Zoological Journal of the Linnean Society, 2020, **XX**, 1–66. With 23 figures.

The Emperor's *Cadlina*, hidden diversity and gill cavity evolution: new insights for the taxonomy and phylogeny of dorid nudibranchs (Mollusca: Gastropoda)

TATIANA KORSHUNOVA[1,2], KARIN FLETCHER[3], BERNARD PICTON[4,5], KENNET LUNDIN[6,7], SHO KASHIO[8], NADEZHDA SANAMYAN[9], KAREN SANAMYAN[9], VINICIUS PADULA[10], MICHAEL SCHRÖDL[11] and ALEXANDER MARTYNOV[2*]

[1]*Koltzov Institute of Developmental Biology RAS, 26 Vavilova Str., 119334 Moscow, Russia*
[2]*Zoological Museum, Moscow State University, Bolshaya Nikitskaya Str. 6, 125009 Moscow, Russia*
[3]*Milltech Marine, PO Box 1074, Port Orchard 98366, Washington, USA*
[4]*National Museums Northern Ireland, Cultra, Northern Ireland, United Kingdom*
[5]*Queen's University, Belfast, Northern Ireland, United Kingdom*
[6]*Gothenburg Natural History Museum, Box 7283, S-40235, Gothenburg, Sweden*
[7]*Gothenburg Global Biodiversity Centre, Box 461, S-40530, Gothenburg, Sweden*
[8]*Natural History Museum, Kishiwada City, 6-5 Sakaimachi, Kishiwada, Osaka Prefecture 596-0072, Japan*
[9]*Kamchatka Branch of Pacific Geographical Institute FEB RAS, Partizanskaya Str. 6, 683000 Petropavlovsk-Kamchatsky, Russia*
[10]*National Museum, Federal University of Rio de Janeiro, Quinta da Boa Vista, São Cristóvão, Rio de Janeiro, RJ, 20940-040, Brazil*
[11]*SNSB-Bavarian State Collection of Zoology, Münchhausenstr. 21, D-81247 München, and Biozentrum and GeoBioCenter LMU Munich, Germany*

Received 9 April 2019; revised 27 September 2019; accepted for publication 30 September 2019

Dorids are one of the largest nudibranch groups, encompassing more than 2000 species. One of the crucial problems with tracing the evolution of dorids is the relationship between cryptobranch dorids (gill cavity present) and phanerobranch dorids (gill cavity absent). Integrative morphological and molecular studies of the enigmatic Japanese dorid species of the cryptobranch genus *Cadlina*, *C. japonica* and '*C.*' *sagamiensis*, which were collected by the Emperor of Japan (Shōwa era), are presented here for the first time. It is shown that while *C. japonica* does belong to the *Cadlina* clade, another Japanese species '*C.*' *sagamiensis* is not part of the cryptobranch dorids of the family Cadlinidae, but is related to both the phanerobranch dorid family, Hexabranchidae, and to the cryptobranch family **Cadlinellidae stat. nov**. A new genus, ***Showajidaia* gen. nov.**, and new family, **Showajidaiidae fam. nov.**, are proposed for '*C.*' *sagamiensis*, and four new species of the genus *Cadlina* are described based on a dorid-wide molecular phylogenetic analysis, which is the first substantial update of the dorid family system since 2010. Integration of phylogenetic data with an ontogenetic model of dorid evolution suggests that cryptobranch organization can be most reliably assessed as the ancestral state for the majority of dorids.

KEYWORDS: molecular systematics – morphology – Mollusca – phylogenetics – taxonomic revision.

INTRODUCTION

Dorids are one of the largest groups of nudibranchs with more than 2000 species (Thompson & Brown, 1984; Rudman, 1998; Willan, 1998; MolluscaBase, 2019a). Members of this group possess a special

---

*Corresponding author. E-mail: martynov@zmmu.msu.ru

http://zoobank.org/urn:lsid:zoobank.org:pub:ED174BE4-86F2-4A5D-B2DC-4E582AEE793A

circular arrangement of gills in the centre or posterior part of the dorsum. The quest to understand dorid taxonomy and evolutionary pathways has a long and disputed history (e.g. Bergh, 1892; Odhner, 1926, 1934; Minichev, 1970; Minichev & Starobogatov, 1979; Martynov, 1999a, b; Wägele & Willan, 2000) without a satisfactory conclusion. Clarification of dorid evolution would not only resolve the evolutionary questions within that group, but would also be an important step for understanding the evolution of nudibranch molluscs as a whole. A detailed model of dorid morphological evolution, based on integrative ontogenetic and phylogenetic evidence has been proposed (Martynov, 2011; Martynov & Schrödl, 2011; Martynov *et al*., 2011, 2016). Here, we build on the previous model by including two enigmatic dorids that were initially placed in the genus *Cadlina*, and were collected by the late Emperor Shōwa (the Emperor Hirohito) in 1935 and later described by Kikutarō Baba (1937) (see: Baba, 1949: 3–4). These Japanese 'Emperor's *Cadlina*' species, *C. japonica* Baba, 1937 and *C. sagamiensis* Baba, 1937, remained enigmatic taxa for a long time, lacking a proper morphological description and a molecular analysis. To date there are no morphological re-descriptions of either species, and molecular data (Johnson, 2010) are available only for a single specimen of *C. japonica* from the Republic of Korea, but not from Japan. It has been suggested that there are morphological differences between *Cadlina sagamiensis* and the genus *Cadlina*, so it is currently placed in the genus *Cadlinella* (Schrödl & Millen, 2001; Molluscabase, 2019b), but this proposal was not evaluated with integrative morphological and molecular data.

In the present study, we investigate the type material of *C. japonica* and '*C.*' *sagamiensis* from the Shōwa Memorial Institute in Tsukuba (where samples collected by Emperor Hirohito are currently stored; see e.g. Imajima, 2003) and we also obtained recently collected specimens of both these species from Japan for morphological and molecular analyses. These data were coupled with a broad taxon sampling of several *Cadlina* species complexes through out the entire Northern Hemisphere from the UK to the Sea of Japan and to the north-eastern American Pacific.

MATERIAL AND METHODS

Material examined

Material for this study was obtained from various expeditions and fieldwork. Specimens were collected in locations in northern Eurasia and Pacific America: Ireland, the United Kingdom, Sweden, Norway, the Barents Sea, the White Sea, Kamchatka, the Commander Islands, Russian Far East, the Kurile Islands, the Sea of Japan (see Martynov *et al.*, 2015a, b), the Pacific side of the Japanese Islands, Vietnam, Alaska, British Columbia and Washington State (Port Orchard and Bainbridge Island). Specimens were studied and deposited in the Zoological Museum of Lomonosov Moscow State University (ZMMU), the National Museum of Nature and Science, including the Showa Memorial Institute, Tsukuba (NSMT), the Natural History Museum, Kishiwada City (KSNHM), the National Museums Northern Ireland, Cultra, Belfast and the Bavarian State Collection of Zoology, Munich (ZSM).

Morphological analysis

External morphology was studied through observation and photographs of living specimens and dissection of preserved specimens under a stereomicroscope. For the description of internal features, we dissected both preserved and fresh specimens (when available) under the stereomicroscope. The buccal mass of each specimen was extracted and processed in 10% sodium hypochlorite solution for one to two minutes. The coated radulae were examined and photographed using a scanning electron microscope (CamScan and JSM). The reproductive systems of different species were also examined and drawn using a stereomicroscope.

Molecular analyses

Small pieces of tissue were used for DNA extraction with Diatom DNA Prep 100 kit by Isogene Lab and the protocol provided by the manufacturer. A commonly used set of markers were sequenced: mitochondrial cytochrome *c* oxidase subunit I (*COI*) and 16S rDNA, nuclear 28S rDNA (C1–C2 domain) and 18S rDNA. The primers and polymerase chain reaction programs used are presented in Supporting Information, Table S1. DNA sequences of both strands were obtained using the ABI PRISM1Big-Dye Terminator v.3.1. on an automated DNA sequencer (Applied Biosystems Prism 3700). *COI* sequences were translated into amino acids for confirmation of the alignment. All new sequences were deposited in GenBank (Supporting Information, Table S2; highlighted in bold). Additional molecular data of other dorid species were obtained from GenBank. All new and publicly available sequences were checked via BLAST searches in GenBank (https://blast.ncbi.nlm.nih.gov/Blast.cgi) to verify identification and against potential contaminations and errors. Original data and publicly available sequences were aligned with the MAFFT algorithm (Katoh *et al.*, 2002). Separate analyses were conducted for *COI* (658 bp), 16S (502 bp), 28S

(306 bp), 18S (1732 bp) and four concatenated markers (3198 bp). GBlocks 0.91b (Talavera & Castresana, 2007) were applied to discard poorly aligned regions for the 18S data set (using less stringent options; 12% of the positions were eliminated). Additionally, analyses were conducted for all available data for *Cadlina* species, including *COI* (658 bp), 16S (467 bp), 28S (331 bp) and three concatenated markers (1456 bp). The GTR+I+G model was chosen for the concatenated datasets using MrModelTest 2.3 (Nylander *et al.*, 2004). Two different phylogenetic methods, Bayesian inference (BI) and maximum likelihood (ML), were used to infer evolutionary relationships. Bayesian estimation of posterior probability was performed in MrBayes 3.2 (Ronquist *et al.*, 2012). Four Markov chains were sampled at intervals of 1000 generations. Analysis was started with random starting trees and 6×10^6 generations. ML analysis was performed using RAxML 7.2.8 (Stamatakis *et al.*, 2008) with 1000 bootstrap replicates. Final phylogenetic tree images were rendered in FigTree 1.4.2. The program MEGA7 (Kumar *et al.*, 2016) was used to calculate the minimum uncorrected p-distances between all the sequences. Also, the maximum intra- and minimum intergroup genetic distances were examined. Automatic Barcode Gap Discovery (ABGD) (Puillandre *et al.*, 2012) was used to estimate the diversity of *Cadlina* species. An alignment of the *COI* marker was submitted and processed in ABGD using the Jukes–Cantor (JC69) and Kimura (K80) models and the following settings: a prior for the maximum value of intraspecific divergence between 0.001 and 0.1, 10 recursive steps.

RESULTS

Molecular phylogeny

For the molecular part of this study, a total of 185 specimens were examined, combining 90 novel sequences with 407 multilocus data sequences from GenBank to represent the full diversity of dorid families. True dorids [= 'infraorder Doridoidea' according to MolluscaBase (2019a)] and bathydoridids have recently been recognized as a separate order, Doridida, by Martynov & Korshunova (2011, 2012) because of the presence of a ctenidium-like gill and developmental patterns similar to the order Pleurobranchida (universally considered a separate order sister to the nudibranchs; Wägele & Willan, 2000; Martynov, 2011; Pabst & Kocot, 2018). Four specimens of bathydoridids (= 'infraorder Bathydoridoidei'; MolluscaBase, 2019c) (11 publicly available sequences) are used as the outgroup. Bayesian inference (BI) and maximum likelihood (ML) analyses based on the combined dataset for the mitochondrial genes *COI* and 16S and the nuclear genes 28S and 18S yield similar results. The same phylogenetic tree resulting from concatenated molecular data (*COI*+16S+28S+18S) is represented in a rectangular tree layout and a radial tree layout (Fig. 1, and see Discussion).

At the initial stage of research for comprehensive taxon sampling, publicly available sequences were checked via BLAST searches in GenBank. Several publicly available sequences of the species of the dorid genus *Dendrodoris* were verified as erroneous during BLAST searches and are not included in the present analysis. The sequences did not return any other mollusc sequences as near matches in BLAST searches, only other *Dendrodoris*, then spiders and insects (see the section 'Footnote to results' for details). Despite the fact that BLAST searches in GenBank verified genetic similarity for only small fragments of these sequences, it is absolutely clear that these sequences are not suitable for inferring dorid nudibranch phylogeny. We suppose that the use of some of these erroneous *Dendrodoris* sequences underlies the 'concerns regarding multiple sequence alignments in estimating the phylogeny of the Nudibranchia suborder Doridina' in Hallas *et al.* (2017). There is no doubt that the long branch clade formed by *Dendrodoris arborescens*, *D. fumata*, *D. guttata* and *D. nigra* is an artefact of non-molluscan mtDNA data that corrupt the phylogenetic analysis as a whole.

Besides, using different methodologies to examine conflicts regarding estimated phylogenies led to the insertion of the erroneous 'N' nucleotides in some *COI* sequences (Hallas *et al.*, 2017). For example, the *COI* sequence for *Hexabranchus sanguineus* (Rüppell & Leuckart, 1828) (GenBank accession number MF958433) has a length of 661 bp and an extra 'N' on positions 483, 484 and 485, whereas the *COI* sequence for *Hexabranchus sanguineus* sequenced for our study has the expected length of 658 bp. Translation into amino acids has also revealed differences in protein sequences. Therefore, the extra 'N's in publicly available sequences were deleted before conducting MAFFT alignment for our analysis. We suggest that these *Dendrodoris* sequences are most likely a pseudogene that is inserted in the nuclear genome and is amplifying preferentially with the Folmer primer set or it could be a result of other events. This error has unfortunately been repeated by previous workers looking at species of *Dendrodoris*, and thus some conclusions based on these *COI* sequences will need to be revisited.

The main goal of the present molecular phylogenetic analysis is to explore the taxonomic relationships of representatives of the genera *Cadlina*, *Cadlinella* and '*Cadlinella*' *sagamiensis* (Baba, 1937). Phylogenetic analyses, based on four molecular markers, show a better resolution at the genus than at the family level. Nevertheless, these results allow for the clarification of

Cadlina and *Cadlinella* relationships and reveal some patterns of evolution. The molecular analysis shows the presence of a well-supported (PP = 1, BS = 100) large clade that encompasses most of the families of true dorids. All *Cadlina* species cluster together (PP = 1, BS = 99) in a highly supported clade that is sister (PP = 1, BS = 99) to the *Aldisa* species clade (PP = 1, BS = 100). The *Dendrodoris* clade (PP = 1, BS = 99), *Doriopsilla* (PP = 1, BS = 100) clade and *Phyllidia* + *Fryeria* + *Phyllidiella* + *Reticulidia* + *Ceratophyllidia* (PP = 1, BS = 83) cluster together (PP = 0.93, BS = 73) and are revealed as closest to the *Cadlina* and *Aldisa* clades. The species of *Cadlinella* (PP = 1, BS = 100) clusters remotely from *Cadlina* and *Aldisa* and forms a common clade (PP = 0.94, BS = 50) together with the *Hexabranchus* clade (PP = 1, BS = 100) and the '*Cadlinella*' *sagamiensis* (PP = 1, BS = 100) clade. Despite the fact that '*Cadlinella*' *sagamiensis* is represented by two specimens, successfully sequenced for all four genetic markers, this clade has an unstable location with low support (PP = 0.72, BS = 33) and demonstrates an intermediate position between *Cadlinella* and *Hexabranchus*. Chromodorididae and Polyceridae (plus Okadaiidae and Gymnodorididae) clades are revealed as closest to the *Cadlinella* + *Hexabranchus* + '*Cadlinella*' *sagamiensis* clade. It is important to note that long branches of the *Vayssierea* clade (PP = 1, BS = 99) are not an artefact, but refer to highly divergent taxa that fit well with the morphological features of *Vayssierea*. The *Vayssierea* clade is recovered as sister to the *Gymnodoris* and *Polycera* clades and provides the opportunity to consider *Vayssierea* as a highly modified descendant with a relationship to Gymnodorididae/Polyceridae. The clade with three specimens of the cryptobranch *Onchimira cavifera* Martynov *et al.*, 2009 (PP = 1, BS = 100) is nested in Onchidorididae.

To define species of the genus *Cadlina*, we used an integrative approach, including phylogenetic tree topologies, ABGD analysis, intra- and intergroup genetic distances and morphological diagnostics. Since there are insufficient data for the 18S marker of representatives of *Cadlina*, the phylogenetic tree is based on three concatenated markers (*COI* + 16S + 28S) (Fig. 2). BI and ML analyses based on the three-genes dataset yielded similar results (Fig. 1). All ten *C. laevis* (Linnaeus, 1767) sequences cluster together (PP = 1, BS = 100%) in a clade that is sister to *C. kamchatica* Korshunova *et al.*, 2015 (PP = 1, BS = 100%), *C. paninae* (PP = 1, BS = 100%) and *C. umiushi* Korshunova *et al.*, 2015 (PP = 1, BS = 96%) clades. *Cadlina sylviaearleae* (PP = 1, BS = 100%) and *C. luteomarginata* MacFarland, 1966 form two separate sister clades which also form a maximum supported lineage (PP = 1, BS = 100%). *Cadlina japonica* (PP = 1, BS = 97%) is sister to *C. klasmalmbergi* (PP = 1, BS = 100%) and clusters together with *C. jannanicholsae* (PP = 1, BS = 100%), which is a well-supported lineage (PP = 1, BS = 95%). Other *Cadlina* species (*C. modesta* MacFarland, 1966, *C. sparsa* (Odhner, 1921), *C. flavomaculata* MacFarland, 1905, *C. rumia* Marcus, 1955 and *C. luarna* Marcus & Marcus, 1967) form five separate clades in a well-supported clade (PP = 1, BS = 86%). The ABGD analysis of the *COI* dataset run with two different models reveals 16 potential *Cadlina* species: *C. flavomaculata*, *C. jannanicholsae*, *C. japonica*, *C. kamchatica*, *C. klasmalmbergi*, *C. laevis*, *C. luarna*, *C. luteomarginata*, *C. modesta*, *C. paninae*, *C. pellucida*, *C. rumia*, *C. sparsa*, *C. sylviaearleae*, *C. umiushi* and *C.* sp. from South Africa. Maximum intragroup and minimum intergroup genetic distances for *COI* and 16S markers also support four new species in the genus *Cadlina* (Tables 1, 2).

Footnote to results: Genetic similarity of 82% for the *COI* marker is shown between *Dendrodoris arborescens* (Collingwood, 1881) (GenBank accession numbers AB917430, AB917431, AB917432, AB917433, AB917434, AB917435, AB917436, AB917437, AB917438, AB917439 and AB917441) and *Drassodes pubescens* (Thorell, 1856) (Arachnida) and *Nesticella jingpo* Lin, Ballarin & Li, 2016 (Arachnida). Genetic similarity of 88% for the *COI* marker is shown between *Dendrodoris guttata* (Odhner, 1917) (GenBank accession numbers AB917444, AB917445, AB917446, MG948855 and MG948856) and *Rugathodes* sp. (Arachnida) and *Argiope amoena* L.Koch, 1878 (Arachnida). Genetic similarity of 81–82% for the *COI* marker was shown between *Dendrodoris fumata* (Rüppell & Leuckart, 1830) (GenBank accession numbers AB917448, AB917449, AB917450, AB917451, AB917452, AB917453, AB917454, AB917455 and AB917456) and *Burmoniscus purpura* Kwon & Taiti, 1993 (Crustacea); 84% *D. fumata* (GenBank accession numbers MF958444, KF408220 and AF249799) and *Apanteles* sp. (Insecta). Genetic similarity of 83% for the *COI* marker was shown between *Dendrodoris grandiflora* (Rapp, 1827) (GenBank accession numbers KT833268 and KT833269) and Aulacidae sp. (Insecta). Genetic similarity of 87% for the *COI* marker was shown between *Dendrodoris nigra* (Stimpson, 1855) (GenBank accession numbers MF958443, AB917447 and AF249795) and *Eridontomerus arrabonicus* Erdös, 1954 (Insecta). Genetic similarity of 84% for the 16S marker was shown between *Dendrodoris nigra* (GenBank accession numbers MF958318 and AF249242) and *Haswellia* sp. (Isopoda). Genetic similarity of 93% for the 16S marker was shown between *Dendrodoris grandiflora* (GenBank accession number KT820538) and *Torresitrachia weaberana* Solem, 1979 (Stylommatophora).

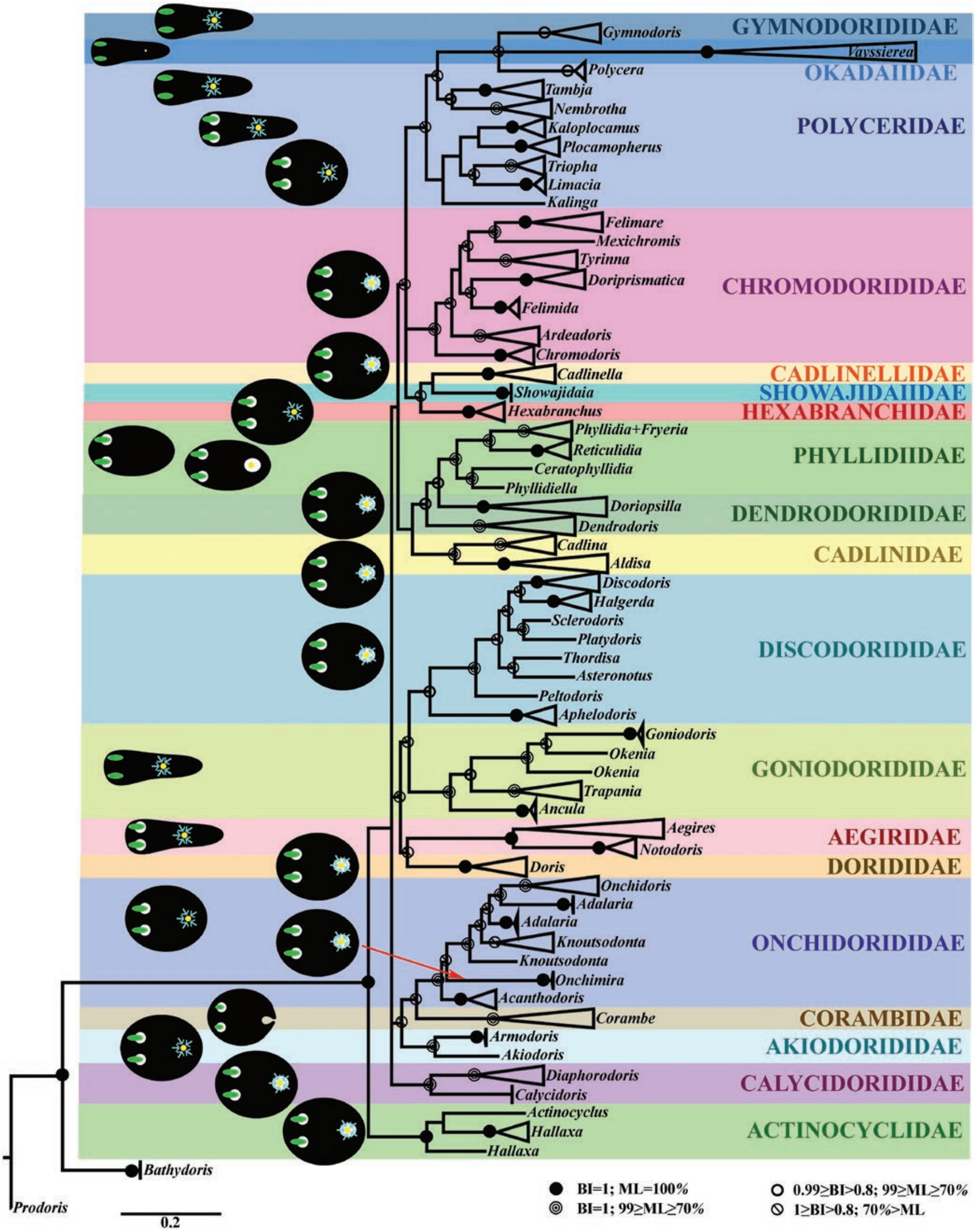

Figure 1. Phylogenetic tree of the dorids based on concatenated molecular data (*COI* + 16S + 28S + 18S) represented by Bayesian inference (BI), represented as rectangular tree layout. Posterior probabilities from BI and bootstrap values for Maximum Likelihood (ML) are indicated on the figure. Presence of the gill cavity (cryptobranch state) and rhinophoral sheaths indicated by white circles on the black dorid body outlines.

