.

Distribution: Indo-West Pacific (Madagascar, Reunion, Red Sea, Taiwan, Philippines, Papua New Guinea, Tasmania, New Caledonia, Hawaii), Mediterranean Sea (Corsica and Alboran Sea), Caribbean Sea (Martinique and French Guiana); 0–214 m deep.

Remarks: The type species, *Marsenia perspicua*, is part of a complex of at least two cryptic species. This widely distributed lineage is present in the tropical areas of the Indo-Pacific and the Atlantic, and in the Mediterranean Sea. It would be difficult to recognize this genus from other lamellarines with a low spire and moderately calcified shell, if it was not for its radula, characterized by a rachidian tooth bifurcated at the base, with small denticles on both sides and elongated lateral teeth with pointed, triangular and external cusps, with small denticles on both sides.

In one species (*Marsenia* sp. L45), a specimen with a shell not completely enclosed by the mantle but presenting a small dorsal fissure (similar to that of some *Variolipallium* specimens) was observed.

We think that, based on the original descriptions, several *taxa inquirenda* described by Bergh (1886b) from Philippines and Cape Verde material (*Marsenia affinis*, *Marsenia cabulana*, *Marsenia dubia*, *Marsenia gemma*, *Marsenia isabellina* and *Marsenia perspicua* var. *lara*) might belong to this genus.

Marseniella Bergh, 1886

Marseniella Bergh, 1886a: 14; type species *Marseniella borealis* Bergh, 1886 by monotypy.

Included species: *Marseniella borealis* Bergh, 1886.

Description: Body of medium size for the subfamily, 2.2 cm total length. Shell thin, membranaceus, weakly calcified; ear shaped, low spire, last whorl wide and detached from the spire at the back, with expanded aperture; completely enclosed by the mantle. Periostracum unknown.

Protoconch unknown.

Mantle flat, outline rounded; with coarse and fine knots on the dorsum; with anterior siphon folds; texture unknown; colour unknown.

Penis to the right of the right cephalic tentacle; with a lateral subterminal papilla. Vas deferens with a free loop and several folds in the haemocoel.

Radula reduced taenioglossate, formula 0:1:1:1:0; rachidian tooth base bifurcated; rachidian cusp with several denticles on both sides; lateral tooth elongated, with a pointed triangular external cusp, with several denticles on both sides.

Jaws short.

Distribution: Known only from Florø, north of Bergen (Norway); depth unknown.

Remarks: Bergh (1886a, b, 1887) described this monotypic genus from a single specimen collected in Norwegian waters. Bergh described it as very similar to velutinids that we call here *Lamellaria* and *Marsenia*, but different enough to deserve a separate name. The radular formula and the 'V'-arched rachidian tooth confirm that it belongs to the Lamellariinae. The rachidian tooth with denticle on both sides and a lateral tooth elongated, with a pointed triangular external cusp, with several denticles on both sides might be compatible with the genus *Marsenia* (but we have not found any *Marsenia* in Norwegian waters, from where we have examined only *Lamellaria* specimens). The vas deferens producing several folds in the haemocoel has been observed in the genus *Lamellaria*, but we do not consider this character as diagnostic at the genus level. Above all, Bergh (1886a, b, 1887) described for *Marsenia borealis* a very unusual corneous shell, only partly calcified, somehow similar in texture to that of *Onchidiopsis*. The described shape is also unusual, flatter than *Lamellaria* and *Marsenia*, with a very wide last whorl detached from the spire at the back (a shell shape not observed in any other velutinid examined so far) (Bergh 1887: pl. X figs 1, 2).

For these reasons, pending further analysis, we provisionally keep *Marseniella* as a valid genus in the subfamily Lamellariinae, not present in our molecular dataset.