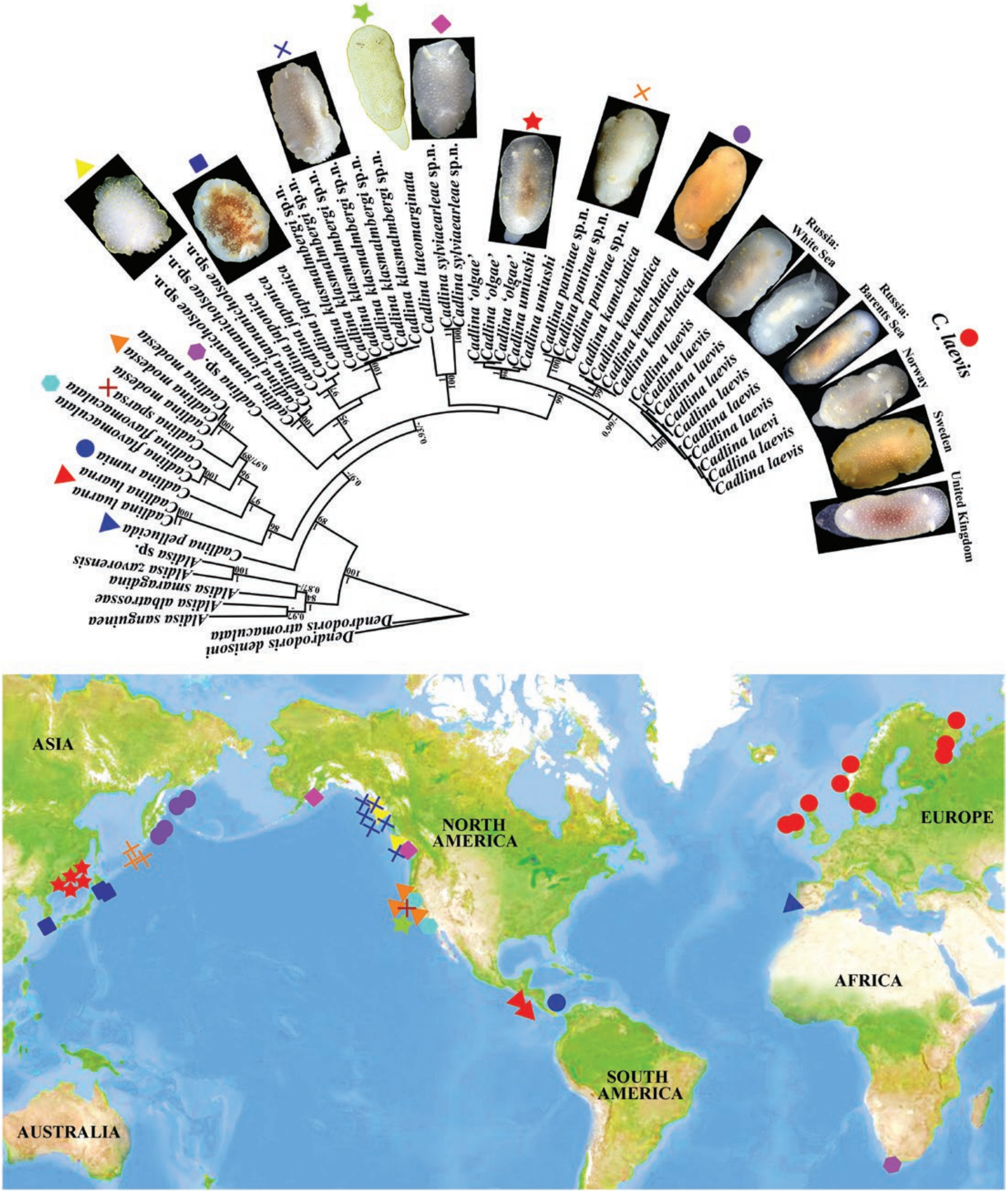

Figure 2. Phylogenetic tree of the genus *Cadlina* based on concatenated molecular data (*COI* + 16S + 28S) represented by Bayesian inference (BI) and combined with distributional data. Numbers left of branches represent posterior probabilities from BI. Numbers right of branches indicate bootstrap values for maximum likelihood. Coloured symbols placed on the map denote the *Cadlina* species distribution used in the above analysis.

SYSTEMATICS

FAMILY CADLINIDAE BERGH, 1891

Synonyms: Echinochilidae Odhner in Franc, 1968, Inudinae Marcus & Marcus, 1967.

Diagnosis: Notal edges well defined, covered with low tubercles or smooth. Gills multipinnate, gill cavity well defined. Labial cuticle with uni-, bi- or tricuspid elements. Radula broad, central teeth present, low trapezoid or elongated with distinct, massive cusps, not directed forward. Vas deferens with narrow ejaculatory duct, penial spines usually present, apparently absent in at least one clade. Receptaculum seminis does not insert directly to base of bursa.

Genera included: *Cadlina* Bergh, 1879, *Aldisa* Bergh, 1878.

CADLINA LAEVIS (LINNAEUS, 1767)

(FIGS 2–6, 15A)

Doris laevis Linnaeus, 1767: 1083.
Cadlina laevis – Iredale & O'Donoghue. 1923: 201–233; Thompson & Brown, 1984: 76–78.
?*Cadlina boscai* Vilella, 1994: 63–72.
?*Doris marginata* Montagu, 1804: 79–80, tab. 7, fig. 7.
Cadlina marginata – Miller, 1980: 170, non *Cadlina marginata* sensu MacFarland, 1905
Doris obvelata Müller, 1776: 229.
Cadlina obvelata – Odhner, 1907: 21.
?*Doris planulata* Stimpson, 1853: 26, fig. 14
Cadlina planulata – Bergh, 1879a: 345.
Doris repanda Alder & Hancock, 1842: 31–36.
Cadlina repanda –Bergh, 1879a: 345; Bergh, 1879b: 115–120, pl. V. fig. 15; pl VI. figs 21, 22; pl. VII. figs 9–18; pl VIII. figs 3–6.
Cadlina sp. A – Just & Edmunds, 1985: 46–47, pl. 19.
Cadlina sp. B – Just & Edmunds, 1985: 48–49, pl. 20.
Neotype (designated here): ZMMU Op-608, *L* (body length) = 10 mm (preserved), north-eastern Atlantic, Norway, Gulen, 10–20 m, stones and rocky substrate, 19 March 2015, coll. T. A. Korshunova, A. V. Martynov.
Paraneotype: ZMMU Op-609, one spc., *L* = 11 mm (preserved), north-eastern Atlantic, Norway, Gulen, 10–20 m, stones and rocky substrate, 18 March 2015, coll. T. A. Korshunova, A. V. Martynov.

Material studied: ZMMU Op-675, one spc., *L* = 10 mm (preserved), dissected, north-eastern Atlantic, Ireland, Co Mayo, S of Inishgallon, Purteen, Achill Island, 10–25 m depth, 5 April 2015, coll. Bernard Picton. ZMMU Op-676, one spc., *L* = 12 mm, same locality as previous, 10–25 m depth, 5 April 2015, coll. Bernard Picton. ZMMU Op-677, one spc., *L* = 11.5 mm (live), Arctic Ocean, White Sea, 5–20 m depth, 13 July 2013, coll. T. A. Korshunova, A. V. Martynov. ZMMU Op-678, one spc., *L* = 17 mm (live), Arctic Ocean, White Sea, 10–15 m depth, 27 September 2015, coll. T. A. Korshunova, A. V. Martynov. ZMMU Op-679, one spc., *L* = 23 mm (live), Arctic Ocean, Barents Sea, 10–20 m depth, 30 August 2012, coll. T. A. Korshunova, A. V. Martynov. ZMMU Op-680, one spc., *L* = 16.5 mm (preserved), Sweden, Smoegen, 5–10 m depth, 12 August 2017, coll. K. Lundin, A. V. Martynov. ZMMU Op-681, one spc., *L* = 12 mm, north-eastern Atlantic, Norway, Gulen, 10–20 m, stones and rocky bottom, 5 March 2018, coll. T. A. Korshunova, A. V. Martynov. ZMMU-682, one spc., *L* = 9 mm (preserved), Arctic Ocean, White Sea, 9–15 m depth, 14 September 2015, coll. T. A. Korshunova, A. V. Martynov. ZMMU-692, one spc., *L* = 19 mm (live), Arctic Ocean, White Sea, 7–10 m, 27 September 2015, coll. T. A. Korshunova, A. V. Martynov.

External morphology

Notum broad, rounded in front and posteriorly. Rhinophores long and retracted into raised soft sheaths bearing small tubercles (Fig. 3). 11–18 rhinophoral lamellae. Notum covered with commonly indistinct small, low to slightly pointed tubercles (Fig. 3). Spicules form sparse network in notum. Six to eight multipinnate gills united by common membrane into circle around anus. Gills retractable into common gill cavity (Fig. 3C). Border of gill cavity moderately raised with smooth edge (Fig. 3C, E). Oral veil small, trapezoid, with oblique notched lateral sides (Fig. 3B, D). Foot broad, anteriorly rounded and slightly thickened to form double edge (Fig. 3); it appears as entire (Fig. 3K) or slightly notched in middle (Fig. 3D); posteriorly it sometimes projects slightly from notum in crawling animals, forming a rounded tail.

Colour

Living specimens commonly rather semitransparent whitish to rarely dark yellowish (Fig. 3). Rhinophores similar to background colour or occasionally darker (Fig. 3O). Gills semitransparent white, similar to ground colour. Digestive gland slightly visible through notum dorsally and shining more clearly through foot ventrally. Subepidermal glands shine near lateral edges of notum. Usually thin yellow line around notum border absent, but in some specimens from the White Sea (Fig. 3N, O) and Ireland it may appear, usually weakly developed.

Table 1. Maximum intragroup (highlighted in bold) and minimum intergroup genetic distances (%) for *COI* marker in *Cadlina* species

	Cadlia laevis	*Cadlina umiushi* + *C.* ‘*olgae*’	*Cadlina kamchatica*	*Cadlina paninae*	*Cadlina luteomarginata*	*Cadlina sylviaearleae*	*Cadlina klasmalmbergi*	*Cadlina jannanicholsae*	*Cadlina japonica*	*Cadlina modesta*	*Cadlina sparsa*	*Cadlina flavomaculata*	*Cadlina rumia*	*Cadlina luarna*	*Cadlina pellucida*	*Cadlina* sp. (Africa)
Cadlina laevis	**1.52**	3.90	4.21	4.24	11.45	12.96	13.97	11.62	12.29	15.15	16.84	15.42	14.48	15.66	10.61	14.81
Cadlina umiushi + *C.* ‘*olgae*’	3.90	**0.34**	4.38	5.05	11.11	12.63	12.12	10.10	11.62	15.32	16.67	15.49	13.47	14.81	11.28	13.64
Cadlina kamchatica	4.21	4.38	**0.17**	4.71	11.62	12.96	13.13	11.45	11.78	15.32	16.67	15.99	13.30	15.32	10.94	13.47
Cadlina paninae	4.24	5.05	4.71	**0**	12.46	13.13	13.64	12.12	11.62	15.32	16.50	15.82	14.31	16.16	11.45	14.48
Cadlina luteomarginata	11.45	11.11	11.62	12.46	-	10.44	12.63	13.37	13.64	15.66	16.16	15.82	14.81	15.66	12.12	13.80
Cadlina sylviaearleae	12.96	12.63	12.96	13.13	10.44	**0**	14.98	14.89	15.15	15.66	17.51	17.17	15.49	17.68	13.80	14.81
Cadlina klasmalmbergi	13.97	12.12	13.13	13.64	12.63	14.98	**0.17**	8.42	8.59	16.33	16.33	16.50	16.33	15.66	14.31	12.96
Cadlina jannanicholsae	11.62	10.10	11.45	12.12	13.37	14.89	8.42	**1.01**	8.42	15.66	16.16	15.99	15.66	14.48	13.37	13.30
Cadlina japonica	12.29	11.62	11.78	11.62	13.64	15.15	8.59	8.42	**0.84**	15.32	15.82	15.66	13.97	16.67	13.13	12.79
Cadlina modesta	15.15	15.32	15.32	15.32	15.66	15.66	16.33	15.66	15.32	**0.67**	9.60	9.52	13.47	16.16	14.48	16.33
Cadlina sparsa	16.84	16.67	16.67	16.50	16.16	17.51	16.33	16.16	15.82	9.60	-	8.75	13.97	15.99	15.99	15.49
Cadlina flavomaculata	15.42	15.49	15.99	15.82	15.82	17.17	16.50	15.99	15.66	9.52	8.75	**0.85**	12.63	15.48	13.78	14.48
Cadlina rumia	14.48	13.47	13.30	14.31	14.81	15.49	16.33	15.66	13.97	13.47	13.97	12.63	-	17.17	14.81	13.30
Cadlina luarna	15.66	14.81	15.32	16.16	15.66	17.68	15.66	14.48	16.67	16.16	15.99	15.48	17.17	-	16.84	17.34
Cadlina pellucida	10.61	11.28	10.94	11.45	12.12	13.80	14.31	13.37	13.13	14.48	15.99	13.78	14.81	16.84	-	15.15
Cadlina sp. (Africa)	14.81	13.64	13.47	14.48	13.80	14.81	12.96	13.30	12.79	16.33	15.49	14.48	13.30	17.34	15.15	-

Table 2. Maximum intragroup (highlighted in bold) and minimum intergroup genetic distances (%) for 16S marker in *Cadlina* species

	Cadlia laevis	*Cadlina umiushi* + *C.* ‘*olgae*’	*Cadlina kamchatica*	*Cadlina paninae*	*Cadlina luteomarginata*	*Cadlina sylviaearleae*	*Cadlina klasmalmbergi*	*Cadlina jannanicholsae*	*Cadlina japonica*	*Cadlina modesta*	*Cadlina sparsa*	*Cadlina flavomaculata*	*Cadlina rumia*	*Cadlina luarna*	*Cadlina pellucida*	*Cadlina* sp. (Africa)
Cadlina laevis	**1.88**	3.70	3.35	3.29	7.67	6.59	4.94	5.41	5.41	7.14	7.14	6.88	7.94	9.18	6.90	8.20
Cadlina umiushi + *C.* ‘*olgae*’	3.70	**1.18**	1.41	1.42	5.90	6.37	4.48	4.95	4.95	7.31	7.55	7.08	7.59	7.31	6.15	6.12
Cadlina kamchatica	3.35	1.41	**0.24**	0.71	6.59	6.12	3.76	4.47	4.24	7.53	7.53	7.29	7.83	7.76	6.13	6.82
Cadlina paninae	3.29	1.42	0.71	**0**	7.06	6.59	4.47	4.94	4.71	7.53	7.76	7.29	8.33	7.76	6.13	7.06
Cadlina luteomarginata	7.67	5.90	6.59	7.06	-	4.24	6.12	6.82	6.12	9.88	9.65	9.18	11.11	9.65	10.14	6.82
Cadlina sylviaearleae	6.59	6.37	6.12	6.59	4.24	-	6.12	6.59	6.12	9.65	10.82	10.35	11.62	10.35	9.91	7.76
Cadlina klasmalmbergi	4.94	4.48	3.76	4.47	6.12	6.12	**0**	1.65	1.41	8.71	9.88	8.00	8.59	8.71	7.55	7.06
Cadlina jannanicholsae	5.41	4.95	4.47	4.94	6.82	6.59	1.65	**0.94**	1.65	8.71	9.41	8.00	8.84	9.18	7.78	7.29
Cadlina japonica	5.41	4.95	4.24	4.71	6.12	6.12	1.41	1.65	**0.47**	8.71	9.41	7.53	8.84	8.71	7.55	6.82
Cadlina modesta	7.14	7.31	7.53	7.53	9.88	9.65	8.71	8.71	8.71	**0.24**	2.59	1.65	4.04	7.53	10.38	9.41
Cadlina sparsa	7.14	7.55	7.53	7.76	9.65	10.82	9.88	9.41	9.41	2.59	-	2.35	5.81	8.71	10.61	10.12
Cadlina flavomaculata	6.88	7.08	7.29	7.29	9.18	10.35	8.00	8.00	7.53	1.65	2.35	**1.41**	4.04	8.24	9.67	9.18
Cadlina rumia	7.94	7.59	7.83	8.33	11.11	11.62	8.59	8.84	8.84	4.04	5.81	4.04	-	8.33	9.87	9.85
Cadlina luarna	9.18	7.31	7.76	7.76	9.65	10.35	8.71	9.18	8.71	7.53	8.71	8.24	8.33	**0**	11.32	9.41
Cadlina pellucida	6.90	6.15	6.13	6.13	10.14	9.91	7.55	7.78	7.55	10.38	10.61	9.67	9.87	11.32	-	9.20
Cadlina sp. (Africa)	8.20	6.12	6.82	7.06	6.82	7.76	7.06	7.29	6.82	9.41	10.12	9.18	9.85	9.41	9.20	-

Figure 3. External features of *Cadlina laevis* from various North Atlantic locations. A–C, Neotype ZMMU Op-608, 10 mm, Norway: dorsal view (A), oral veil and rhinophores (B), gills within gill cavity (C). D, ZMMU Op-609, 11 mm, Norway, ventral view. E, ZMMU Op-681, 12 mm, Norway, dorsal view. F, ZMMU Op-680, 16.5 mm, Sweden. G,H, ZMMU Op-675, 10 mm, Ireland: dorsal view (G), lateral view (H). I, ZMMU Op-676, 12 mm, Ireland, dorsal view. J, K, ZMMU Op-679, 23 mm, Barents Sea (Russia): dorsal view (J), ventral view (K). L, ZMMU Op-677, 11.5 mm, White Sea (Russia), dorsal view. M, ZMMU Op-678, 17 mm, White Sea, ventral view. N,O, ZMMU-692, 19 mm, White Sea, dorsal view. Photos: A–F, J–O, Tatiana Korshunova and Alexander Martynov; G–I, Bernard Picton.

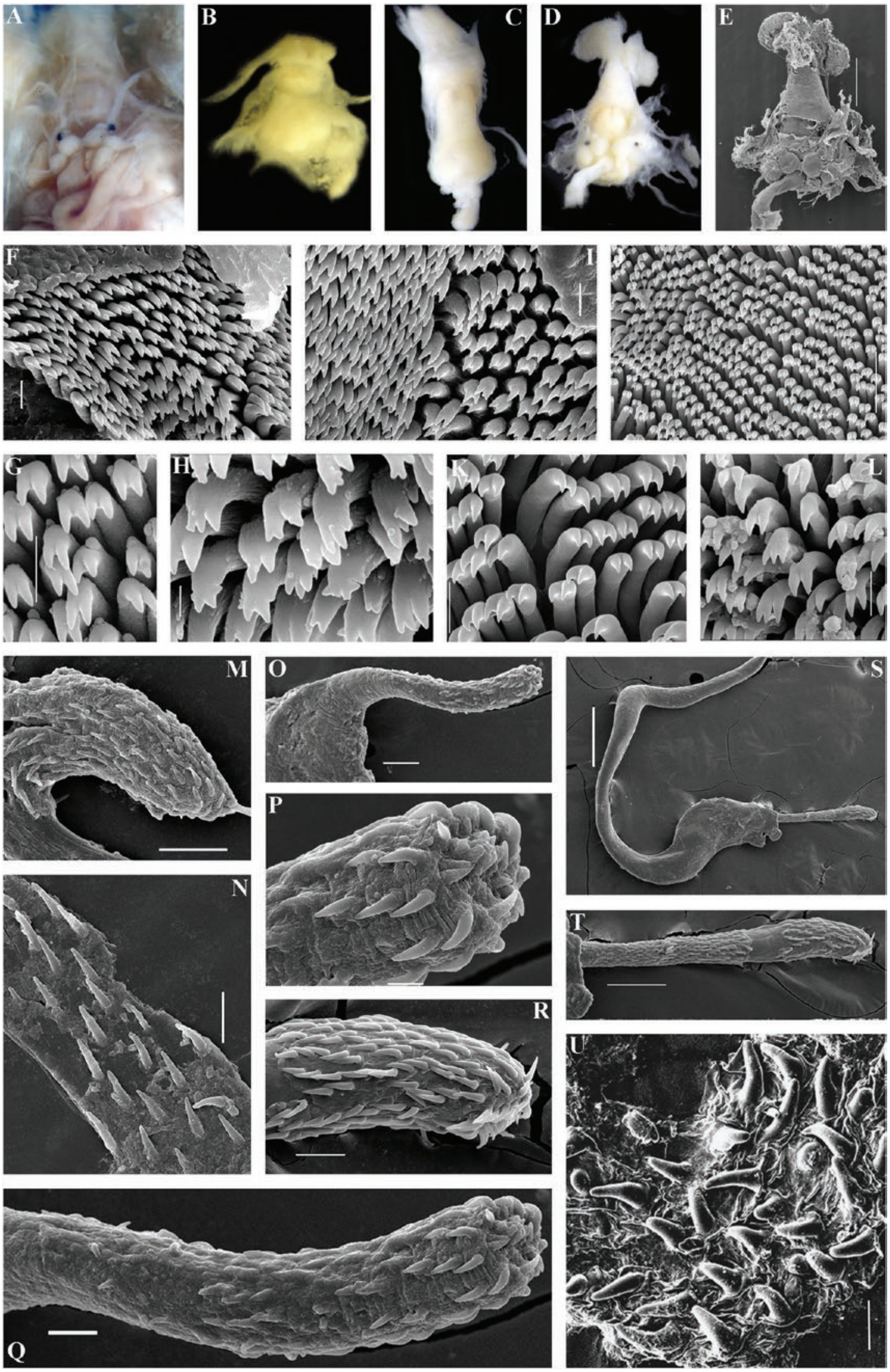

Figure 4. *Cadlina laevis*, buccal bulbs (A–E, light microscopy, LM and E–U, scanning electron microscopy, SEM), labial cuticle elements (F–L, SEM) and penial spines (M–U, SEM). A, M, N, ZMMU Op-681, Norway. B, I, O, P, Q, ZMMU Op-680, Sweden. C, J, K, R, S, T, ZMMU Op-675, UK. D, E, L, U, ZMMU Op-677, White Sea. F–H, ZMMU Op-609, Norway. Scale bars: E, 1 mm; F, G, I, K, L, P, U, 10 µm; J, R, 30 µm; H, 3 µm; N, Q, 20 µm; M, O, 50 µm; T, 100 µm; S, 300 µm. Light microscopy and SEM images here and in all subsequent figures by Alexander Martynov.

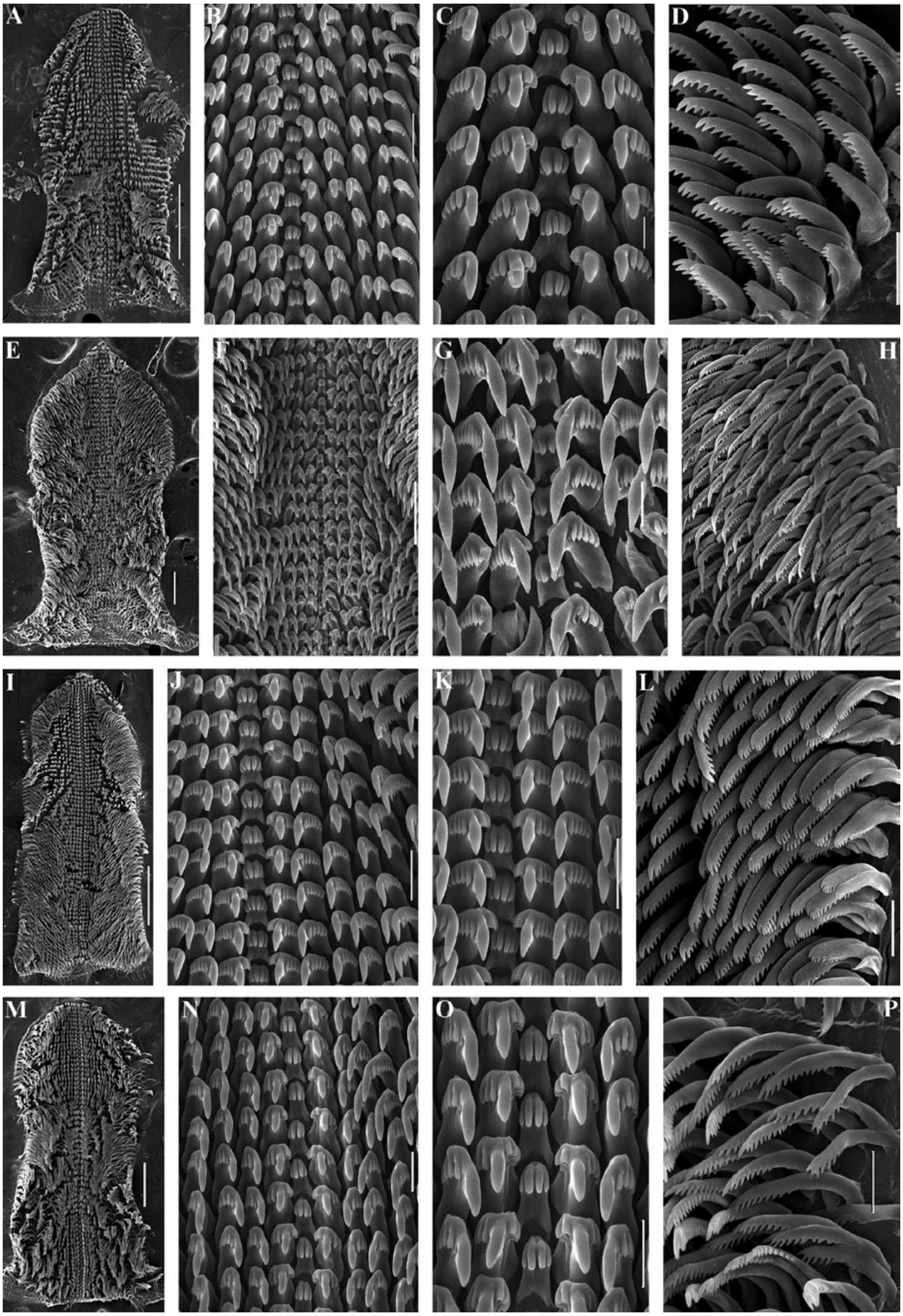

Figure 5. *Cadlina laevis*, complete radula, central part, enlarged central part to show central teeth, and outer teeth are given for every specimen, respectively. SEM. A–D, ZMMU Op-609, Norway. E–H, ZMMU Op-680, Sweden. I–L, ZMMU Op-675, Ireland. M–P, ZMMU Op-677, White Sea. Scale bars: A, I, M, 300 μm; C, 10 μm; B, D, K, L, N, O, P, 30 μm; E, 200 μm; G, 20 μm; H, 50 μm.

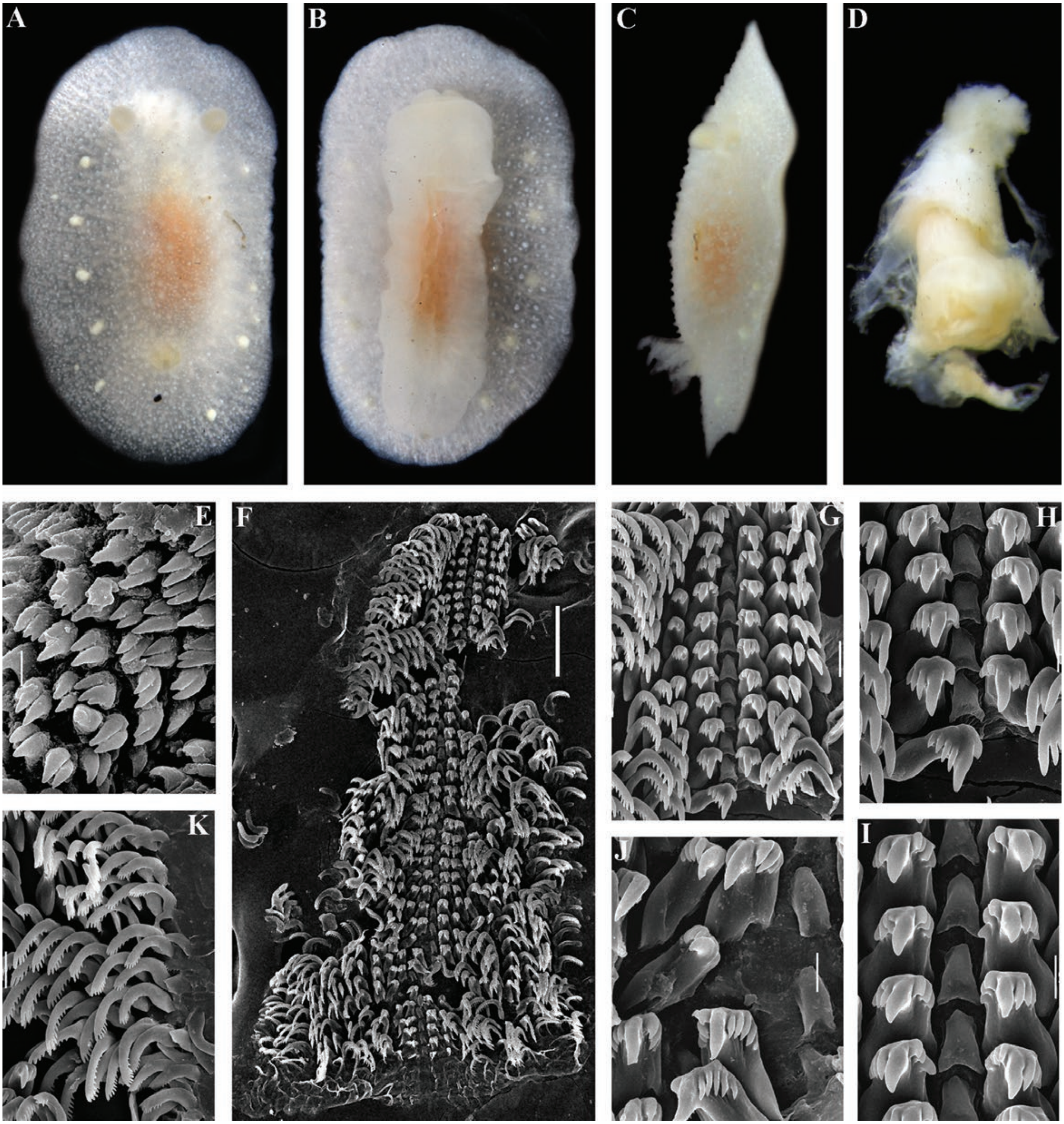

Figure 6. *Cadlina laevis*, ZMMU-682, White Sea, subadult 9 mm, external and internal features. A, dorsal view. B, ventral view. C, lateral view. D, buccal bulb. E, elements of labial cuticle. F, complete radula. G, central part of radula. H, J, I, enlarged central part of radula to show central teeth and first lateral teeth. K, outer lateral teeth. Scale bars: E, 5 μm; F, 100 μm; G, K, 20 μm; H, I, J, 10 μm. Photos: Tatiana Korshunova and Alexander Martynov.

Buccal bulb and oral tube

Buccal bulb relatively long, similar in length to oral tube (Fig. 4A–E). Salivary glands relatively long and narrow.

Jaws

Rounded labial disk covered by dark brown cuticle bearing distinct labial elements with commonly double to more rarely triple hook-shaped tips (Fig. 4F–L).

Radula

Radular formulae 59 × 26.1.26 (Op-609, Norway, Fig. 5A–D), 78 × 29.1.29 (Op-680, Sweden, Fig. 5E–H), 86 × 28.1.28 (Op-675, UK, Fig. 5I–L), 70 × 36.1.36 (Op-677, Russia, White Sea, Fig. 5M–P) and 43 × 18.1.18 (Op-682, White Sea, Fig. 6F–H). Radular teeth slightly yellowish. Central tooth rectangular, elongate to broad, and bears four to six distinct cusps (Fig. 5C, G, K, O). Central teeth of late juveniles (subadults) almost devoid of cusps (Fig. 6H, I). Inner lateral tooth massive with wide base and short, strong, slightly curved cusp and five to seven denticles on outer edge and two or three on inner edge (Fig. 5B–C, F–G, J–K, N–O). Outer lateral teeth elongated hook-shaped, bearing up to 18 comb-shaped denticles (Fig. 5D, H, L, P).

Reproductive system

Ampulla comprised of at least four thickened compartments (Fig. 15A, a). Ampulla bifurcates into moderately long vas deferens and oviduct. Uterine duct emerges some distance from female gland mass (Fig. 15A, ud). Prostatic part of vas deferens long, narrow and not distinct (Fig. 15A, pr). Prostate transits to long, narrow vas deferens with several loops (Fig. 15A, vd), which slightly widens towards penial sheath that encloses evertable ejaculatory duct (Fig. 15A, psh). Penial spines conical with a relatively narrow base (Fig. 4M–U). Vagina narrow (Fig. 15A, v), and enters medium-sized rounded bursa copulatrix (Fig. 15A, b). Uterine duct short and narrow (Fig. 15A, ud); it begins from female gland mass (Fig. 15A, fgm) and then enters near base of small oval receptaculum seminis (Fig. 15A, rs). A small genital lobe (15A, gl) placed near female genital openings.

Habitat

Commonly feeds on the spiculeless sponge *Halisarca dujardinii* Johnston, 1842 (personal observations at the White Sea; McDonald & Nybakken, 1997), but also has been reported feeding on *Dysidea fragilis* (Montagu, 1814) (Picton & Morrow, 1994), *Stylotella columella* (Bowerbank, 1874) and *Sycon* sp. (McDonald & Nybakken, 1997). Verified depth range c. 0–30 m.

Distribution

North-eastern Atlantic south to the Gibraltar Strait and north to the the Barents and White seas (Arctic Ocean), but it most commonly occurs in the north-east Atlantic (Fig. 2).

Remarks

Morphological and molecular data provided here for the first time encompass broad geographical coverage from Ireland to the White Sea (Russia) and confirm *C. laevis* as a single species in the shallow waters of the eastern North Atlantic (Fig. 2). At the same time, contrary to previous estimations (e.g. Thompson & Brown, 1984; Roginskaya, 1987), *C. laevis* does not show amphiboreal distribution and is replaced by several species in the northern Pacific, including *C. kamchatica* and *C. umiushi* (re-described below). To avoid potential confusion with the latter externally similar species, we designate a neotype of *C. laevis* from Norway, because the type locality of this species is Scandinavia (Linnaeus, 1767). Linnaeus gave this species the epithet 'laevis', which means 'soft' or 'smooth', likely due to the indistinct dorsal tubercles. From the present wide-ranging material (Fig. 3) we confirm that, despite some specimens demonstrating recognizable low tubercles (e.g. on Fig. 3I from Ireland), the general appearance of *C. laevis* is smooth, especially compared to many North Pacific species, including those from the *C. laevis* clade (like *C. kamchatica*, see Fig. 8B, and C. *umiushi*, see Fig. 7C). While *C. laevis* is commonly white without a yellow notum border, some specimens from Ireland and the White Sea demonstrate the presence of a weakly developed yellow line (Fig. 3G–I, N–O), partly similar to *C. umiushi* (see Fig. 7A–E), or dark yellow to brownish ground colour (Fig. 3F) resembling *C. kamchatica* (Fig. 8A). Those cases are remarkable because intraspecific external variability in one species (i.e. *C. laevis*) partly overlaps with the diagnostic features of evidently separate species (i.e. *C. umiushi* and *C. kamchatica*), thus further undermining the 'cryptic' species concept (see also: Korshunova *et al.*, 2017a). The brownish morph and the yellow-line morphs of *C. laevis* studied here correspond with locality data and coloration of those that were mentioned in Just & Edmunds (1985) as *Cadlina* sp. A and sp. B, respectively. Thus, we here confirm that both these morphs belong to *C. laevis*. We also detected variability in the degree of the height of the central teeth (Fig. 5C, G, K, O) that needs to be considered when comparing such characters with other species. See Table 3 for a morphological comparison of all of the known species of *Cadlina* (except *C. luarna*, see Discussion). Maximum intragroup distances in *C. laevis* are 1.52% for the *COI* marker and 1.88% for the 16S marker. The lowest *COI* intergroup distance of 3.9% is found between *C. laevis* and *C. umiushi*.

The lowest 16S intergroup distance of 3.29% is found between *C. laevis* and *C. paninae* (Tables 1, 2).

One of the commonly recognized synonyms of *C. laevis* (e.g. Iredale & O'Donoghue, 1923; Miller, 1980), *Doris repanda* Alder & Hancock, 1842 corresponds to the diagnosis of *C. laevis*, whereas the first description of *Doris marginata* (Montagu, 1804) does not include characters clearly attributable to *C. laevis* and may represent a different species. Thompson & Brown (1984) did not include *D. marginata* into their synonymy of *C. laevis*. We, therefore, hesitantly include *Doris marginata* into the synonymy of *C. laevis*. The original description of *Doris planulata* (Stimpson, 1853) from the North American Atlantic coast matches *C. laevis*, but in the absence of molecular data for western Atlantic *Cadlina* we place *D. planulata* into the synonymy also with uncertainty. We question the synonymy of *Cadlina boscai* Vilella, 1994 from the Catalan coast of the Mediterranean. While it is similar to *C. laevis*, and that species biologically could inhabit the north-western Mediterranean, the synonymy of *C. boscai* needs to be proven with molecular data before a decision can be made. Finally, *Cadlina glabra* Friele & Hansen, 1876 from deeper waters (*c.* 365 m) off southern Norway, and sometimes included, with reservation, into the synonymy of *C. laevis* (Thompson & Brown, 1984), was never recorded again after the first description and may represent a distinct species (Odhner, 1939).

CADLINA UMIUSHI KORSHUNOVA *ET AL.* IN MARTYNOV *ET AL.*, 2015

(FIGS 7, 15B)

Cadlina sp. nov. (under a preliminary name): Martynov, 1999b: 104–107, figs 78, 81–83.
Cadlina umiushi Korshunova *et al.* in Martynov *et al.*, 2015b: 65, fig. 1.
Cadlina olgae Chichvarkhin, 2016: 12–14, fig. 4., syn. nov.
Holotype: ZMMU Op-445, *L* = 10 mm (live), north-west Pacific, Russia, Sea of Japan, Peter the Great Bay, Bolshoi Pelis Island, stones, 5–7 m depth, 7 September 2014, coll. T. A. Korshunova, A. V. Martynov.

Paratypes: ZMMU Op-455, one spc, *L* = 8 mm (preserved), north-west Pacific, Sea of Japan, Spokoinaya Bay, stony and rocky substrate, 20 m depth, 25 September 2014, coll. T. A. Korshunova, A. V. Martynov. ZMMU Op-458, *L* = 10 mm (live), north-west Pacific, Sea of Japan, Peter the Great Bay, Vostok Bay, stones with algae, 5–7 m depth, 7 July 1993, coll. A. V. Martynov.

External morphology

Notum broad, rounded in front and posteriorly. Rhinophores long and retracted into raised soft sheaths bearing small tubercles (Fig. 7). 11–18 rhinophoral lamellae. Notum covered with distinct, small, rounded tubercles (Fig. 7A, D, E), which can be more protruding in some specimens (Fig. 7C). Spicules form sparse network in notum. Six to eight multipinnate gills united by common membrane into circle around anus. Gills retractable into common gill cavity. Border of gill cavity moderately raised with tuberculated edge (Fig. 7D). Oral veil small, trapezoid, with oblique notched lateral sides (Fig. 7B). Foot broad, anteriorly rounded and slightly thickened to form double edge; it appears as entire (Fig. 7B); posteriorly it sometimes projects slightly from notum in crawling animals, forming a rounded tail.

Colour

Notum semitransparent white (Fig. 7A–E). Gills and rhinophores similar in colour to notum. Digestive gland slightly visible through the notum dorsally (Fig. 7A, D, E). Subepidermal glands especially conspicuous dorsally. Yellow line around notum always well defined (Fig. 7A–E).

Buccal bulb and oral tube

Buccal bulb relatively short, similar in length to oral tube (Fig. 7F). Salivary glands relatively long and narrow.

Jaws

Rounded labial disk covered by yellowish brown cuticle bearing rod-shaped labial elements with double hook-shaped tips (Fig. 7G).

Radula

Radular formula 70 × 30.1.30 (Op-455, 8 mm). Central tooth moderately high, bears five or six cusps (Fig. 7I, J). Inner lateral teeth with four to six denticles on outer edge, and two or three on inner edge (Fig. 7I, J). Middle and outer teeth comb-shaped, bearing up to 15 denticles (Fig. 7K).