A DRAMATICALLY INCREASED VELUTINID DIVERSITY

Velutinid systematics has been long neglected, and few authors have produced sounding descriptions of taxa including detailed diagnoses. In addition, the velutinid shell, often internal and vestigial, lacks the diagnostic power of shells in other gastropod groups. Last, but not least, in most of the species the variation of the dorsal mantle coloration is very likely to be a result of selective pressure for host–parasite crypsis; therefore, distant species can have similar colours because they live on the same (or on morphologically similar) ascidian species. In contrast, the same velutinid species can have a variety of different colour patterns if parasitizing different hosts or a host with a great chromatic variability. All this has led to a velutinid diversity, as estimated before the present revision, of 99 accepted species (plus 19 *taxa inquirenda*), belonging to 19 genera (plus one uncertain), grouped into two subfamilies (MolluscaBase, 2021). Our molecular dataset included 50% of the described genera, yielded three newly described ones and recovered a species diversity within the assayed dataset of ≥ 86 species, 58 of which are very likely to be new to science (67%). At the subfamily level, velutinids were found to be more diversified than previously estimated, with two newly described taxa, Marseniopsinae and Hainotinae, and an overall inter-subfamily *COI* genetic distance of 18–34%. The velutinid diversification in four subfamilies could be explained by a co-evolution with different hosts (e.g. solitary, social and colonial

ascidians), although the available trophic data do not support this hypothesis. However, information on host–parasite associations is scattered, and its reliability is weakened by the challenging systematics of both the gastropods and the tunicates.

The species diversity of Velutininae and Marseniopsinae has been addressed extensively in recent studies (Gulbin, 2005; Fassio *et al.*, 2019). This is the first modern attempt to reassess the diversity of Lamellariinae within a phylogenetic framework.

To the 49 currently accepted species of Velutininae, four new candidate species identified in the present study can be added. The diversity of Lamellariinae, counting 37 currently accepted species, should be increased by ≥ 41 new candidate species, making Lamellariinae by far the most diverse velutinid subfamily. Part of this diversity was described throughout the last centuries under the genus name *Lamellaria*, currently including 25 accepted species names (plus ten *taxa inquirenda*). Our analyses recovered four distinct phylogenetic lineages (*Lamellaria*, *Marsenia Pacifica* and *Variolipallium*) and 43 candidate species, increasing the corresponding diversity by 72%. It is worth noting that both traditional species of '*Lamellaria*' reported for the well-known Mediterranean/north-eastern Atlantic fauna, *Lamellaria latens* and *Marsenia perspicua*, each conceal a species complex. The *Lamellaria latens* complex includes at least four species, and probably more considering that the only Eastern Mediterranean specimen belongs to a distinct species. A similar situation is found in the *Marsenia perspicua* complex, which includes two species, one exclusively Mediterranean and one amphi-Atlantic. Another paradigmatic example can be found in the genus *Djiboutia*, originally monotypic and reported only from the Gulf of Tadjoura (Djibouti), for which we found seven distinct candidate species from Madagascar to New Caledonia.

Our data confirmed frequent interspecific overlap in features of the external morphology and coloration patterns, and of shell and radula morphology, even among phylogenetically distant taxa. Velutininae underwent a morphological diversification that produced significantly different body and shell shapes (e.g. shell enclosed or not; one or two mantle siphons). Conversely, the two other species-rich subfamilies, Marseniopsinae and Lamellariinae, are mostly composed of taxa hardly identifiable at species level, relying exclusively on a single morphological feature, and often even with a combination of characters. For this reason, describing a new velutinid species today, without molecular data as support, can easily lead to the description of either a synonym or of a new species hardly recognizable in the future.

Our samples originated primarily from dredging for deep-water species and by hand picking in shallow water. Velutinid habitat preferences are obviously driven by the presence of their ascidian hosts. However, specimens do not live permanently attached to their host and can often be found attached to the lower surface of flat stones. In shallow waters, they are mostly found on rocky and stony ground, among algae, seagrasses, hydroids, sponges and, obviously, ascidians (Gulbin, 2005). At greater depths, they inhabit mixed cobble–sandy–muddy surfaces and, less frequently, sandy and muddy–sandy terrains and, even less frequently, cobble–sandy terrains and pure mud (Gulbin, 2005). For these reasons, ARMS seem to provide a particularly suitable habitat for velutinids. Autonomous reef monitoring structures are composed of stacks of plates and are often colonized by ascidians, artificially recreating a habitat similar to that on which velutinids are generally found, especially in shallow waters. In fact, 13 specimens included in our dataset were collected on ARMS deployed in New Caledonia, Florida (USA) and Red Sea waters. In addition, one of them, MNHN-IM-2019-9031 (New Caledonia), is the only collected specimen of a *Marsenia* species new to science.