Reproductive system

Ampulla relatively thin, comprised of several compartments (Fig. 15B, a). Ampulla bifurcates into moderately long vas deferens and oviduct. Uterine

Table 3. Morphological comparision of species of the genus *Cadlina*

	Type locality	Geographic range	Dorsum colour	Rhinophores & gills colour
Cadlina abyssicola Valdés, 2001	Pacific, East of New Caledonia, 20°54'S, 165°53'E, 394–397 m	off New Caledonia	White to cream	Same as the dorsum
Cadlina affinis Odhner, 1934	Antarctic, Ross Sea, McMurdo, 92–547 m	Antarctic, Ross Sea	Unknown	Unknown
Cadlina dubia Edmunds, 1981	Atlantic, Ghana, off Tema, 10 m	Ghana, 10 m	Creamy white, small white spots	Rhinophores yellow with brown suffusion, gills white
Cadlina excavata (Pruvot-Fol, 1951)	Mediterranean: Banyul	Mediterranean: Banyul	Yellow to pale white, one large blackish spot on each side of the middle part of the dorsum	? Not specified, but according to drawing on Fig. 105d (Pruvot-Fol, 1954) probably same colour with background light coloration of dorsum
Cadlina flavomaculata MacFarland, 1905		NE Pacific: Vancouver Island to Baja California, 0–201 m	White, light cream to yellow	Rhinophores dark brown to black, gills white
Cadlina georgiensis Schrödl, 2000	Subantarctic, South Georgia, 16 m	Subantarctic, South Georgia	Unknown	Unknown
Cadlina glabra (Friele et Hansen, 1876)	North East Atlantic, Norwegian Sea, off Florø, 365.7 m	North East Atlantic	White	Rhinophores and gills yellow
Cadlina jannanicholsae	NE Pacific, Washington State, Bainbridge Island, Shangri-la site	Northeastern Pacific, Canada (British Columbia) and USA (Washington State), c. 8 m	Opaque whitish	Rhinophores yellowish. Gills are semitransparent white, but up to 1/3 covered with yellow
Cadlina japonica Baba, 1937	North Pacific, off central Honshu, Sagami Bay, Amadaiba, 100–350 m	North Pacific, Japanese Islands (from Akkeshi Bay to Kii), South Korea, 5–350 m	Grayish white with large amount of irregular dark brown patching, scattered yellow relatively small spots	Rhinophores brownish to greenish, gills white with yellow punctuated markings
Cadlina kamchatica Korshunova, Picton, Sanamyan & Martynov in Martynov *et al.*, 2015	NW Pacific, Kamchatka, Starichkov Island	NW Pacific: Kamchatka, possibly, Commander Islands and Northern Kurile Islands, c. 6–15 m	Creamy to dark yellow/ light brown; numerous yellow/light yellow spots	Rhinophores and gills similar in colour to dorsum
Cadlina kerguelensis Thiele, 1912	Subantarctic,Keguelen Island, Observatory Bay, 'low depth'	Subantarctic, Keguelen Island	Unknown	Unknown
Cadlina klasmalmbergi	NE Pacific, Washington state, Port Orchard	NE Pacific, Canada (British Columbia) and USA (Washington state), 11–18 m	Opaque whitish (adult), translucent whitish (subadult)	Rhinophores light brownish, tipped with light yellow, gills are semitransparent white, similar to ground colour, tipped with yellow
Cadlina laevis (Linnaeus, 1767)	Norway	North Eastern Atlantic from Barents and White Seas to Northern Spain and Portugal, 0–30 m	Semitransparent whitish to rarely dark yellowish	Rhinophores and gills similar in colour to dorsum
Cadlina limbaughorum Lance, 1962	La Jolla, California	California (Santa Barbara) to Mexico (Los Coronados Islands, Baja California Johnson's Seamount), 15–47 m	White with small opaque white spots	Black to dark brown (both gills and rhniphores)
Cadlina luteomarginata MacFarland, 1905	Eastern North Pacific, Monterey Bay, intertidal	We limit distribution of real *C. luteomarginata* mostly from the type locality and neighbouring areas, and also at least for one sequence from British Columbia. Such records as in Alaska (Lynn Canal), and especially Southern Californian and Mexican ones (Point Eugenia) (MacFarland, 1966; Rudman, 1984; Behrens & Hermosillo, 2005) we consider as belonging to other species	White with moderately sized yellow spots at the top of tubercles	White rhinophores and gills (slightly tipped with yellow)

Yellow line around notal margin	Mantle glands	Dorsal tubercles	Spicules in dorsum	Maximal length, mm
Absent	Present, simple, isolated, yellow	Simple, conical, some larger and sparsely arranged	No data	20 (preserved)
Unknown	'Numerous' (Schrödl, 2000)	Large, knob-like	Present	20
Absent	Present, simple, 6–9 on each side, creamy	Absent	Present	7 (live)
Absent	No data	Small tubercles	Not specified	23 (live)
Present, narrow, faint	Present, simple, clearly seen through the dorsum, rounded, sometimes double, 7–12 on each side, yellow	Small, low rounded tubercles	Present	24 (preserved)
Unknown	Present	Knob-like tubercles of different sizes (up to 0.8 mm)	Present	13 (preserved)
Absent	Present ('sulphureous spots near the mantle margin')	Absent	No data	10 (live?)
Present, broad	Scarcely visible	Large, relatively high irregular in shape to rounded tubercles	Present	45 (live)
Present, rather narrow	Present, yellow, relatively small, more evident in smaller specimens (21 mm – up to 13 glands; 39 mm – up to 10 glands)	Tubercles of various sizes, in middle part of dorsum bigger rounded tubercles	Present	70 (live)
Absent in all specimens invariably	Present, hardly seen through dorsum, simple rounded, or double or rarely triple, *c.* 5–11 on each side, yellow	Small, low rounded tubercles	Present	37 (live)
Unknown	Present	Knob-like tubercles	Unknown	13.5 (preserved)
Present, relatively narrow (adult) to indistinct (subadult)	Not visible in adult and shine through the dorsum in subadult	Moderate in size, low rounded tubercles in adult, much smaller subrounded tubercles in subadult	Present	55 (live)
Commonly absent, rarely present a thin line	Present, clearly seen from dorsum, commonly yellow, numerous	Small low to slightly pointed tubercles	Present	Up to 32
Absent	Numerous, white, of different size	Low pointed tubercles	Present	33 (live)
Present	Scarcely visible in adults	Elevated round to oval somewhat prominent tubercles	Present	45 (live)

Table 3. Continued

	Type locality	Geographic range	Dorsum colour	Rhinophores & gills colour
Cadlina magellanica Odhner, 1926	South Pacific, Chile, Punta Arenas, 27 m	Chile, Falkland Id., 2–270 m	Whitish	Same as dorsum
Cadlina modesta MacFarland, 1966	North-East Pacific, California, La Jolla	Alaska (Point Lena) to California (La Jolla), 0–50 m	Light yellowish to light brown, small to moderate yellow spots mid-laterally	Gills simlar to dorsum, rhinophores often darker, yellow-orange to brown
Cadlina nigrobranchiata Rudman, 1985	Southern Indian Ocean, Western Australia, Figure of 8 Island, Esperance, 10 m	Western Australia, Figure of 8 Island, 10 m	Translucent white, sometimes with few moderate yellow spots laterally	Gills and rhinophores dark brown to black
Cadlina pacifica Bergh, 1879	North East Pacific, Unalashka, Captain's Bay; Shumagin Island Coal harbor, intertidal		Bluish-white	Unknown
Cadlina paninae	Matua Islands, Middle Kurile Islands	Middle Kurile Islands, c. 11–14 m	Opaque whitish, sometimes with some yellowish shadow	Similar to ground colour
Cadlina pellucida (Risso, 1826)	Mediterranean, Nice region	Eastern Atlantic from France (Belle-ile, Brittany) to Strait of Gibraltar, including Portugal); Cabo Verde; Canary Islands; Mediterranean (Nice, Liguria Sea, Naples,), 0–60 m	White	Dark brown to black rhinophores and gills
Cadlina rumia Marcus, 1955	South Atlantic, Brazil, São Sebastião	Tropical Western Atlantic: Florida, Jamaica, Belize, Panama, Domincan Republics, Curaçao, St. Martin, Puerto Rico, Brazil, intertidal	Translucent white	Pale brown rhinophores, whitish to pale brown/yellowish gills
Cadlina scabriuscula (Bergh, 1890)	Atlantic between Florida and Cuba, 24° 44' N, 83° 26' W, 68 m	Atlantic between Florida and Cuba, 24° 44' N, 83° 26' W, 68 m	No data	No data
Cadlina sparsa (Odhner, 1921)	Juan Fernandez, Chile to California	Juan Fernandez, Chile, 2–40 m	Opaque creamy whitish to salmon	Opaque white
Cadlina sylviaearleae	North-eastern Pacific, Washington State, Port Orchard, Rich Passage	Northeastern Pacific, Washington State and Alaska, c. 12 m	Opaque whitish, with some small dorsal tubercles tipped with yellow	Rhinophores with slight yellow tint. Gills are semitransparent white, similar to ground colour.
Cadlina tasmanica Rudman, 1990	Southern Indian Ocean, Tasmania, Bicheno, 6 m	Southern Indian Ocean, Tasmania, 6 m	Translucent white, scattered small opaque white and yellow granules	Gills and rhinophores translucent white
Cadlina umiushi Korshunova, Picton, Sanamyan & Martynov in Martynov *et al.*, 2015	Sea of Japan, Peter the Great Bay	NW Pacific: Sea of Japan, possibly Sakhalin and South Kurile Islands, and Northern Hokkaido, 0–20 m	White; numerous yellow small spots	Rhinophores and gills white
Cadlina willani Miller, 1980	New Zealand	Throughout New Zealand, 0–20 m	Translucent white, broad yellow stripe throughout dorsum midline from rhinophores to gills	Rhinophores and gills white

Yellow line around notal margin	Mantle glands	Dorsal tubercles	Spicules in dorsum	Maximal length, mm
Absent	'Numerous' (Schrödl, 2000)	Knob-like tubercles, diameter up to 0.2 mm	Present	9 (live)
Absent	Numerous	Low rounded tubercles, small and large intermingled	Present	33 (live)
Present	'No sign of mantle glands' (Rudman 1985)	Absent, dorsum is smooth	Unknown	25 (live)
Unknown	Unknown	Small compressed or rounded tubercles	Present	28 (preserved)
Absent	Subepidermal glands shine near lateral edges of notum through dorsal side	Low indistinct tubercles	Present	29 (preserved)
Absent	Few small, simple on each side, white to yellow	Small, disperse	Present	20 (live)
Absent	Present, clearly seen through dorsum, simple rounded, or double or rarely triple, 2–14 on each side, yellow	Rounded small tubercles	Present	15 (live)
No data	No data	Small tubercles		12 (preserve.)
Absent	Present, clearly seen through dorsum, simple rounded, or double or rarely triple, yellowish dark pinkish	Conical to semispherical	Present	36 mm (live)
Present, thin	Present, white, clearly shine near lateral edges of notum	Small pointed tubercles	Present	25 mm (live)
Present, but thin	Not evident	Tiny, granule-like	Not specified	4.5 mm (live)
Present in all specimens invariably, narrow	Present, clearly seen through dorsum, simple rounded, or double or rarely triple, 4–9 on each side, yellow	Small, low rounded tubercles	Present	20 (pre serv.)
Present, moderate	Present, clearly seen through dorsum, simple rounded, up to 30, on each side, white	Small, conical, apically rounded tubrecles	Present	Up to 21 mm (live)

Table 3. Continued

	Jaws	Radula formula (maximal and minimal)	Central teeth	Innermost teeth	Inner lateral teeth	Mid- lateral teeth
Cadlina abyssicola Valdés, 2001	Unicuspid elements only	59 × 45.1.45 (20 mm)	Elongated, 4–5 small similar in size denticles	Hamate, similar to mid laterals, no distinction between cusp and tooth body, 3–4 short, not conspicuous denticles on inner side, 6–7 in outer side	Hamate, 7–10 denticles on outer side only	Hamate, high, completely lacking denticles
Cadlina affinis Odhner, 1934	Bifid and trifid elements	56 × 20.1.20 (13 mm); 62 × 23.1.21 (15 mm); 71 × 27.1.27 (19 mm);	Moderately high, trapezoid (ratio height/breadth somewhat varied), 4–6 distinct denticles, two middle equal to outer or slightly larger	Massive, with 1–2 large inner denticles, strong distinct cusp *c.* 2/3 of tooth body, 2–4 distinct outer denticles	Hamate, low, 4–6 distinct outer denticles only	Hamate, low, up to 8 distinct outer denticles only, gradually diminishing toward outer laterals
Cadlina dubia Edmunds, 1981	Unicuspid elements only	78 × 21.1.21 (7 mm)	Low, trapezoid, 4 distinct denticles, two middle 1.5–2 times larger than outer ones	Massive, with single small blunt inner denticle, strong distinct cusp slightly longer than tooth body, 5 distinct outer denticles	Three following teeth massive, similar to innermost, cusp becoming shorter than tooth body, 5–6 outer denticles	Hamate, low, 5–8 distinct outer denticles only
Cadlina excavata (Pruvot-Fol, 1951)	Bifid elements	Not specified	Moderately high, trapezoid, 4 distinct denticles, those on the left side slightly larger than on the right side	Rather massive, with 4 distinct inner denticles strong distinct cusp as long as tooth body (?), at least 2 distinct outer denticles	Not specified	Hamate, low, 9 distinct outer denticles only
Cadlina flavomaculata MacFarland, 1905	Bifid and trifid, deeply divided, recurved denticles	77 × 23.1.23 (MacFarland, 1966, from La Jolla to Crescent city, exact length unknown,); 80 × 21.1.21 (Rudman, 1984, Palos Verdes Peninsula, California, 10 mm); 70 (+2) × 22.1.22 (Rudman, 1984; Monterey Bay, California,10 mm); 51–77 × 22–28.1.22–28 (Behrens, 1991, California, average length 15 mm)	Low, trapezoid, 4–6 distinct denticles, two middle equal to outer or slightly larger	Massive, with 2–3 large inner denticles, strong distinct cusp *c.* half shorter than tooth body, 4–7 distinct outer denticles	Two following teeth massive, similar to innermost, no inner denticles, 6–7 outer denticles	Hamate, low, strongly denticulated, evidently comb-shaped low, 11–12 distinct outer denticles only; 'Laterals bear 11 to 15 denticles'
Cadlina georgiensis Schrödl, 2000	No data (still in situ in dissected holotype, according to Schrödl, 2000)	53 × 17.1.17 (13 mm)	Moderately high, trapezoid, 4 distinct denticles, two middle equal to outer	Massive, with 3 large inner denticles, strong distinct cusp *c.* half shorter than tooth body, 4 distinct outer denticles	Two following teeth massive, similar to innermost, no inner denticles, 4–6 outer denticles	Hamate, low, *c.* 8 distinct outer denticles
Cadlina glabra (Friele & Hansen, 1876)	No data	70 × 40.1.40 (10 mm)	No data	No data	No data	No data
Cadlina japonica Baba, 1937	Unicuspid	63 × 50.1.50, 102 × 110–115.1.110–115, 90 × 72–80.1.72–80 (Baba, 1937; 1949); 67 × 60.1.60 (present study)				

Outer lateral teeth	Ampulla	Vaginal duct	Bursa & receptaculum semenis	Vas deferens	Ejucalotory duct spines	References
Hamate (reduced), 10–12 small not conspicuous, but sharpened denticles	Long, convoluted	Long, wide	Irregular bursa ten times larger than oval receptaculum	Long tubular prostate (*c.* 5 loops), short deferent duct	Absent (?)	Valdés, 2001
Hamate (reduced) to almost straight, 4–7 denticles	Unclear data (thin apparent hermaphroditic duct (?), no ampulla described or figured)	Relatively long and wide	Round bursa 2 – 3 times larger than oval receptaculum	Long tubular prostate (*c.* 3 loops), relatively long deferent duct	Absent (?)	Odhner, 1934; Schrödl, 2000
Hamate (reduced) to almost straight, few inconspicuous denticles	No data	No data	No data	No data	No data	Edmunds, 1981
Not specified	Relatively short slightly bent ampulla	Long, narrow vagina	Oval receptaculum; damaged bursa	Short (half-loop) vas deferens: no distinction between prostate and deferent duct	No data	Pruvot-Fol 1951, 1954
Hamate (reduced) to almost straight, elongated (?), 2–4 inconspicuous denticles	Long, narrow, convoluted	Moderate, wide	Pear-shaped bursa 2–3 times larger than similarly shaped receptaculum	Long tubular prostate (*c.* 5–6 loops), long (2–3 loops) deferent duct	Penial spines, 'bullet-shaped', about 0.004 mm. in height, with basal widths of 0.002 mm.	MacFarland, 1905, 1966; Rudman, 1984; Behrens, 1991
Hamate to almost straight, 0–10 denticles	Long, moderately narrow, slightly convoluted	Short, narrow	Round bursa 3–times larger than narrow oval receptaculum	Long tubular prostate (*c.* 2–3 loops), no distinction between prostate and deferent duct	Absent (?)	Odhner 1934; Schrödl 2000
No data	No data	No data	No data	No data	No data	Friele & Hansen 1876; Odhner 1907
						Baba 1937; Baba 1949; Nakano, 2018 Rudman 1984; Schrödl, Millen 2001; Present study

Table 3. Continued

	Jaws	Radula formula (maximal and minimal)	Central teeth	Innermost teeth	Inner lateral teeth	Mid- lateral teeth
Cadlina jannanicholsae	Unicuspid	95 × 65.1.65	Hamate, with 2–3 inner denticles and 3–4 outer denticles	Hamate, with almost reduced denticles	Hamate, with almost reduced denticles	Hamate, with almost reduced denticles
Cadlina kamchatica Korshunova, Picton, Sanamyan & Martynov in Martynov *et al.*, 2015	Bifid, denticles deeply divided, slightly recurved – almost straight denticles, rarely trifid	82 × 35.1.35	Moderately high, trapezoid, 5–6 denticles, two middle usually more distinct and larger (up to 1.5–2 times) than outer ones	Massive, with 4–6 large inner denticles, strong distinct cusp *c.* half shorter than tooth body, 5–6 distinct outer denticles	Two following teeth massive, similar to innermost, no inner denticles, 5–6 outer denticles	Hamate, low, rather comb-shaped, up to 17 distinct outer denticles only
Cadlina kerguelensis Thiele, 1912	Bifid	60 × 25.1.25		Massive, with large inner denticles, strong distinct cusp *c.* half shorter than tooth body, distinct outer denticles	Hamate, low, distinct outer denticles only	Hamate, low, rather comb-like, up to distinct outer denticles only, gradually diminishing toward outer laterals
Cadlina klasmalmbergi	Bifid to unicuspid	90 × 97.1.97 (adult) 60 × 55.1.55 (sub-adult)	High, with 3–5 distinct cusps	Hamate, 2–4 inner denticles and 3–5 outer denticles	Elongated hook-shaped, up to 7 denticles	Elongated hook-shaped, up to 7 denticles
Cadlina laevis (Linnaeus, 1767)	Bifid and trifid (rarely four denticles), deeply divided, recurved denticles,	43–70 × 22–28.1.22–28 (8–25 mm)	Moderately high, trapezoid, 6–7, more rarely 4 in adults, distinct denticles, two middle equal to outer or slightly larger, sometimes smaller adjacent between middle and outer ones	Massive, 2–3 denticles on inner edge, and 5–7 on outer edge	Two following teeth hamate, with up to 10 denticles on outer side	Elongated hook-shaped, up to 18 comb-shaped denticles
Cadlina limbaughorum Lance, 1962	Bifid, slightly curved	102 × 44.1.44 (27 mm)	Moderately high, trapezoid, 4–6 distinct denticles, two middle equal to outer	Massive, with large 3 inner denticles, strong distinct cusp *c.* half shorter than tooth body, 6 distinct outer denticles	Two following teeth massive, similar to innermost, no inner denticles, 3–5 outer denticles	Hamate, low, rather comb-like, up to 14 distinct outer denticles only, gradually diminishing toward outer laterals
Cadlina luteomarginata MacFarland, 1905	Bifid (rarely unicuspid), straight to slightly curved	90–114 × 47–58 .1.47–58 (*c.* 37 mm) (MacFarland, 1966)	Elongated, 2–4 larger denticles sometimes supplemented with 2 –4 smaller denticles	Hamate, similar to mid laterals, no distinction between cusp and tooth body, 2–4 short, not conspicuous denticles on inner side, 6–10 in outer side	Hamate, up to 14 denticles on outer side only	Hamate, gradually diminishing denticles on outer side only
Cadlina magellanica Odhner, 1926	Bifid to trifid, slightly curved to straight, moderately divided	58 × 21–27.1.27–1 (6 mm) (Odhner, 1926); 58 × 15.1.15 (9 mm) (Schrödl, 2000); 60 × 23.1.23 (Odhner, 1926, *C. falklandica*, 8 mm);	Moderately high, trapezoid, 4–5 denticles, two middle equal or slightly larger than outer ones	Massive, with large 3 inner denticles, strong distinct cusp *c.* half shorter than tooth body, 4 distinct outer denticles	Hamate, somewhat similar to innermost, no inner denticles, 3–6 outer denticles	Hamate, low, rather comb-like, up to 15 distinct outer denticles only, gradually diminishing toward outer laterals

Outer lateral teeth	Ampulla	Vaginal duct	Bursa & receptaculum semenis	Vas deferens	Ejucalotory duct spines	References
Hamate, with almost reduced denticles	Moderately wide, convoluted,	Moderatly long, narrow	Pear-shaped bursa, at least two times larger than receptaculum seminis	Long tubular prostate (*c.* 3–4 loops), relatively short (1–2 loops) deferent duct	Absent (needs to be confirmed)	Present study
Hamate (reduced), elongated with pointed slightly curved apex, up to 19 sharp denticles	Long, narrow, convoluted	Long, narrow	Round to pear-shaped bursa 1.5–2 times larger than elongate oval receptaculum	Long tubular prostate (*c.* 2–3 loops), relatively short (1–2 loops) deferent duct	Elongate spines	Martynov *et al.*, 2015b; Present study
Hamate (reduced) to almost straight, denticles	Unknown	Long, moderate in width	Bursa is in form of spherical swelling similar in size to round receptaculum	Moderate tubular prostate (*c.* 2 loops), no distinction between prostate and deferent duct	Absent (?)	Thiele, 1912; Schrödl, 2000
Elongated hook-shaped, up to 7 denticles	Long, strongly convoluted	Relatively long, narrow	Triangular bursa similar in size to receptaculum	Relatively long tubular prostate (*c.* 2–3 loops), deferent duct short	Absent (needs to be confirmed)	Present study
Elongated hook-shaped, up to 18 comb-shaped denticles	Long, strongly convoluted	Relatively long and wide	Oval bursa 2 –3 times larger than oval to pear-shaped receptaculum	Relatively long tubular prostate (*c.* 2–3 loops), deferent duct short relatively long and thin (2 –3 loops)	Conical with a relatively narrow base	Alder & Hancock, 1845 – 1855; Bergh, 1879a, b; Odhner, 1907; Thompson & Brown, 1984; Rudman, 1984; Roginskaya, 1987; Present study
Hamate (reduced) to almost straight, denticles	Unknown	Unknown	Unknown	Unknown	Unknown	Lance, 1962; Behrens, 1991
Hamate (reduced) to almost straight, short, broad 3–6 small not conspicuous, but sharpened denticles	Long, narrow, 3–4 loops	Moderate, narrow	Oval bursa 2– times larger than oval receptaculum	Long tubular prostate, short deferent duct	'Minute hooks'	MacFarland, 1905, 1906, 1966; Behrens, 1991; Rudman, 1984
Hamate (reduced) to almost straight, short, broad 5–8 small not conspicuous, but sharpened denticles	Moderate, convoluted to two loops	Moderate, distally widened	Oval bursa 1.5 –4 times larger than oval receptaculum	Long tubular prostate (2–3 loops), long (2–3 loops) narrow deferent duct	Elongate conical spines	Odhner, 1926; Schrödl, 2000

Table 3. Continued

	Jaws	Radula formula (maximal and minimal)	Central teeth	Innermost teeth	Inner lateral teeth	Mid- lateral teeth
Cadlina modesta MacFarland, 1966	Bifid, slightly curved to rather straight, moderately divided	70 × 21.1.21 (length unknown) 94 × 24.1.24 (24 mm) (MacFarland, 1966); 106 (+4) × 39.1.39 (28 mm) (Rudman, 1984) 43–94 × 21–28.1.28 –21 (up to 33 mm) (Behrens, 1991)	Rather low, trapezoid, 4 denticles, two middle equal or considerably larger than outer ones	Massive, somewhat similar in shape to rachidians, with 2 – 4 inner denticles, strong distinct cusp *c.* half to 2/3 to tooth body, 4–5 distinct outer denticles	Two following teeth massive, similar to innermost, 1 inner denticle, 4–5 outer denticles	Hamate, low, rather comb-like, up to 15 distinct outer denticles only, gradually diminishing toward outer laterals
Cadlina nigrobranchiata Rudman, 1985	Unicuspid, rarely bicuspid,slightly curved to straight	87 (+4) × 48.1.48 (25 mm)	Rather high elongate, 2 –4 denticles, two middle larger than outer ones	Not massive, rather hamate, more similar to mid laterals, cusp only *c.* 1/3 of tooth body, 2–4 distinct denticles on inner side, 3–4 on outer side	Hamate, somewhat similar to innermost, no inner denticles, 5–6 outer denticles	Hamate, high, ‘cryptobranch-like’, up to 14 small outer denticles only, towards outer teeth became less conspicuous, sometimes almost smooth (*c.* 1–2 barely visible denticles)
Cadlina pacifica Bergh, 1879	Bifid, recurved	85 × 33.1.33 (28 mm) 73 × 30.1.30 (14 mm)	Low to moderately high, trapezoid, 6–8 denticles, two middle equal or slightly larger than outer ones	Massive, with large 5–6 inner denticles, strong distinct cusp *c.* half to 1/3 of tooth body, 6–7 distinct outer denticles	Two following teeth massive, similar to innermost, no inner denticles, 6 outer denticles	Hamate, low, rather comb-like, up to 22 distinct outer denticles only, gradually diminishing toward outer laterals
Cadlina paninae	Bifid	90 × 38.1.38	Low rectangular, 3–5 distinct cusps, often bifurcated at tips	Massive, 2–3 inner denticles and 3–4 outer denticles	Two following teeth massive, similar to innermost, no inner denticles, up to 4 outer denticles	Elongate hook-shaped, up to 20 comb-shaped denticles
Cadlina pellucida (Risso, 1826)	Bifid, recurved; mace-shaped elements (Eliot 1906)	? × 22.1.22 (10 mm, *Cadlina clarae*, Ihering 1880) 70 × 23.1.23 (4.5 mm Eliot 1906, 1910)	Moderately high, trapezoid, serrated inconspicuous denticles (Ihering 1880); Four distinct denticles, middle slightly longer that outer ones (Eliot 1906)	Massive, with 2 inner distinct denticles, strong distinct cusp *c.* 1/3 of tooth body, 3 distinct outer denticles	Two following teeth massive, similar to innermost, both have 1–2 inner denticles, 3–4 outer denticles	Massive to hamate, some rather comb-like, 2–8 outer denticles
Cadlina rumia Marcus, 1955	Bifid and trifid, slightly curved to rather straight, moderately divided	50–77 × 12–5.12–25	Moderately high, trapezoid, 6–8 distinct denticles, two middle equal to outer or slightly larger	Massive, with large 1–3 inner denticles, strong distinct cusp *c.* half of tooth body, 4–6 distinct outer denticles	Two following teeth massive, similar to innermost, no inner denticles, 5–6 outer denticles	Hamate, low, rather comb-like, up to 6 distinct outer denticles only, gradually diminishing toward outer laterals
Cadlina scabriuscula (Bergh, 1890)	Bifid, slightly curved to rather straight, moderately divided	108 × 30.1.30	Moderately high, trapezoid, *c.* 6 distinct denticles, two middle equal to outer or slightly larger	Massive, with large 4 – 5 inner denticles, strong distinct cusp of unknown ratio to tooth body, 8–10 distinct outer denticles	Two following teeth massive, similar to innermost, no inner denticles, 5–6 outer denticles	Hamate, low, rather comb-like, 3 –5 distinct outer denticles only, gradually diminishing toward outer laterals

Outer lateral teeth	Ampulla	Vaginal duct	Bursa & receptaculum semenis	Vas deferens	Ejucalotory duct spines	References
Hamate (reduced) to almost straight, short, broad 0–10 small denticles	Moderate, narrow, *c.* 2 loops	Moderate, distally widened	Oval bursa 2–3 times larger than oval receptaculum	Moderate, broad tubular prostate (2–3 loops), long (ca 5 loops) narrow deferent duct	Broad conical spines	MacFarland, 1966; Rudman, 1984; Bertsch, 1969; Behrens, 1991
Hamate to reduced hamate, short, broad 4–6 small denticles	Moderate, bent	Moderate, widened	Rounded bursa 1.5–2 times shorter than elongate receptaculum	Long tubular prostate (3–4 loops), short narrow deferent duct	Unknown	Rudman, 1985
Hamate (reduced) to almost straight, 0–11 denticles	Long, narrow , bending	Unknown	Rounded bursa *c.* 2 times larger than rounded receptaculum	Long tubular prostate, short narrow deferent duct	Conical elongated spines	Bergh, 1879a, b
Elongate hook-shaped, up to 20 comb-shaped denticles	Relatively short, widened, slightly convoluted	Long, narrow	Oval bursa *c.* 1.5 times larger than similar in shape receptaculum	Relatively short tubular prostate (*c.* 1.5 loops), long (2–3 loops) narrow deferent duct	Conical spines with widened base	Present study
No data	No data	No data	No data	No data	No armature (Ihering 1880); 'No armature found on verge' (Eliot 1910); Conical, elongate spines, sometimes even bifid (?) (Pruvot-Fol 1954)	Risso 1826; Ihering 1880; Eliot 1906; Eliot 1910; Pruvot-Fol 1936a, b; 1954; Marcus 1958; Bouchet & Tardy 1976; Ortea & Urgorri 1981; Cattaneo-Vietti 1986; Ortea 1988; García-Gomez *et al* 1989; Calado *et al.* 1999; Calado *et al.* 2005; Cervera *et al.* 2004; Trainito 2005
Hamate (reduced) to almost straight, 0–5 denticles	Long, convoluted	Long	Oval bursa *c.* 2 times larger than rounded receptaculum	Long tubular prostate (*c.* four loops), long (*c.* four loops) narrow deferent duct	Present	Marcus, 1955; Marcus & Marcus, 1967; Bertsch, 1975; Rudman, 1984; Valdes *et al.*, 2006; Domínguez *et al.*, 2006; García *et al.*, 2008
Hamate (reduced) to almost straight, *c.* 3 denticles	Convoluted	Long	Pear-shaped bursa, sausage-shaped smaller receptaculum	Long vas deferens, prostatic part shorter (?)	Uncertain	Bergh, 1890; Marcus & Marcus, 1967

Table 3. Continued

	Jaws	Radula formula (maximal and minimal)	Central teeth	Innermost teeth	Inner lateral teeth	Mid- lateral teeth
Cadlina sparsa (Odhner, 1921)	Bifid	54 (+2) × 20.1.20 (Odhner, 1921) 37–69 × 24–28.1.28–24 (Marcus, 1959, 1961; Behrens & Hermosillo, 2005)	Relatively low, trapezoid, *c.* 5 cusps	Massive, with 1–3 inner denticle, and 3–5 outer denticles	Two following teeth massive, similar to innermost, no inner denticles, 4–5 outer denticles	Hamate to almost straight, up to 15 denticles
Cadlina sylvia earleae	Bifid	92 × 45.1.45	Relatively low, bears 3–4 distinct cusps	Massive, 2–3 inner denticles and 4–5 inner denticles	Two following teeth hamate, no inner denticles, up to six outer denticles	Hamate to almost straight, up to 14 denticles
Cadlina tasmanica Rudman, 1990	Bifid to strongly asymmetrical, almost unicuspid	108 × 17.1.17	Low, trapezoid, no distinct denticles, rather serrated edge with numerous fine hardly distinguished denticles	Massive, with large 4 – inner denticles, strong distinct but short cusp of *c.* 1/3 to tooth body, 7 distinct outer denticles	Four following teeth massive, similar to innermost, 4 inner denticles, 7 outer denticles	Hamate to almost straight, bifid
Cadlina umiushi Korshunova *et al.* in Martynov *et al.*, 2015	Bifid, denticles deeply divided, strongly recurved denticles, rarely trifid	70 × 30.1.30 (*c.* 10 mm); 100 × 36.1.36 (20 mm)	Moderately high, trapezoid, 6 (rarely 5) distinct denticles, two middle equal to outer or slightly larger	Massive, with 2–3 large inner denticles, strong distinct cusp *c.* half shorter than tooth body, 4–6 distinct outer denticles	Two following teeth massive, similar to innermost, no inner denticles, 3–5 outer denticles	Hamate, low, rather comb-shaped, 8–15 distinct outer denticles (rarely up to 20–30)
Cadlina willani Miller, 1980	Bifid or unicuspid	88 × 26.1.26	Low, trapezoid, up to 6 cusps, all similar in size	Massive, with *c.* 2 large inner denticles, strong distinct cusp, *c.* 3 distinct outer denticles	Up to six following inner laterals	Hamate, low, rather comb-shaped, up to 11

Outer lateral teeth	Ampulla	Vaginal duct	Bursa & receptaculum semenis	Vas deferens	Ejucalotory duct spines	References
Almost straight, up to 25 denticles	-	-	-	Tubular prostate	‘Hooks’	Berhrens & Hemosillo, 2005; Odhner, 1921; Marcus, 1959, 1961
Almost straight, up to 14 denticles	Narrow, convoluted	Relatively broad	Pear-shaped bursa, oval receptaculum smaller *c.* 1.5	Relatively short tubular prostate (*c.* 2 loops), short (1–1.5 loops) wide deferent duct	Spines with distinctly broad base	Present study
Hamate (reduced) to almost straight, *c.* 5 denticles	No data	No data	No data	No data	No data	Rudman, 1990, 2010
Hamate to almost straight, elongated (?), 8–11 inconspicuous denticles	Long, narrow, convoluted	Moderate, relatively narrow	Round to pear-shaped bursa 1.5–2 times larger than similarly shaped receptaculum	Long tubular prostate (*c.* 2–4 loops), long (4–5 loops) deferent duct	Conical spines	Martynov *et al.*, 2015b, Present study
Hamate to almost straight, *c.* 6 distinct denticles	Relatively long, thickened, at least three compartments	Moderate, relatively narrow	Oval bursa *c.* 1.5 times larger than similarly shaped receptaculum	Long tubular prostate (*c.* 3 loops), relatively short (2–3 loops) deferent duct	Spines slightly bent and sometimes constricted close to base	Miller, 1980

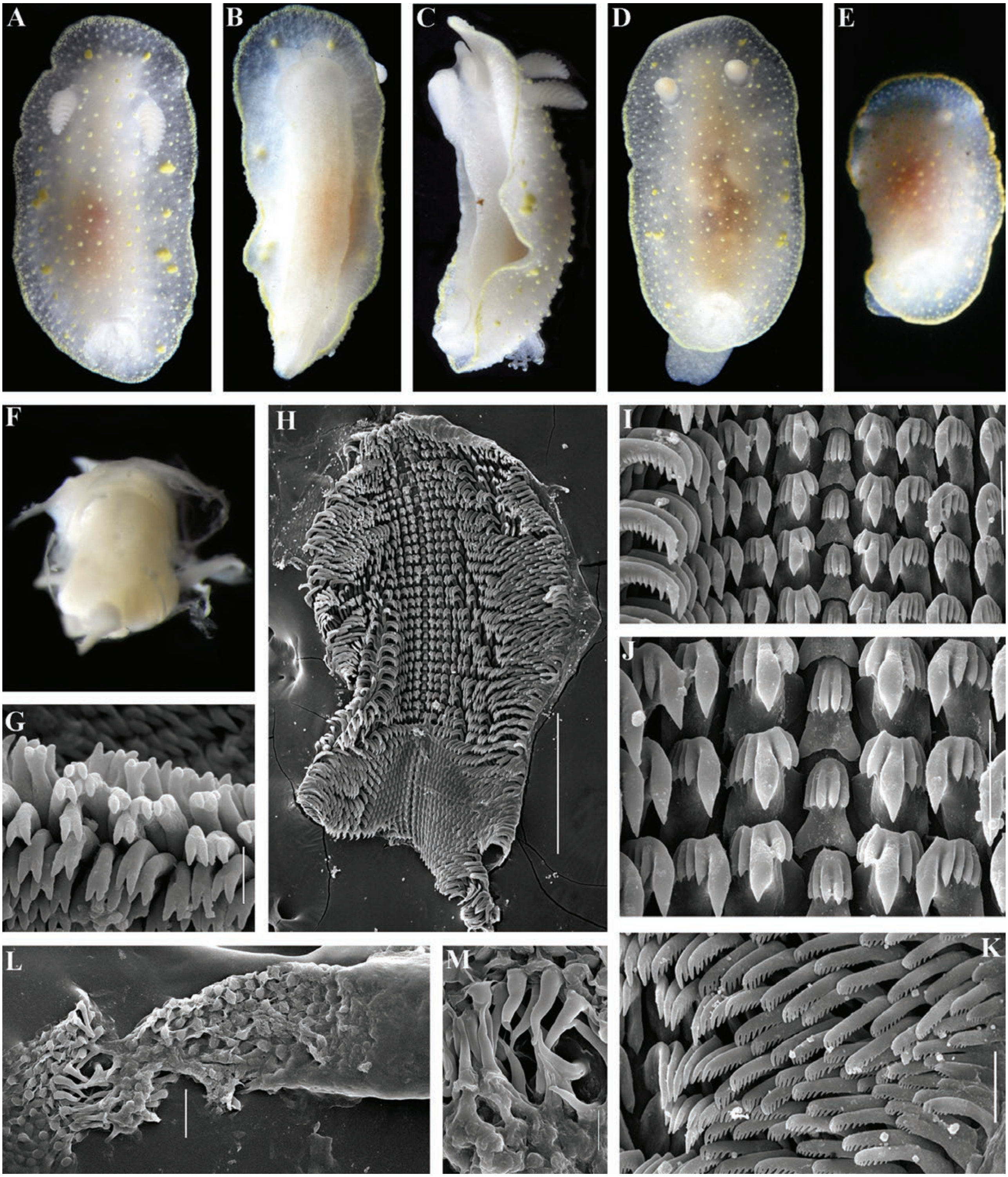

Figure 7. *Cadlina umiushi*, the Sea of Japan, external and internal features. A–C, holotype ZMMU Op-445, 10 mm, dorsal, ventral and lateral views, respectively. D, paratype ZMMU Op-455, 8 mm, dorsal view. E, paratype ZMMU Op-458, 10 mm, dorsal view. F–K, internal features (ZMMU Op-455): F, buccal bulb, LM. G, elements of labial cuticle, SEM (and following images). H, complete radula. I, central part of radula. J, enlarged central part of radula to show central teeth and first lateral teeth. K, outer lateral teeth. L, M, penial spines. Scale bars: G, M, 10 µm; H, 300 µm; I, J, K, L, 30 µm. Photos: Tatiana Korshunova and Alexander Martynov.

duct emerges some distance from female gland mass (Fig. 15B, ud). Prostatic part of vas deferens long, narrow and not distinct (Fig. 15B, pr). Prostate transits to long, narrow vas deferens with several loops (Fig. 15B, vd), which slightly widens towards penial sheath that encloses evertable ejaculatory duct. Penial spines conical (Fig. 7L, M). Vagina narrow (Fig. 15B, v) entering relatively large, rounded to pear-shaped bursa copulatrix (Fig. 15B, b). Uterine duct short and narrow (Fig. 15B, ud); it begins from female gland mass and then enters near base of rounded to slightly oval receptaculum seminis (Fig. 15B, rs).

Habitat

On stony and rocky substrates, intertidal – 20 m.

Distribution

Sea of Japan, particularly in its northern part (Fig. 2).

Remarks

Morphologically, *C. umiushi* partly overlaps with a rare variant of *C. laevis* that has a weak yellow notal border, but clearly differs from the latter species, because this yellow line is always present in *C. umiushi* specimens and is much more distinct. *Cadlina umiushi* is also robustly supported as distinct from the *C. laevis* clade, according to our molecular analysis (Fig. 2). Maximum intragroup distances in *C. umiushi* (including data for C. *olgae*) are 0.34% for the *COI* marker and 1.18% for the 16S marker. The lowest *COI* intergroup distance of 3.9% is found between *C. umiushi* and *C. laevis*. The lowest 16S intergroup distance of 1.41% is found between *C. umiushi* and *C. kamchatica* (Tables 1, 2). Chichvarkhin (2016) published *Cadlina olgae* from the Sea of Japan with similar morphology to *C. umiushi*. The molecular results of the present analsysis revealed that *C. umiushi* and *C. olgae* are the same species. Genetic distances in *C. umiushi* are 0% and in *C. olgae* are 0% for the *COI* marker. The maximum distance between *C. umiushi* and *C. olgae* is 0.34% for the *COI* marker. Genetic distances in *C. umiushi* are 0.24% and in *C. olgae* range from 0.00–0.24% for the 16S marker. The maximum distance between *C. umiushi* and *C.* ‘*olgae*’ is 1.18% for the 16S marker. Results of phylogenetic and ABGD analyses confirm that *Cadlina umiushi* and *C. olgae* are the same species. The morphological description of *C. olgae* Chichvarkhin, 2016 raises many questions. Specifically, the size of *C. olgae* is confusing: ‘lengths to 25 mm (14 mm in holotype, 11 mm in paratype) in fully extended living specimens’. Furthermore, the description of the radula of *C. olgae* in Chichvarkhin (2016: 12) does not corresponded with those provided in the associated figure (Chichvarkhin, 2016: fig. 4) as the lateral teeth in the middle and outer parts have a distinctly different shape and different number of denticles. The original description of *C. olgae* stated: ‘First lateral teeth with bigger central denticle and four smaller denticles on both sides. The other lateral teeth are similar, with 4–5 outer denticles’ (Chichvarkhin, 2016: 12). However, the differences in the shapes of the lateral teeth are clear, and the number of denticles on the outer lateral teeth is higher than five (Chichvarkhin, 2016: fig. 4). Martynov discovered a species of *Cadlina* in the northern part of the Sea of Japan (from the same area as *C. olgae*) and a detailed morphological description was presented in his dissertation (Martynov, 1999b). This species was ultimately described as *Cadlina umiushi* Korshunova *et al*., 2015. Thus, in the absence of any taxonomically reliable differences, *C. umiushi* and *C. olgae* refer to the same species and *C. olgae* is here regarded as a junior synonym.

CADLINA KAMCHATICA KORSHUNOVA *ET AL.* IN MARTYNOV *ET AL.*, 2015

(FIGS 2, 8, 15C)

Cadlina kamchatica Korshunova *et al*. in Martynov *et al*., 2015b: 63–65, fig. 1.

Holotype: ZMMU Op-446, *L* = 25 mm (preserved, 37 mm alive), north-west Pacific, Russia, Kamchatka, Avachinskiy Bay, Laperousa stones, 10–15 m, large boulders and rocky substrate, 3 August 2008, coll. T. A. Korshunova, A. V. Martynov.

Paratypes: ZMMU Op-452, two spcs., one dissected, *L* = 19 mm and 25 mm (preserved), north-west Pacific, Kamchatka, Avachinskiy Bay, Starichkov Id., 6–7 m, large boulders and rocky substrate, 25 July 2008, coll. T. A. Korshunova, A. V. Martynov. ZMMU Op-453, one spc., *L* = 20 mm (preserved), same locality and date as previous. ZMMU Op-454, one spc., *L* = 27 mm (preserved), north-west Pacific, Kamchatka, Avachinskiy Bay, Starichkov Id., 10–15 m, large boulders and rocky substrate, 19 August 2008, coll. T. A. Korshunova, A. V. Martynov.

External morphology

Notum broad, rounded in front and posteriorly. Rhinophores long and retracted into raised soft sheaths with small tubercles on the rims (Fig. 8A, D). Approximately 15 rhinophoral lamellae. Notum covered with distinct low to slightly raised tubercles (Fig. 8D). Spicules form sparse network in notum. Approximately ten multipinnate gills united by common membrane into circle around anus. Gills

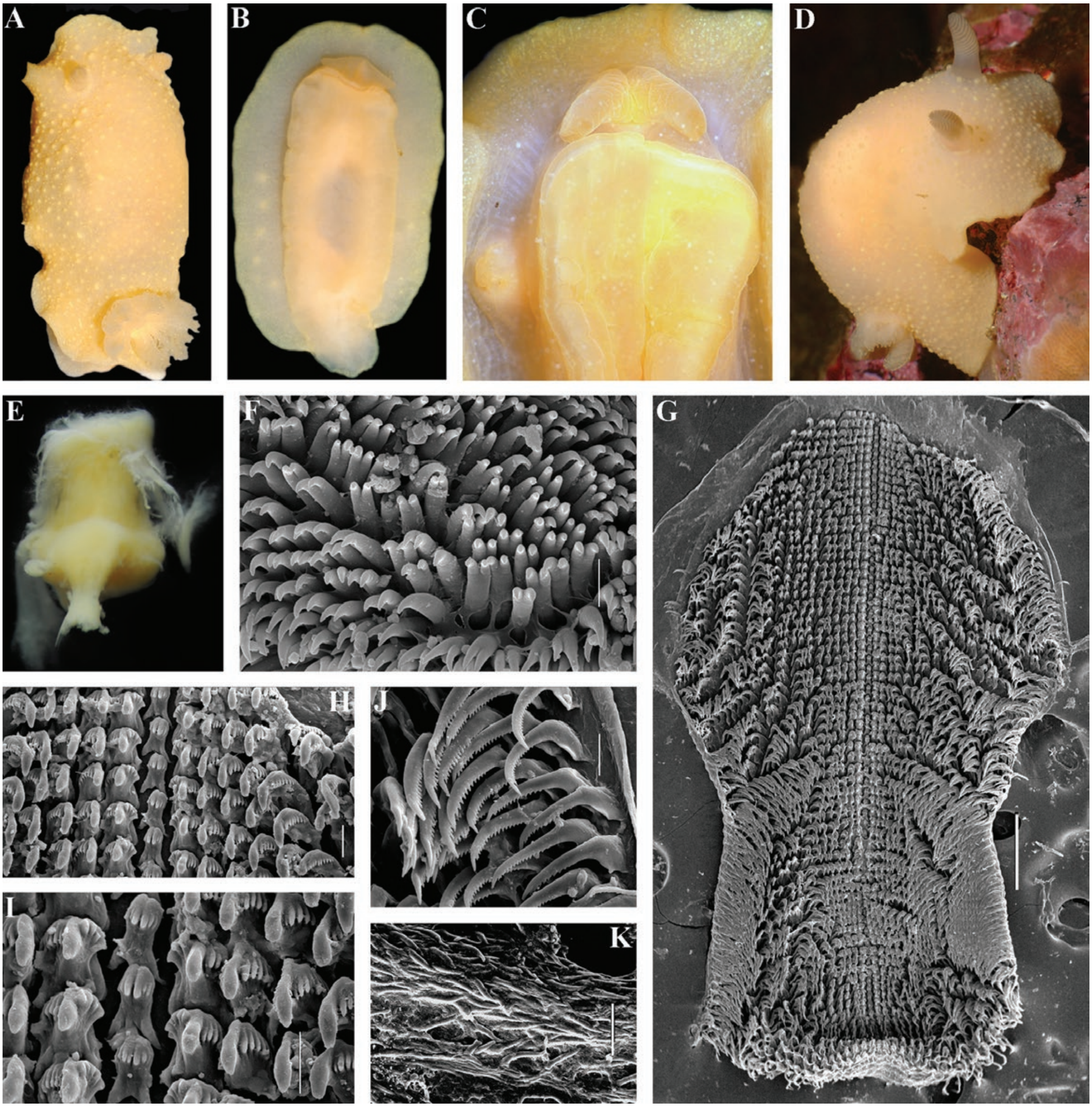

Figure 8. *Cadlina kamchatica*, Kamchatka, external and internal features. A–C, holotype ZMMU Op-446, 37 mm, dorsal, ventral and enlarged oral views, respectively. D, paratype ZMMU Op-452, 25 mm, lateral view. E–K, internal features (ZMMU Op-452): E, buccal bulb, LM. F, elements of labial cuticle, SEM (and following images). G, complete radula. H, central part of radula. I, enlarged central part of radula to show central teeth and first lateral teeth. J, outer lateral teeth. K, penial spines. Scale bars: F, 10 μm; K, 20 μm; G, 300 μm; H, I, J, 30 μm. Photos: Tatiana Korshunova and Alexander Martynov.

retractable into common gill cavity. Border of gill cavity moderately raised with slightly tuberculated rim (Fig. 8D). Oral veil forms relatively large, triangular, lateral sides, with no evidence of notches (Fig. 8B, C). Foot broad, anteriorly rounded and slightly thickened to form a double edge; it appears as entire (Fig. 8B) or somewhat notched in the middle (Fig. 8C); posteriorly it sometimes projects slightly from notum in crawling animals, forming a rounded tail.