The other key factor to take into consideration for the success of a molecular study on this group is the specimen fixation–conservation protocol. Our experience and results clearly suggest that, owing to the high amount of mantle tissue and therefore of water that can be released in the fixing reagent, velutinid vouchers are often badly preserved, making it difficult to amplify molecular markers using standard extraction protocols and Sanger sequencing. Our results suggest that fixation of a small piece of foot tissue in a separate tube (as detailed in the Material and Methods section) can dramatically increase the success of the subsequent molecular analyses.

Biogeographical and bathymetric patterns

The available geographical data, combined with our phylogenetic results, allow for a preliminary hypothesis on the origin and evolution of this widespread family, to be tested when a time-calibrated phylogeny is available.

The position on the tree of Marseniopsinae (from Antarctica and the cold tip of South America), Hainotinae (from temperate Pacific) and Velutininae (from the Arctic to temperate Atlantic and Pacific), along with the lamellarine *Calyptoconcha* lineage (sister to the rest of Lamellarinae and exclusive to deep waters of the temperate northern Atlantic) are suggestive of an origin in cold-temperate areas (Fig. 2). Only the Lamellariinae have radiated (secondarily) also in the warm tropical realm.

Velutinids have a reduced shell in terms of calcification, with many lineages that are characterized by a vestigial shell that is completely or almost

completely enclosed by the mantle. Some genera have only a partly enclosed shell (e.g. *Marsenina*; Fig. 4C, D) or a completely exposed shell (e.g. *Velutina*; Fig. 4E, F). Our phylogenetic pattern does not fit the currently held hypothesis of a completely exposed shell as the ancestral state (reflecting the typical gastropod condition) and a progressive enclosure during the evolution of the group. Indeed, the shell is completely enclosed by the mantle in the Hainotinae and in most of the Marseniopsinae and Lamellarinae (except for some specimens included in the genera *Marsenia*, *Marseniopsis* and *Variolipallium*). Furthermore, the genus *Onchidiopsis* has a reduced, leaf-like shell completely enclosed within a fused mantle, but is supported as sister to the rest of the subfamily Velutininae. These observations would suggest that an internal shell could be plesiomorphic in velutinids, whereas a partly or completely exposed shell would be a secondary acquisition attributable to some sort of mantle reduction. According to our phylogeny, this mantle reduction would have occurred at least once during velutinid evolution, in the common ancestor of the genera *Marsenina* and *Velutina*, culminating in the completely exposed shell with a rich periostracum in the genus *Velutina*. The presence of specimens with and without a mantle fissure in several marseniopsine and lamellariine species suggests that this character is rather plastic.

Shell exposure seems to be linked to the reacquisition of a harder shell, possibly with an increased protective value, as in the case of *Velutina*. Shell robustness is probably driven also by other factors; for example, differences in calcification rates can be observed also among those velutinids possessing an internal shell (Fig. 6D). In particular, the three genera with membranaceus shells, *Calyptoconcha*, *Marseniopsis* and *Variolipallium*, are found at greater depths, ≤ 4500, 668 and 1574 m, respectively (Fig. 2). In contrast, the genus with the most calcified shell is *Coriocella*, the genus with the shallowest depth distribution (0–18 m). Although further data would be necessary to address this topic properly, it seems likely that the level of calcification of the velutinid shell is driven by several factors, including depth and/or temperature. A similar trend has been observed in other shelled molluscs, both gastropods and bivalves (Irie & Morimoto, 2016; Aranda & Manzano, 2017; Mancuso *et al.*, 2019), and in other marine taxa with calcium carbonate skeletons, such as corals and foraminiferans (Baker & Weber, 1975; Stainbank *et al.*, 2019). For example, a meta-analysis on coral reef ecosystems showed that depth was a significant driver of net ecosystem calcification and that temperature was influential (Davis *et al.*, 2021).

Velutinidae also show a high genetic connectivity even between distant populations, as a result of the long-lasting planktotrophic larval development (Modica *et al.*, 2017), despite a shortening of the larval phase in some Antarctic species of Marseniopsinae (Fassio *et al.*, 2019). In addition to the case of the amphi-Atlantic species of the *Marsenia perspicua* complex already discussed, another species worthy of mention for its distribution is *Marsenia herberti* (= *Coriocella herberti*, clade L44; Fig. 3). This species ranges throughout the Indo-West Pacific, from Tanzania to Hawaii, including Madagascar, Reunion, the Red Sea, Philippines, Papua New Guinea and New Caledonia, with two specimens collected 14 000 km apart showing a *COI* genetic divergence of 0.82%.