Colour

Living specimens opaque dark yellowish to light brownish (Fig. 8). Rhinophores similar to background colour. Gills semitransparent, similar to background colour. Digestive gland almost visible through notum dorsally (Fig. 8A) and shines more clearly through foot ventrally (Fig. 8B). Subepidermal glands not visible through dorsal side of notum (Fig. 8A), partly shine through near lateral edges of notum on ventral side (Fig. 8B). No thin yellow line around notum.

Buccal bulb and oral tube

Buccal bulb relatively short, similar in length to oral tube (Fig. 8E). Salivary glands relatively long and narrow (Fig. 8E).

Jaws

Rounded labial disk covered by yellowish to brownish cuticle bearing rod-shaped labial elements commonly with double hook-shaped tips (Fig. 8F).

Radula

Radular formula 82 × 35.1.35 (Op-452, 25 mm). Central tooth moderately high, bears five to six cusps (Fig. 8H, I). Inner lateral teeth with five or six denticles on outer edge, and four to six on inner edge (Fig. 8H, I). Middle and outer teeth comb-shaped, bearing up to 19 denticles (Fig. 8J).

Reproductive system

Ampulla comprised of at least five thickened compartments (Fig. 15C, a). Ampulla bifurcates into moderately long vas deferens and oviduct. Uterine duct emerges some distance from female gland mass (Fig. 15C, ud). Prostatic part of vas deferens long, narrow and not distinct (Fig. 15C, pr). Prostate transits to long, narrow vas deferens (Fig. 15C, vd), which considerably widens towards penial sheath that encloses evertable ejaculatory duct (Fig. 15C, psh). Penial spines elongated (Fig. 8K). Vagina narrow (Fig. 15C, v) and enters medium-sized rounded bursa copulatrix (Fig. 15C, b). Uterine duct short and narrow (Fig. 15C, ud); it begins from female gland mass and then enters near base of relatively large pear-shaped receptaculum seminis (Fig. 15C, rs).

Habitat

Inhabits shallow waters with rocky and stony substrates at depths *c.* 6–15 m.

Distribution

Currently it is only known from the Pacific side of Kamchatka (Fig. 2). Potential distribution includes the Commander Islands and the most northern Kurile Islands (e.g. Paramushir Island).

Remarks

Cadlina kamchatica shows external and internal differences from *C. laevis* (including dark-yellow to brownish coloration, larger number of rows in radula and differently shaped penial spines; see Figs 2–6 and Table 3 for comparison). These morphological characters are robustly supported by the molecular data (Fig. 2). Among *C. laevis* sometimes brownish morphs can occur (Fig. 3F, see above). However, these still have a smaller number of radular teeth just like the more common white *C. laevis* specimens. The constancy of the dark-yellow coloration in *C. kamchatica* needs to be further investigated, because at least in some subadult specimens a more whitish ground is observed. From *C. paninae*, which is geographically closest to *C. kamchatica*, the former differs in having a predominantly white ground colour, different radula and penial spines (see below and compare Figs 8 and 9).

Maximum intragroup distances within *C. kamchatica* are 0.17% for the *COI* marker and 0.24% for the 16S marker. The lowest *COI* intergroup distance of 4.21% is found between *C. kamchatica* and *C. laevis*. The lowest 16S intergroup distance of 0.71% is found between *C. kamchatica* and *C. paninae* (Tables 1, 2).

CADLINA PANINAE KORSHUNOVA *ET AL.*, **SP. NOV.**

(FIGS 2, 9, 15D)

Holotype: ZMMU Op-683, *L* = 18 mm (preserved), north-west Pacific, Russia, Kurile Islands, Matua Island, Cape Klyuv, stones and rocky substrate, 14 m depth, 19 August 2017, coll. N. P. Sanamyan.
LSID:urn:lsid:zoobank.org:act:AA1F30F1-1B14-46E0-86C6-F78E254B9402

Paratypes: ZMMU Op-684, one spc., *L* = 29 mm (preserved), north-west Pacific, Kurile Islands, Matua Island, Cape Krokodil, stones and rocky substrate, 11 m depth, 19 August 2016, coll. N. P. Sanamyan.

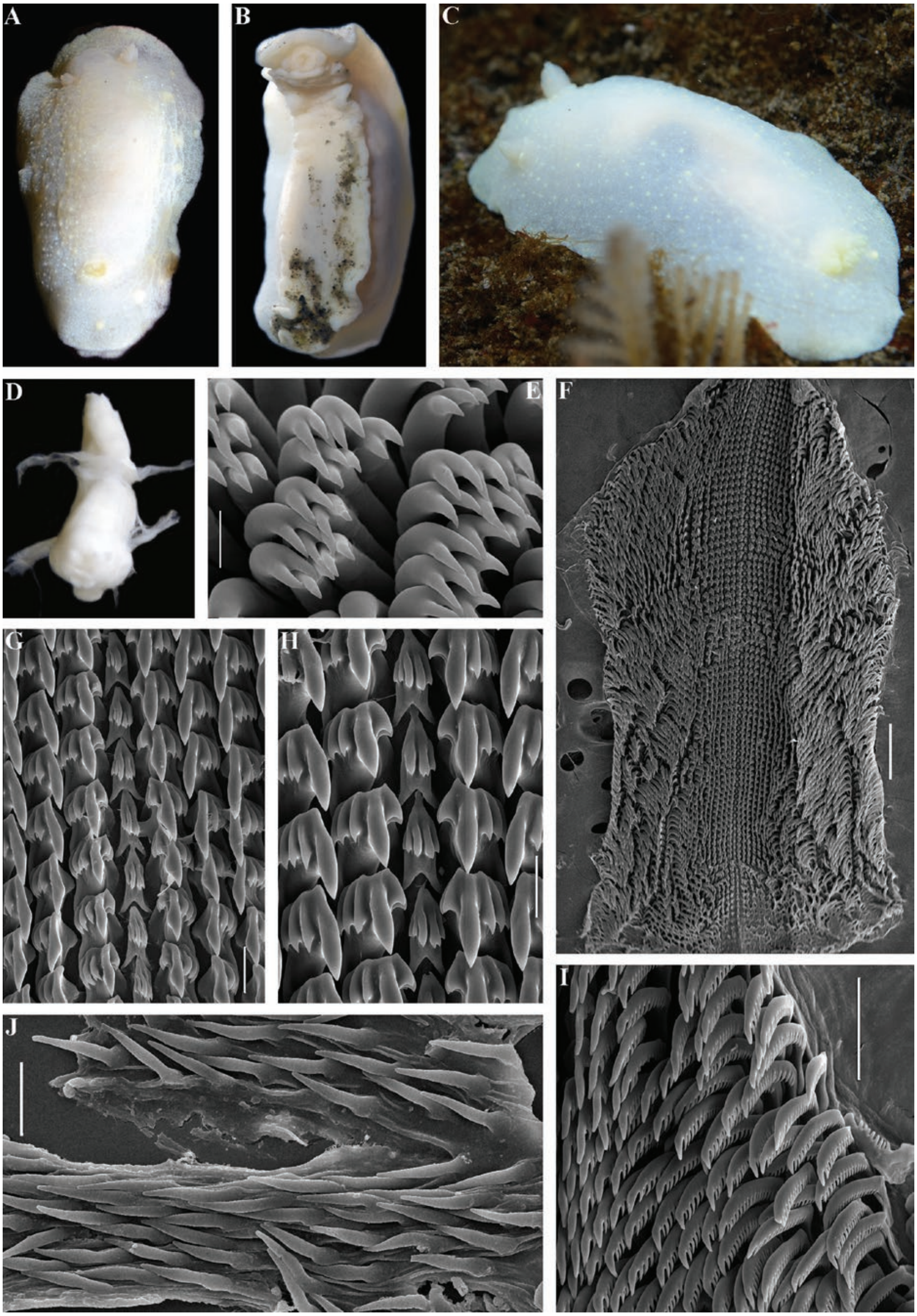

Figure 9. *Cadlina paninae*, external and internal features. A, B, holotype ZMMU Op-683, 18 mm, Kurile Islands, dorsal and ventral views, respectively. C, paratype ZMMU Op-685, 20 mm, lateral view. D–I, internal features (ZMMU Op-685): D, buccal bulb, LM. E, elements of labial cuticle, SEM (and following images). F, complete radula. G, central part of radula. H, enlarged central part of radula to show central teeth and first lateral teeth. I, outer lateral teeth. J, penial spines. Scale bars: E, 10 μm; J, 20 μm; G, H, 30 μm; F, 100 μm; I, 100 μm. Photos: Nadezhda Sanamyan.

ZMMU Op-685, one spc., L = 20 mm (preserved), north-west Pacific, Kurile Islands, Matua Island, Cape Klyuv, stones and rocky substrate, 14 m depth, 4 August 2017, coll. N. P. Sanamyan.

Etymology

Named for Elena Panina, biologist from Petropavlovsk-Kamchatsky, who considerably helped in the collection of marine invertebrates during expeditions to the Kurile Islands.

External morphology

Notum broad, rounded in front and posteriorly. Rhinophores long and retracted into raised sheaths, bearing indistinct tubercles (Fig. 9C). Approximately 15–18 rhinophoral lamellae. Notum covered with low indistinct tubercles (Fig. 9A, C). Spicules form sparse network in notum. Approximately six to seven multipinnate gills united by a common membrane into circle around anus. Gills retractable into common gill cavity (Fig. 9A). Border of gill cavity moderately raised (Fig. 9A, C). Oral veil with short triangular lobes with oblique notched lateral sides (Fig. 9B). Foot broad, anteriorly rounded and slightly thickened to form double edge; it appears as entire (Fig. 9B); posteriorly it sometimes projects slightly from notum in crawling animals, forming a rounded tail.

Colour

Living specimens opaque whitish, sometimes with yellowish cast (Fig. 9A, C). Rhinophores similar to ground colour. Gills semitransparent white, similar to ground colour. Digestive gland barely visible through the notum dorsally (Fig. 9A, C). Subepidermal glands shine near lateral edges of notum through dorsal side. No yellow line around notum.

Buccal bulb and oral tube

Buccal bulb longer than oral tube (Fig. 9D). Salivary glands relatively long and narrow.

Jaws

Rounded labial disk covered by yellowish to brownish cuticle bearing rod-shaped labial elements with double hook-shaped tips (Fig. 9E).

Radula

Radular formula approximately 90 × 38.1.38 (Op-684). Radular teeth slightly yellowish. Central tooth rectangular and bears three to five distinct cusps, often bifurcated at tips (Fig. 9G, H). Inner lateral tooth massive with wide base and short, strong, slightly curved cusp and three or four outer denticles and two or three inner denticles (Fig. 9G, H). Outer lateral teeth are elongated and hook-shaped, bearing 15–20 comb-shaped denticles (Fig. 9I).

Reproductive system

Ampulla comprised of at least three thickened compartments (Fig. 15D, a). Ampulla bifurcates into moderately long vas deferens and oviduct. Uterine duct emerges some distance from female gland mass (Fig. 15D, ud). Prostatic part of vas deferens relatvely short, narrow and not distinct (Fig. 15D, pr). Prostate transits to long, narrow vas deferens (Fig. 15D, vd) that considerably widens toward the penial sheath that encloses evertable ejaculatory duct (Fig. 15D, psh). Penial spines conical with widened base (Fig. 9J). Vagina narrow (Fig. 15D, v), and enters medium-sized oval, compressed bursa copulatrix (Fig. 15D, b). Uterine duct short and narrow (Fig.15D ud); it begins from female gland mass and then enters near base of medium-sized oval receptaculum seminis (Fig. 15D, rs).

Habitat

Inhabits shallow waters with rocky and stony substrates at depth *c.* 11–14 m.

Distribution

Currently it is known from the Middle Kurile Islands (Matua Island) (Fig. 2). Potential distribution includes at least other Middle Kurile Islands and adjacent parts of the Okhotsk Sea and Pacific Ocean.

Remarks

Cadlina paninae is the sister species to *C. kamchatica* according to the present phylogenetic analysis (Fig. 2). Morphologically *C. paninae* differs from *C. kamchatica* in predominantly whitish and not yellowish coloration, higher number of radular rows, shape of the ampulla, seminal reservoirs and penial spines. Morphological intraspecific variation in *C. paninae* needs further investigation. See also Table 3 for a detailed morphological comparison with other species of *Cadlina*. No intragroup divergence was observed for *COI* and 16S sequences of *C. paninae*. The lowest *COI* intergroup distance of 4.24% is found between *C. paninae* and *C. laevis*. The lowest 16S intergroup distance of 0.71% is found between *C. paninae* and *C. kamchatica* (Tables 1, 2).

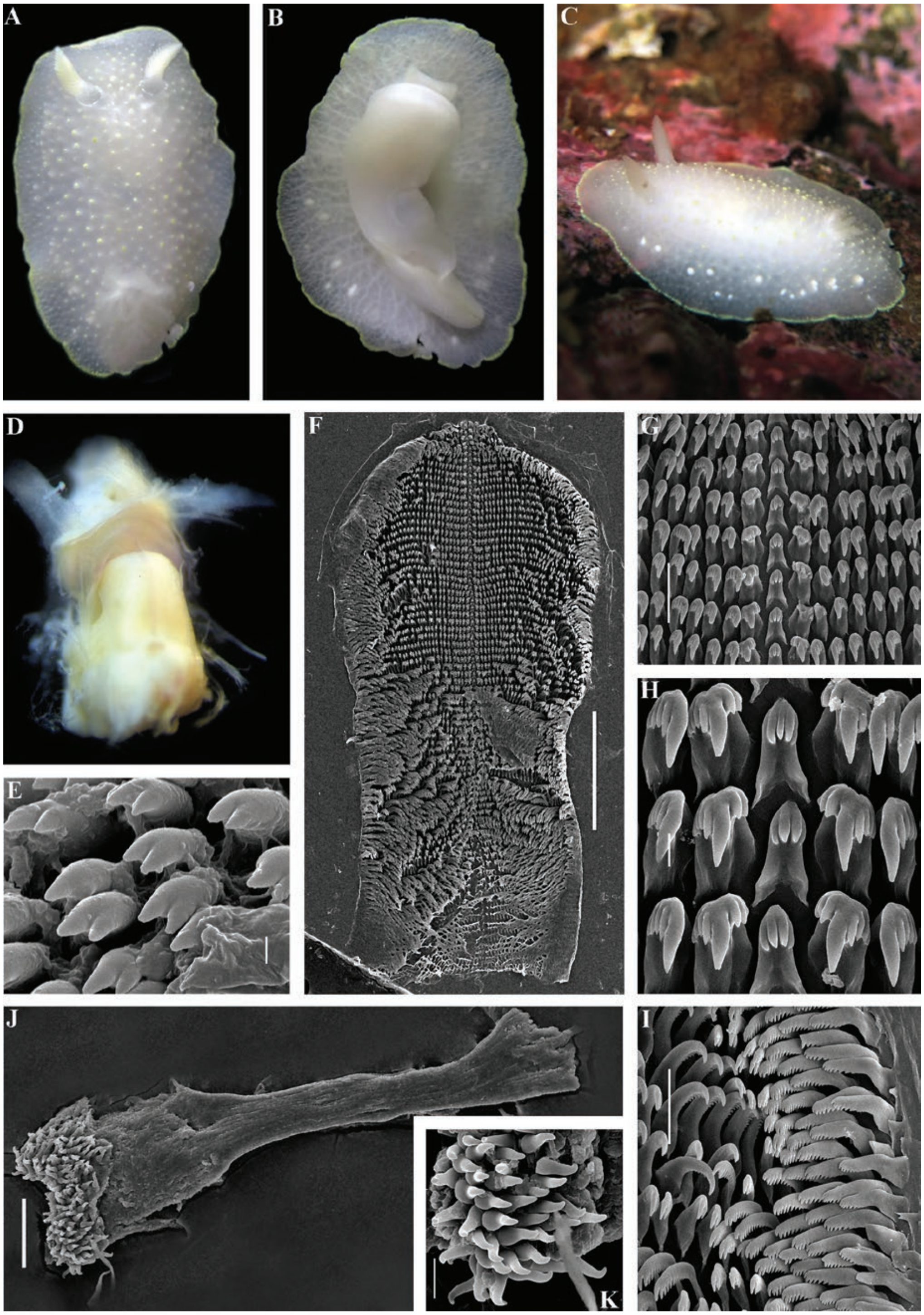

Figure 10. *Cadlina sylviaearleae*, Washington State, external and internal features. A–C, holotype ZMMU Op-686, 25 mm, dorsal, ventral and lateral views, respectively. D–K, internal features (ZMMU Op-686): D, buccal bulb, LM. E, elements of labial cuticle, SEM (and following images). F, complete radula. G, central part of radula. H, enlarged central part of radula to show central teeth and first lateral teeth. I, outer lateral teeth. J, K, penial spines. Scale bars: E, 2 μm; F, 500 μm; G, I, J, 20 μm. Photos: Karin Fletcher. SEM Photos Alexander Martynov.

CADLINA SYLVIAEARLEAE KORSHUNOVA *ET AL.*, SP. NOV.

(FIGS 2, 10, 15E)

Cadlina luteomarginata auct. non MacFarland, 1966.
Holotype: ZMMU Op-686, *L* = 25 mm (live), dissected, north-eastern Pacific, USA, Washington State, Salish Sea, Rich Passage, Watauga Beach, stones, 12.2 m depth, 28.xii.2013, coll. K. Fletcher.
LSID: urn:lsid:zoobank.org:act:22BDFF50-61E3-4DAC-876C-6A2BCA30AD93

Etymology

Named for Sylvia Earle, an American marine biologist, explorer, author and lecturer, whose ongoing efforts to protect the ocean and its wildlife are inspirational.

External morphology

Notum broad, rounded in front and posteriorly. Rhinophores long and retracted into raised sheaths, bearing tiny indistinct tubercles (Fig. 10A, C). 18 rhinophoral lamellae. Notum covered with small, pointed tubercles (Fig. 10A, C). Spicules form sparse network in notum. Six or seven multipinnate gills united by common membrane into a circle around the anus (Fig. 10A, C). Gills retractable into common gill cavity. Border of gill cavity moderately raised with indistinct tubercles (Fig. 10A, C). Oral veil small, trapezoid, with obliquely notched lateral sides (Fig. 10B). Foot broad, anteriorly rounded and slightly thickened to form double edge; it appears as entire (Fig. 10B); posteriorly it sometimes projects slightly from notum in crawling animals, forming a rounded tail.

Colour

Living specimens commonly opaque whitish, with some small, dorsal tubercles tipped with yellow (Fig. 10A, C). Rhinophores with slight yellow tint (Fig. 10A). Gills are semitransparent white, similar to ground colour. Digestive gland barely visible through the notum or through the foot. Subepidermal glands white, clearly shining near lateral edges of notum (Fig. 10C). Yellow line around notum present, thin (Fig. 10A, C).

Buccal bulb and oral tube

Buccal bulb longer than oral tube (Fig. 10D). Salivary glands relatively long and narrow.

Jaws

Rounded labial disk covered by yellowish to brownish cuticle bearing rod-shaped labial elements with double hook-shaped tips (Fig. 10E).

Radula

Radular formula approximately 92 × 45.1.45 (Op-684). Radular teeth slightly yellowish. Central tooth rectangular and bears three or four distinct cusps (Fig. 10G, H). Inner lateral tooth massive with wide base and short, strong, slightly curved cusp; four or five outer denticles and two or three inner denticles (Fig. 10G, H). Outer lateral teeth are elongated hook-shaped, bearing up to 14 comb-shaped denticles (Fig. 10I).

Reproductive system

Ampulla comprised of at least five small but thickened compartments (Fig. 15E, a). Ampulla bifurcates into short, thickened vas deferens and oviduct. Uterine duct emerges some distance from female gland mass (Fig. 15E, ud). Prostatic part of vas deferens long, narrow and not distinct (Fig. 15E, pr). Prostate transits to slightly widened penial sheath that encloses evertable ejaculatory duct (Fig. 15E, psh). Conical penial spines with distinctly broad base present (Fig. 10J, K). Vagina narrow (Fig. 15E, v), and enters medium-sized oval bursa copulatrix (Fig. 15E, b). Uterine duct short and narrow (Fig. 15E, ud); it begins from female gland mass and then enters near base of small kidney-shaped receptaculum seminis (Fig. 15E, rs).

Habitat

Found on stony substrate with sponge prey at approximately 12 m.

Distribution

Presently described from Washington State (Port Orchard, Rich Passage); matched sequences occur in GenBank (voucher # 11BIOAK-0009, see Table S2) from Alaska (Fig. 2).

Remarks

This species is a sister to *Cadlina luteomarginata* MacFarland, 1966, with which it was previously confused (sequences of the latter available from GenBank from a specimen collected in Mendocino County, California; Johnson, 2010), relatively close to the type locality of *C. luteomarginata* in Monterey Bay

(MacFarland, 1966); see also Table S2. Morphologically, *Cadlina sylviaearleae* differs from *C. luteomarginata* [according to the original description in MacFarland (1905, 1966)] by the considerably less tuberculated notum, more weakly developed yellow line around notum and by patterns of the radula. The radula of *C. luteomarginata* has a larger number of rows and has relatively high, more hamate first lateral teeth, whereas *Cadlina sylviaearleae* has lower and squarish first lateral teeth, similar to *C. laevis*. See also Table 3 for a detailed morphological comparison with other species of *Cadlina*. *Cadlina sylviaearleae* differs both molecularly and in a number of morphological features from all other described *Cadlina* species.