Focusing on the subfamily Lamellariinae, for which we have a rather large molecular dataset (235 specimens), it is striking that more than half (65%; 36 of 55 species) of the assayed diversity originates in the Indo-West Pacific, from where the large majority of the nominal species not included in our dataset have been described. Of the six lamellarine genera included in the dataset, five are present in the Indo-West Pacific, three of them exclusively. Lower species diversities are observed in the Mediterranean Sea/Northern Atlantic (seven species), in the Caribbean Sea (four species), along the west coast of Panama (three species), in New Zealand (two species) and at the tip of South America (two species). Although our dataset is biased by the more intensive sampling effort conducted in the Indo-West Pacific, our data suggest that most of the diversification of the Lamellariinae occurred in this area. This pattern is consistent with those of other mollusc groups, corals and fishes from the Indo-West Pacific and, in particular, from the so-called 'Coral Triangle' (from the Philippines to the Solomon Islands) (Briggs, 1999; Bouchet *et al.*, 2002; Veron *et al.*, 2011).

Conclusion

An integrative taxonomy approach is widely recognized as a powerful tool for alpha-taxonomy, especially in those groups that present challenges owing to a lack of diagnostic morphological characters and have thus long been neglected by systematic studies. Here, we have shown that this is especially true for the family Velutinidae, in which a fragile and often internal shell, combined with a remarkable chromatic plasticity resulting from host–parasite interaction, have been hiding a great deal of taxonomic diversity.

Velutinids emerge from our work as a more diversified group than previously known, comprising four independent subfamily-level lineages, with a worldwide distribution, a broad depth range and a long-lasting planktotrophic larva ensuring a high genetic connectivity even between distant populations.

Our results emphasize that the shell morphology of this group is remarkably variable, even at intraspecific levels, hampering the usefulness of

shell characters alone for the distinction of closely related species and even of some genera. In addition, the dorsal mantle colour patterns are highly plastic, shared by different genera, but also a single species can present a great intraspecific diversity. This observation strongly suggests that the chromatic features of this group are driven by host–parasite interactions rather than being the result of species-specific characteristics.

Velutinids show a striking variability in the proportion of shell covered by the mantle, and this can vary even at the individual level, with some species including specimens either with or without a small dorsal fissure. For those velutinid genera presenting an internal shell, the rate of calcification seems to be influenced primarily by the depth at which they live. Instead, for those genera with an exposed shell, the calcification rate seems to be driven by prey–predator interactions.

Given the great phenotypic plasticity observed in this family, we stress the importance of using molecular tools for confident species-level identification, while at higher taxonomic levels a combination of morphological (e.g. radula and shell) and ecological (e.g. depth and locality) characters might be sufficient.

This study provides a comprehensive phylogenetic and taxonomic framework of the Velutinidae as a starting point for further studies on the systematics of this no longer neglected group.

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CONFLICT OF INTEREST

All the authors declare to have no conflcit of interest.

DATA AVAILABILITY

The data underlying this article are available in the GenBank Nucleotide Database (available at: https://www.ncbi.nlm.nih.gov) and can be accessed with the following accession numbers: *COI*, ON524175–ON524379; 16S, ON520952–ON521113; 28S, ON525229–ON525268; ITS2, ON529004–ON529104.

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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. Collection data for specimens and GenBank/BOLD accession numbers.
Figure S1. ASAP analysis on the *COI* dataset.
Figure S2. Bayesian phylogenetic inference on the *COI* dataset.
Figure S3. Maximum likelihood phylogenetic inference on the *COI* dataset.
Figure S4. Bayesian phylogenetic inference on the 16S dataset.
Figure S5. Maximum likelihood phylogenetic inference on the 16S dataset.
Figure S6. Bayesian phylogenetic inference on the 28S dataset.
Figure S7. Maximum likelihood phylogenetic inference on the 28S dataset.
Figure S8. Bayesian phylogenetic inference on the ITS2 dataset.
Figure S9. Maximum likelihood phylogenetic inference on the ITS2 dataset.