No divergence was observed between *COI* sequences of *C. sylviaearleae*. The lowest *COI* intergroup distance of 10.44% is found between *C. sylviaearleae* and *C. luteomarginata*. The lowest 16S intergroup distance of 4.24% is found between *C. sylviaearleae* and *C. luteomarginata* (Tables 1, 2).

CADLINA JAPONICA BABA, 1937

(FIGS 2, 11, 12, 15F)

Cadlina japonica: Baba, 1937: 76–78, fig. 1;
Baba, 1949: 57, pl XXI, figs 75–77, text fig. 67;
Nakano, 2018: 275.

Syntypes: NSMT-Op R:12, two spc., *L* = 15 mm and 53 mm (preserved), north-western Pacific, Japan, Sagami Bay, off Kameki-sho, 73.1 m depth, 7 May 1935, coll. Household Emperor Laboratory.
NSMT-Op R:4, one spc., *L* = 47 mm (preserved), north-western Pacific, Japan, Sagami Bay, off Kameki-sho, 82.2 m depth, 18 August 1935, coll. Household Emperor Laboratory.

Additional material

NSMT-Op R:1006, one spc., *L* = 46 mm (preserved), north-western Pacific, Japan, Sagami Bay, off Kameki-sho, Mosaki, 9.0–12.8 m depth, 15 July 1956, coll. Household Emperor Laboratory.

KSNHM–M10746, two spec., *L* = 28 and 25 mm, dissected, north-western Pacific, Japan, Hokkaido, Usujiri, stones rocky substrate, 5–20 m depth, 19 June 2019, coll. Sho Kashio.

External morphology

Notum broad, rounded in front and posteriorly. Rhinophores long and retracted into raised sheaths, bearing small tubercles or almost smooth (Figs 11C, 12A). Approximately 30 rhinophoral lamellae. Notum covered with moderate to large, distinct, rounded tubercles (Figs 11A, 12A, C). Six or seven multipinnate gills united by common membrane into a circle around the anus (Fig. 12A). Gills retractable into common gill cavity (Fig. 11D). Border of gill cavity moderately raised with almost smooth edge or bearing small tubercles (Figs 11D, 12A, C). Oral veil with large, notched, lateral triangular lobes (Figs 11B, 12B). Foot broad, anteriorly rounded and slightly thickened to form double edge; it appears as entire (Fig. 11B); posteriorly it sometimes projects slightly from notum in crawling animals, forming a rounded tail.

Colour

Living specimens commonly opaque with yellowish-brownish to dark brownish extended areas on the dorsum (Figs 11A, 12A). Rhinophores (including lamellae) similar to ground colour. Gills semitransparent white, similar to ground colour. Digestive gland not visible through the notum nor through the foot. Subepidermal glands shine near lateral edges of notum in lighter coloured specimens. Yellow line around notum present and relatively thin. Similar line borders gill cavity and rhinophoral sheaths.

Buccal bulb and oral tube

Buccal bulb relatively long compared to shorter oral tube (Fig. 12D). Salivary glands relatively long and narrow.

Jaws

Rounded labial disk covered by yellow to light brownish cuticle bearing rod-shaped labial elements with double or unicuspid hook-shaped tips (Figs 11F, G, 12E).

Radula

Radular formula approximately 67 × 60.1.60 (KSNHM–M10746) (Fig. 12F). Radular teeth slightly yellowish. Central tooth elongate and bears two to four distinct main cusps and up to seven, if additional smaller denticles are counted (Figs 11I, J, 12G, H). Inner lateral tooth hamate with relatively narrow base and short, strong, slightly curved cusp; four to six outer denticles and three to six inner denticles (Figs 11I, J, 12G, H). Outer lateral teeth are elongated hook-shaped, bearing up to ten sharpened denticles (Figs 11K, 12I).

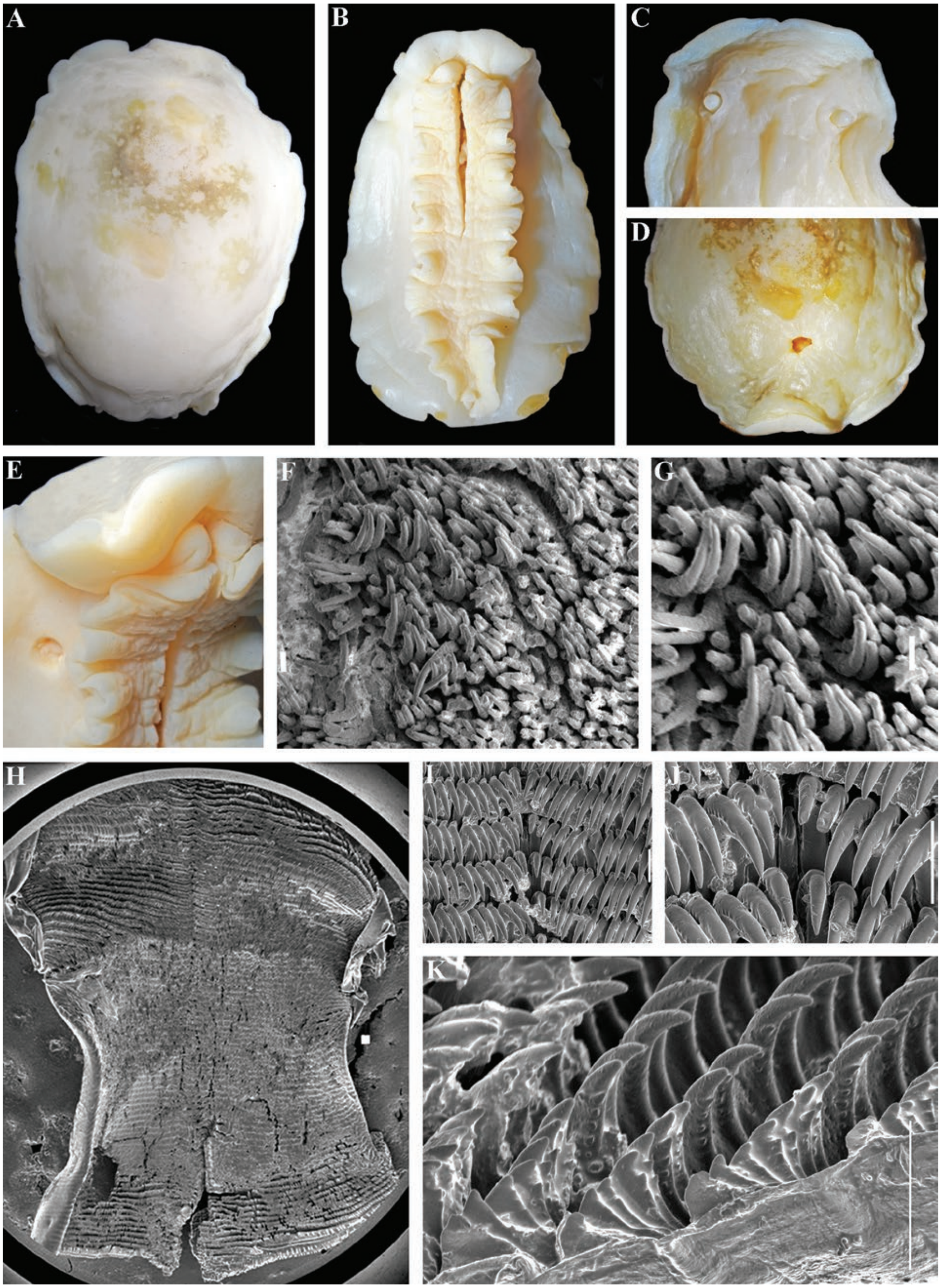

Figure 11. *Cadlina japonica* (Showa Memorial Collection), syntype NSMT-Op R:4, 47 mm, Sagami Bay, Japan, external and internal features. A, dorsal view. B, ventral view. C, dorsal view, anterior part. D, dorsal view, posterior part. E, ventral view, anterior part. F, G, elements of labial cuticle, SEM (and following images). H, complete radula. I, central part of radula. J, enlarged central part of radula to show central teeth and first lateral teeth. K, outer lateral teeth. All scale bars: 100 µm. Photos: Alexander Martynov.

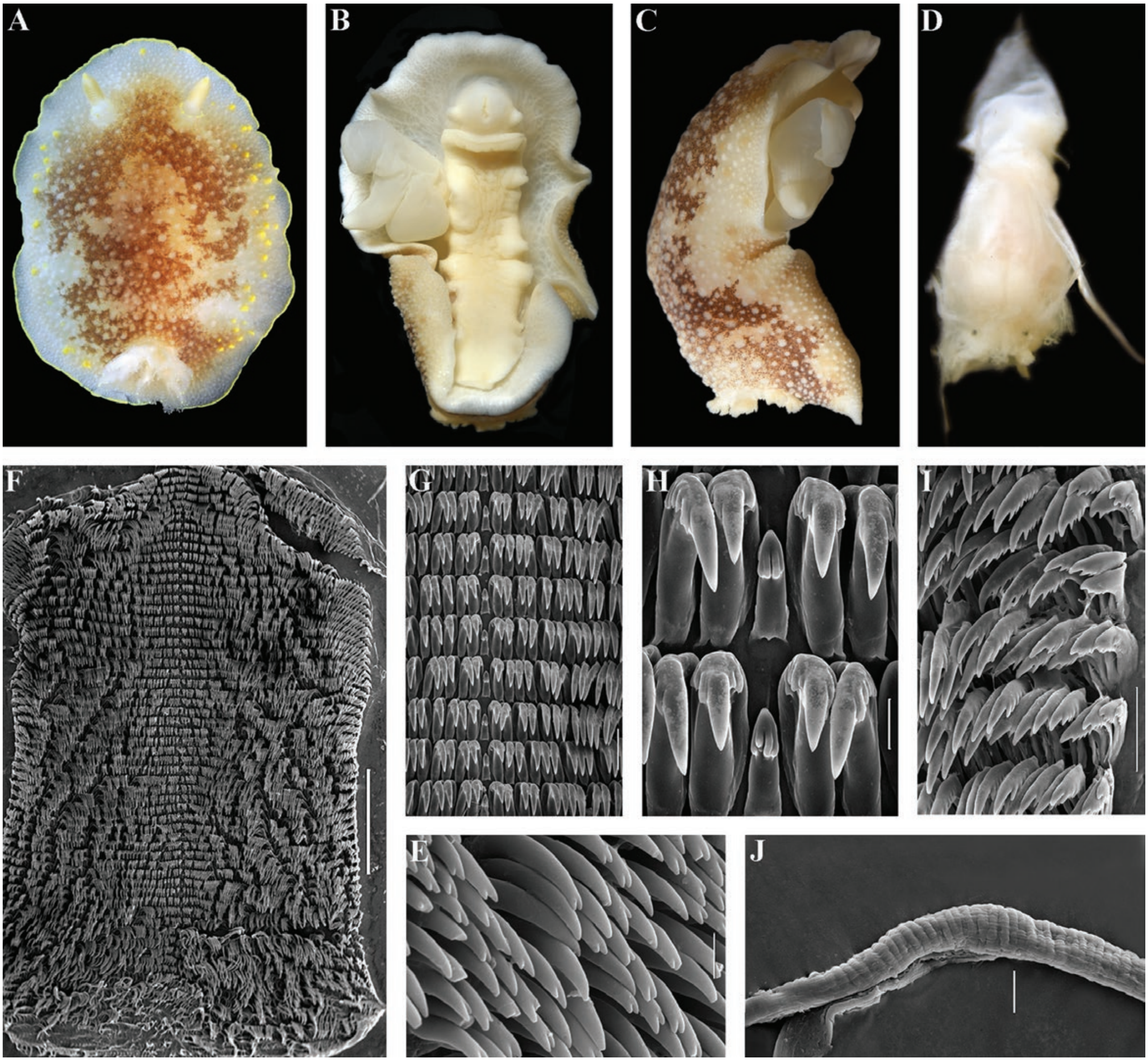

Figure 12. *Cadlina japonica*. KSNHM–M10746, 25 mm, Hokkaido, Japan, external and internal features. A, dorsal view. B, ventral view. C, lateral view. D, buccal bulb, LM. E, elements of labial cuticle SEM (and following images). F, complete radula. G, central part of radula. H, enlarged central part of radula to show central teeth and first lateral teeth. I, outer lateral teeth. J, dissected ejaculatory duct without penial spines. Scale bars: E, 10 µm; F, 100 µm; H, J, 10 µm; G, I; Photos: A, Sho Kashio; B, C, Alexander Martynov.

Reproductive system

Ampulla comprised of at least six small, thickened compartments (Fig. 15F, a). Ampulla bifurcates into long vas deferens and oviduct. Uterine duct emerges some distance from female gland mass (Fig. 15F, ud). Prostatic part of vas deferens long, narrow, moderately distinct (Fig. 15F, pr). Prostate transits towards penial sheath (Fig. 15F, psh) that encloses thin and long evertable ejaculatory duct (Fig. 15F, ied), which is surrounded by huge genital lobe (Fig. 15F, gl). Penial spines were not found in two dissected specimens (Fig. 12J). Vagina narrow (Fig. 15F, v), and enters medium-sized triangular bursa copulatrix (Fig. 15F, b), which is at least two times larger than receptaculum seminis. Uterine duct short and narrow (Fig. 15F, ud); it begins from female gland mass and then enters near base of small oval receptaculum seminis (Fig. 15F, rs).

Habitat

Soft and stony substrates, upper subtidal to 350 m.

Distribution

Southern Hokkaido to southern Honshu (up to Kii peninsula) in Japan and in the Republic of Korea (Fig. 2).

Remarks

Newly collected specimens studied here agree with both the original description (Baba, 1937, 1949) and type specimens at the Showa Memorial Institute investigated for the present study (Figs 11, 12) in most characters, with the exception of the number of cusps on the central teeth, which are somewhat larger (although they overlap in range) from that indicated in the original description and in the type material. Labial cuticle in the new material is comprised of both bi- and unicuspid elements, whereas in the original description Baba reported only unicuspid elements, and in the type material we also found only unicuspid elements. This needs to be investigated further in order to uncover potential hidden diversity. *Cadlina japonica* differs completely from any other species of the genus in the combination of the large brownish areas on the dorsum, thin yellow notal line, elongate central teeth and hamate first laterals. After careful investigations of the ejaculatory ducts of the reproductive systems of two specimens, we did not find any penial spines (Fig. 12J). Absence of penial spines is unusual for species of the genus *Cadlina*, but we cannot completely exclude the possibility that there might be tiny spines in some restricted parts of the ejaculatory ducts that we missed during our study. However, according to the present molecular analysis, *C. japonica* together with *C. klasmalmbergi* and *C. jannanicholsae* described below, form a separate clade from both the *C. laevis* and *C. luteomarginata* groups (Fig. 2). This clade includes large species with elongate central teeth and hamate laterals (*Cadlina* s.str, i.e. members of the *C. laevis* group commonly possess massive first laterals, low central teeth and spines in the ejaculatory duct) and in both *C. klasmalmbergi* and *C. jannanicholsae* we also did not find penial spines (see below). If this feature is confirmed in future studies, this group may require its own genus. Maximum intragroup distances within *C. japonica* are 0.84% for the *COI* marker and 0.47% for the 16S marker. The lowest *COI* intergroup distance of 8.42% is found between *C. japonica* and *C. jannanicholsae*. The lowest 16S intergroup distance of 1.41% is found between *C. japonica* and *C. klasmalmbergi* (Tables 1, 2).

CADLINA KLASMALMBERGI KORSHUNOVA *ET AL.*, **SP. NOV.**

(FIGS 2, 13, 15G)

Cadlina luteomarginata auct. non MacFarland, 1966.

Holotype: ZMMU Op-687, L = 55 mm (live, adult), dissected, north-eastern Pacific, USA, Washington State, Bainbridge Island, Shangri-la site, stony and rocky substrates, 18.3 m depth, 21 July 2018, coll. D. Miller.

Paratypes: ZMMU Op-688, one spc., L = 14 mm (preserved, subadult), dissected, north-eastern Pacific, Canada, British Columbia, Galiano Island, Barnes Bay, stony and rocky substrates, 11.8 m depth, 19 June 2018, coll. K. Fletcher.

LSID: urn:lsid:zoobank.org:act:A5FF0726-9D7C-4CD5-B94F-666191A632E7

Etymology

For Klas Malmberg, Swedish marine biologist, for his contributions to the understanding of the nudibranch fauna.

External morphology

Notum broad, rounded in front and posteriorly. Rhinophores long and retracted into raised sheath, bearing small tubercles (Fig. 13A, D). Approximately 20 rhinophoral lamellae. Notum covered with moderate in size, low, rounded tubercles in adult specimen (Fig. 13A) and much smaller subrounded tubercles in subadult (Fig. 13D). Six multipinnate gills united by common membrane into a circle around the anus (Fig. 13A). Gills retractable into common gill cavity (Fig. 13D). Border of gill cavity moderately raised with tubercles (Fig. 13A, C). Oral veil trapezoid, with obliquely notched lateral sides (Fig. 13B). Foot broad, anteriorly rounded and slightly thickened to form double edge; it appears as entire (Fig. 13B); posteriorly it sometimes projects slightly from notum in crawling animals, forming a rounded tail.

Colour

Living adult specimen opaque whitish (Fig. 13A), subadult translucent whitish (Fig. 13D). Rhinophores light brownish, tipped with light yellow (Fig. 13A, D). Gills are semitransparent white, similar to ground colour, tipped with yellow. Digestive gland not visible through the notum in adults (Fig. 13A), but shows through the notum in subadults (Fig. 13D). Subepidermal glands not visible in adults (Fig. 13A), but shine through the

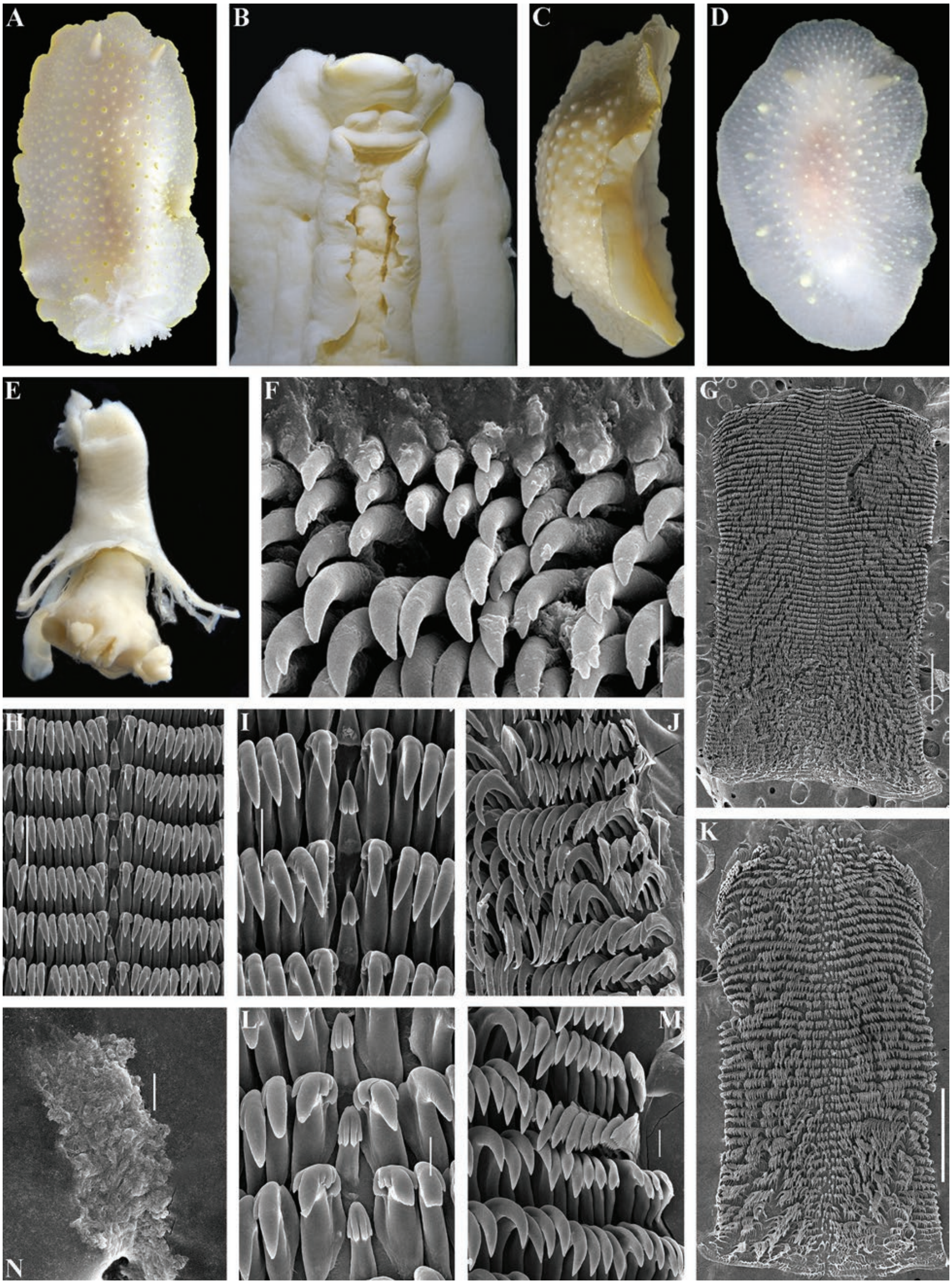

Figure 13. *Cadlina klasmalmbergi*. A–C, E–J, N, holotype ZMMU Op-687, 55 mm, Washington State. D, K, L, M, paratype ZMMU Op-688, 14 mm, British Columbia, external and internal features. A, dorsal view. B, ventral view. C, lateral view. D, dorsal view. E, buccal bulb, LM. F, elements of labial cuticle, SEM (and following images). G, complete radula. H, central part of radula. I, enlarged central part of radula to show central teeth and first lateral teeth. J, outer lateral teeth. K, complete radula. L, enlarged central part of radula. M, outer lateral teeth. N, dissected ejaculatory duct without penial spines. Scale bars: E, 10 μm; F, 10 μm; G, 1 mm; H, J, 100 μm; I, 50 μm; L, M, N, 20 μm. Photos: Karin Fletcher. SEM, Alexander Martynov.

dorsum in subadults (Fig. 13D). Yellow line around notum present, relatively narrow in adult (Fig. 13A) and much less distinct in subadults (Fig. 13D).

Buccal bulb and oral tube

Buccal bulb shorter than long oral tube (Fig. 13E). Salivary glands relatively long and narrow.

Jaws

Rounded labial disk covered by dark-yellow to light brownish cuticle bearing rod-shaped labial elements with double to single hook-shaped tips (Fig. 13F).

Radula

Radular formula approximately 90 × 97.1.97 (ZMMU Op-687, adult, Fig. 13G) and approximately 60 × 55.1.55 (ZMMU Op-688, subadult; Fig. 13K). Radular teeth slightly yellowish. Central tooth moderately elongate and bears three to five distinct cusps (Fig. 13H, I, L). Inner lateral tooth hamate with relatively narrow base (Fig. 13I) (more widened in subadult specimens; Fig. 13L) and short, strong, slightly curved cusp; three to five outer denticles and two to four inner denticles (Fig. 13H, I, L). Outer lateral teeth are elongated hook-shaped, bearing up to seven sharpened denticles (Fig. 13J, M).

Reproductive system

Ampulla comprised of at least ten moderately sized, thickened compartments (Fig. 15G, a). Ampulla bifurcates into long vas deferens and oviduct. Uterine duct emerges some distance from female gland mass (Fig. 15G, ud). Prostatic part of vas deferens relatively long, narrow, slightly distinct (Fig. 15G, pr). Prostate transits towards penial sheath (Fig. 15G, psh) that encloses thin relatively short evertable ejaculatory duct. Penial spines were not found in adult specimen (Fig. 13N). Vagina narrow (Fig. 15G, v), and enters medium-sized triangular bursa copulatrix (Fig. 15G, b), which is similar in size to receptaculum seminis. Uterine duct short and narrow (Fig. 15G, ud), starting from a female gland mass and then entering near the base of the oval receptaculum seminis (Fig. 15G, rs).

Habitat

Inhabits stony and rocky substrates with sponge prey at depths *c.* 11–18 m.

Distribution

So far, known only from Washington State (USA) and British Columbia (Canada).

Remarks

Until recently, *C. luteomarginata* has been considered a single species with a whitish notum and yellow marginal line with a broad range in the north-eastern Pacific from Alaska to California (e.g. MacFarland, 1966; Behrens, 1991; Behrens & Hermosillo, 2005). Present integrative morphological and molecular analysis reveals that there is considerable hidden diversity among *Cadlina* from the north-eastern Pacific. Despite its superficial similarity to *C. luteomarginata*, *C. klasmalmbergi* belongs to a different clade that also includes *C. japonica* and *C. jannanicholsae*, but not *C. sylviaearleae* (Fig. 2). *Cadlina klasmalmbergi* readily differs from *C. luteomarginata* by its hamate first lateral teeth and elongate central teeth, and from *C. jannanicholsae* by the shape of the central and inner lateral teeth (Fig. 13I). In addition, the sympatric *C. klasmalmbergi* and *C. jannanicholsae* are also different externally: the latter species has larger, higher tubercles and a more distinct yellow notal line (Fig. 14A). See also detailed comparison in Table 3. A species from southern California recorded in Rudman (1984) under the name '*C. luteomarginata*', judging from the morphology of the radula (Rudman, 1984: fig. 89), definitely differs from typical *C. luteomarginata* – that has its type locality in central California as described in MacFarland (1905, 1966), but potentially belongs to the same clade with *C. japonica*, *C. klasmalmbergi* and *C. jannanicholsae*, and thus may be an undescribed species.

Maximum intragroup distances in *C. klasmalmbergi* are 0.17% for the *COI* marker and 0% for the 16S marker. The lowest *COI* intergroup distance of 8.42% is found between *C. klasmalmbergi* and *C. jannanicholsae*. The lowest 16S intergroup distance of 1.41% is found between *C. klasmalmbergi* and *C. japonica* (Tables 1, 2).

CADLINA JANNANICHOLSAE KORSHUNOVA ***ET AL.*, SP. NOV.**

(FIGS 2, 14, 15H)

Cadlina luteomarginata auct. non MacFarland, 1966.
Holotype: ZMMU Op-689, *L* = 45 mm (live), dissected, north-eastern Pacific, USA, Washington State, Bainbridge Island, Shangri-la site, stony and rocky substrate, 7.9 m depth, 21 July 2018, coll. K. Fletcher.
LSID: urn:lsid:zoobank.org:act:1EA41008-25A4-4D4E-9E3F-9F4981B1AB7C

Etymology

For Janna Nichols, REEF's Citizen Science Program Manager, working extensively with the Volunteer Fish and Invertebrate Survey Project database, training programmes and volunteer teams. She has

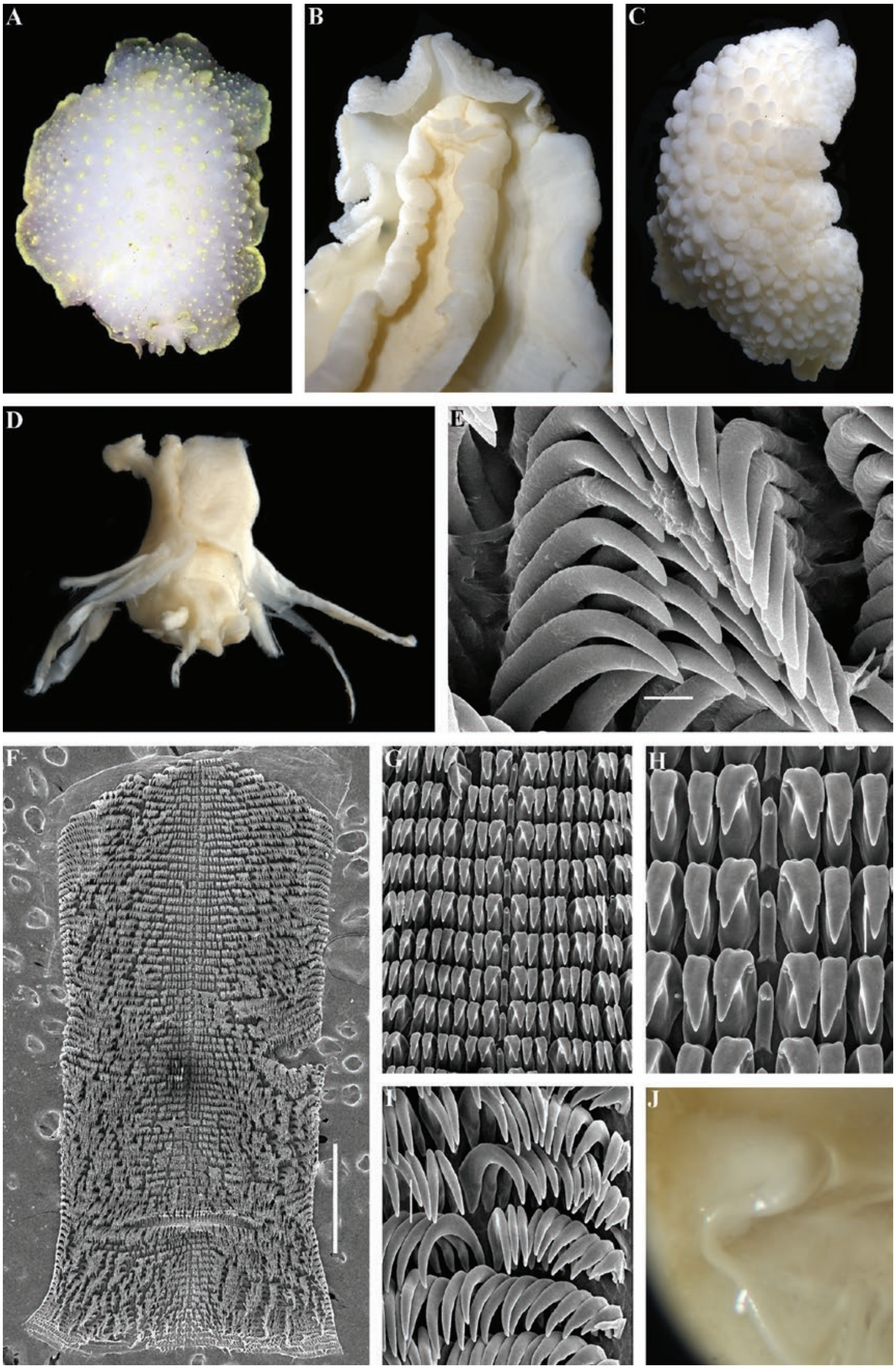

Figure 14. *Cadlina jannanicholsae*, holotype ZMMU Op-689, 45 mm, Washington State, external and internal features. A, dorsal view. B, ventral view. C, lateral view. D, buccal bulb, LM. E, elements of labial cuticle, SEM (and following images). F, complete radula. G, central part of radula. H, enlarged central part of radula to show central teeth and first lateral teeth. I, outer lateral teeth. J, dissected ejaculatory duct without penial spines, LM. Scale bars: E, 10 μm; F, 100 μm; H, J, 10 μm; G, I; Photos: Karin Fletcher. LM and SEM photos by Alexander Martynov.

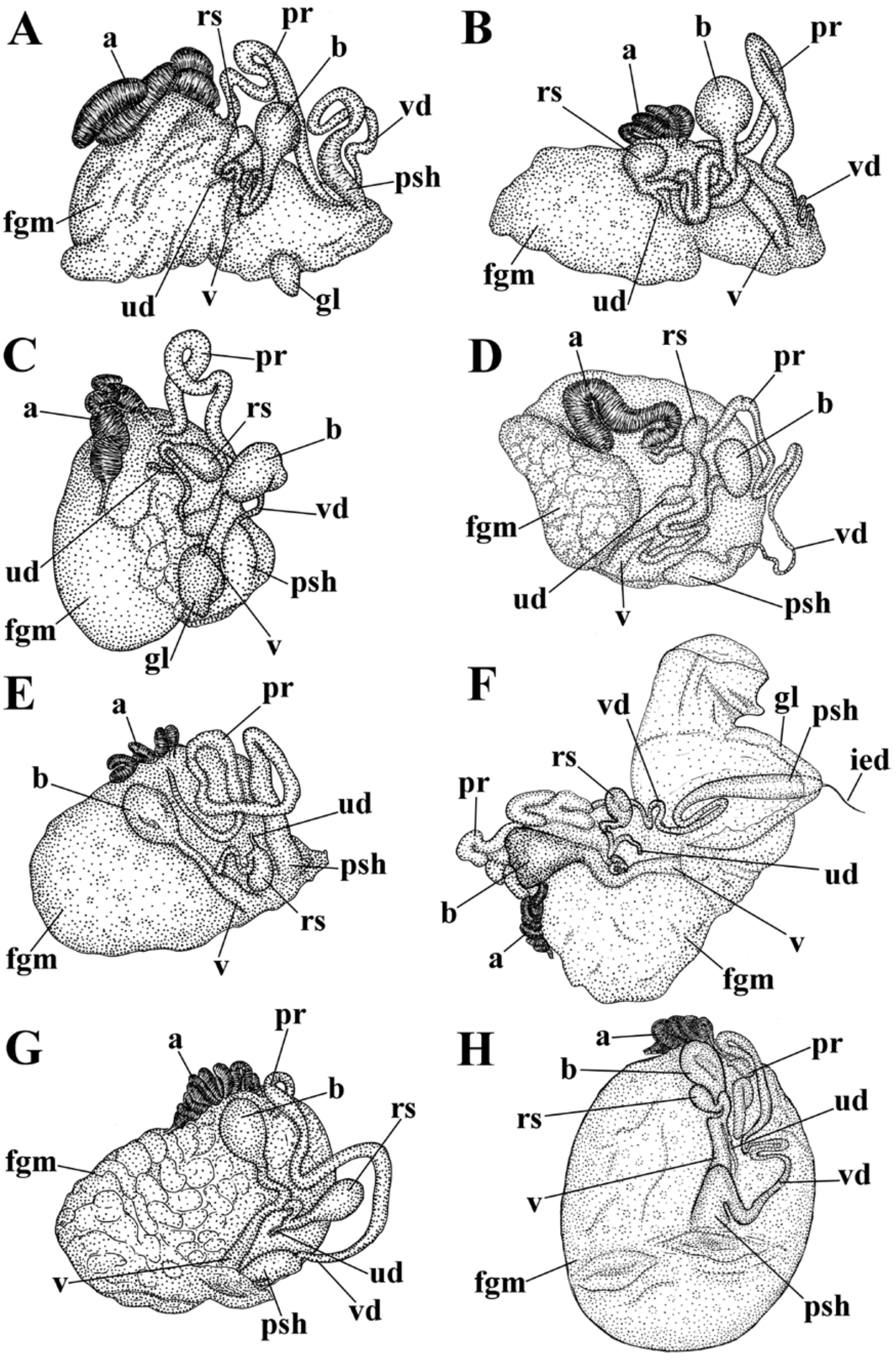

Figure 15. Reproductive systems of the genus *Cadlina*. A, *Cadlina laevis*; B, *Cadlina umiushi*; C, *Cadlina kamchatica*; D, *Cadlina paninae*; E, *Cadlina sylviaearleae*; F, *Cadlina japonica*; G, *Cadlina klasmalmbergi*; H, *Cadlina jannanicholsae*. Abbreviations: a, ampulla; b, bursa; fgm, female gland mass; gl, genital lobe; ied, inverted ejaculatory duct; rs, receptaculum seminis; pr, prostate; psh, penial sheath; ud, uterine duct; v, vaginal duct; vd, vas deferens.

worked tirelessly for citizen science programme development in the Pacific north-west of the USA and globally.

External morphology

Notum broad, rounded in front and posteriorly. Rhinophores long and retracted into raised sheaths, bearing small to larger tubercles (Fig. 14A, C). Approximately 15–20 rhinophoral lamellae. Notum covered with large, relatively high, irregularly shaped to rounded tubercles (Fig. 14A, C). Six multipinnate gills united by common membrane into a circle around the anus (Fig. 14A). Gills retractable into common gill cavity (Fig. 14C). Border of gill cavity moderately raised and surrounded with small and larger tubercles (Fig. 14A, C). Oral veil trapezoid, with obliquely notched lateral sides (Fig. 14B). Foot broad, anteriorly rounded and slightly thickened to form double edge; it appears as entire (Fig. 14B); posteriorly it sometimes projects slightly from notum in crawling animals, forming a rounded tail.

Colour

Living adult specimen opaque whitish (Fig. 14A). Rhinophores yellowish (Fig. 14A). Gills semitransparent white, but up to one-third covered with yellow (Fig. 14A). Digestive gland not visible through notum. Subepidermal glands scarcely visible. Yellow line around notum present, conspicuously broad (Fig. 14A).

Buccal bulb and oral tube

Buccal bulb shorter than oral tube (Fig. 14D). Salivary glands relatively long and narrow.

Jaws

Rounded labial disk covered by yellowish to brownish cuticle bearing distinct, rod-shaped unicuspid labial elements (Fig. 14E).

Radula

Radular formula approximately 95 × 65.1. 65. (Fig. 14F). Radular teeth slightly yellowish. Central tooth elongate and bearing two or three (commonly two) small cusps (Fig. 14G, H). Inner lateral tooth hamate with relatively narrow base and short, strong, slightly curved cusp; three or four outer denticles and two or three inner denticles (Fig. 14G, H). Outer lateral teeth are elongated hook-shaped, with strongly reduced denticles (Fig. 14I).

Reproductive system

Ampulla comprised of at least four moderately sized, thickened compartments (Fig. 15H, a). Ampulla bifurcates into long vas deferens and oviduct. Uterine duct emerges some distance from female gland mass (Fig. 15H, ud). Prostatic part of vas deferens long, narrow, slightly distinct (Fig. 15H, pr). Prostate transits towards penial sheath (Fig. 15H, psh) that encloses thin long evertable ejaculatory duct. Penial spines were not found in adult specimen (Fig. 14J). Vagina narrow (Fig. 15H, v) and enters medium-sized, pear-shaped bursa copulatrix (Fig. 15H, b), which is at least two times larger than receptaculum seminis. Uterine duct short and narrow (Fig. 15H, ud); it begins from female gland mass and then enters near base of oval receptaculum seminis (Fig. 15H, rs).

Habitat

Inhabits stony and rocky substrates with sponge prey at depths of *c.* 8 m.

Distribution

North-eastern Pacific, so far know only from Washington State, USA (present study) and from British Columbia, Canada (GenBank data; see Supporting Information, Table S2).

Remarks

This analysis shows that, despite the superficial similarity to *C. luteomarginata*, *C. jannanicholsae* belongs to a different clade that also includes *C. japonica* and *C. klasmalmbergi*, but not *C. sylviaearleae* (Fig. 2). *Cadlina jannanicholsae* readily differs from *C. luteomarginata* in the hamate first lateral teeth and elongate central teeth, and from *C. klasmalmbergi* in the shape of the central and inner lateral teeth (Fig. 14H). In addition, the sympatric *C. jannanicholsae* and *C. klasmalmbergi* also differ externally: the latter species has lower tubercles and a less distinct yellow notal line in the adult stage (compare Figs 13A and 14A). See also detailed comparison of these species in Table 3. Maximum intragroup distances in *C. jannanicholsae* are 1.01% for the *COI* marker and 0.94% for the16S marker. The lowest *COI* intergroup distance of 8.42% is found between *C. jannanicholsae* and *C. klasmalmbergi* and *C. japonica*. The lowest 16S intergroup distance of 1.65% is found between *C. jannanicholsae* and *C. klasmalmbergi* and *C japonica*. (Tables 1, 2).

FAMILY **CADLINELLIDAE** ODHNER, 1934, **STAT. NOV.**

LSID: urn:lsid:zoobank.org:act:FB2D4DC3-0FC7-4CC2-B37F-D10DE2E45475

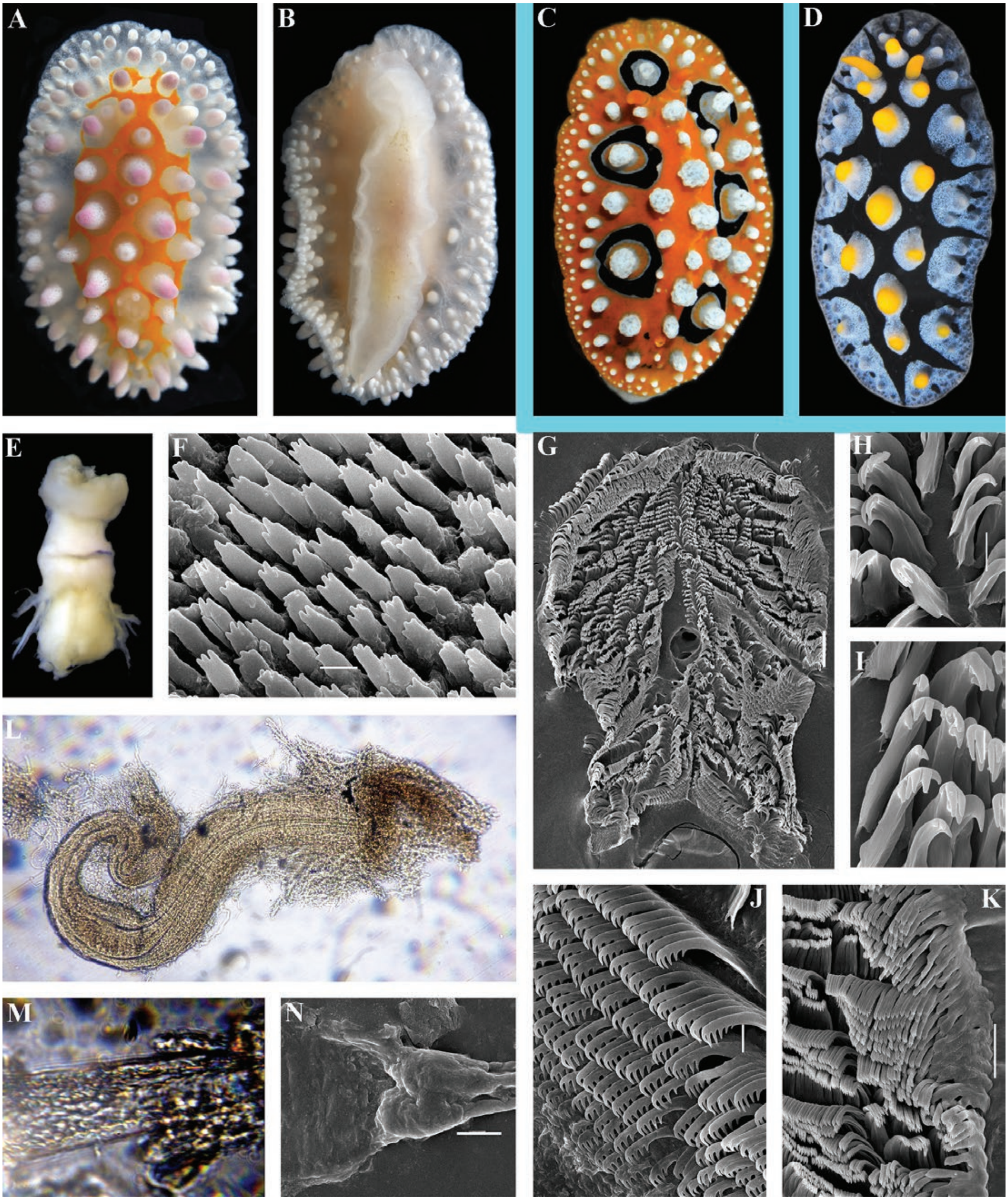

Figure 16. *Cadlinella subornatissima* (family Cadlinellidae) and representatives of the family Phyllidiidae. A, B, E–N, *C. subornatissima*, ZMMU Op-693, 10 mm, Osezaki, Japan, external and internal features. C, *Phyllidia ocellata*, 35 mm, Vietnam, external view. D, *Fryeria picta*, 23 mm, Vietnam, external view. A, dorsal view. B, ventral view. C, dorsal view. D. dorsal view. E, buccal bulb. F, elements of labial cuticle. G, complete radula (SEM). H, I, central part of radula enlarged to show central and first lateral teeth. J, K, outer teeth. L, penial sheath with ejaculatory duct inside (LM). M, ejaculatory duct, enlarged, with apparent penial spines (LM). N, same, SEM, no penial spines visible. Scale bars: F, I, 10 µm; G, 100 µm; H, J, 10 µm; K, 50 µm; N, 20 µm. Photos: Tatiana Korshunova and Alexander Martynov.

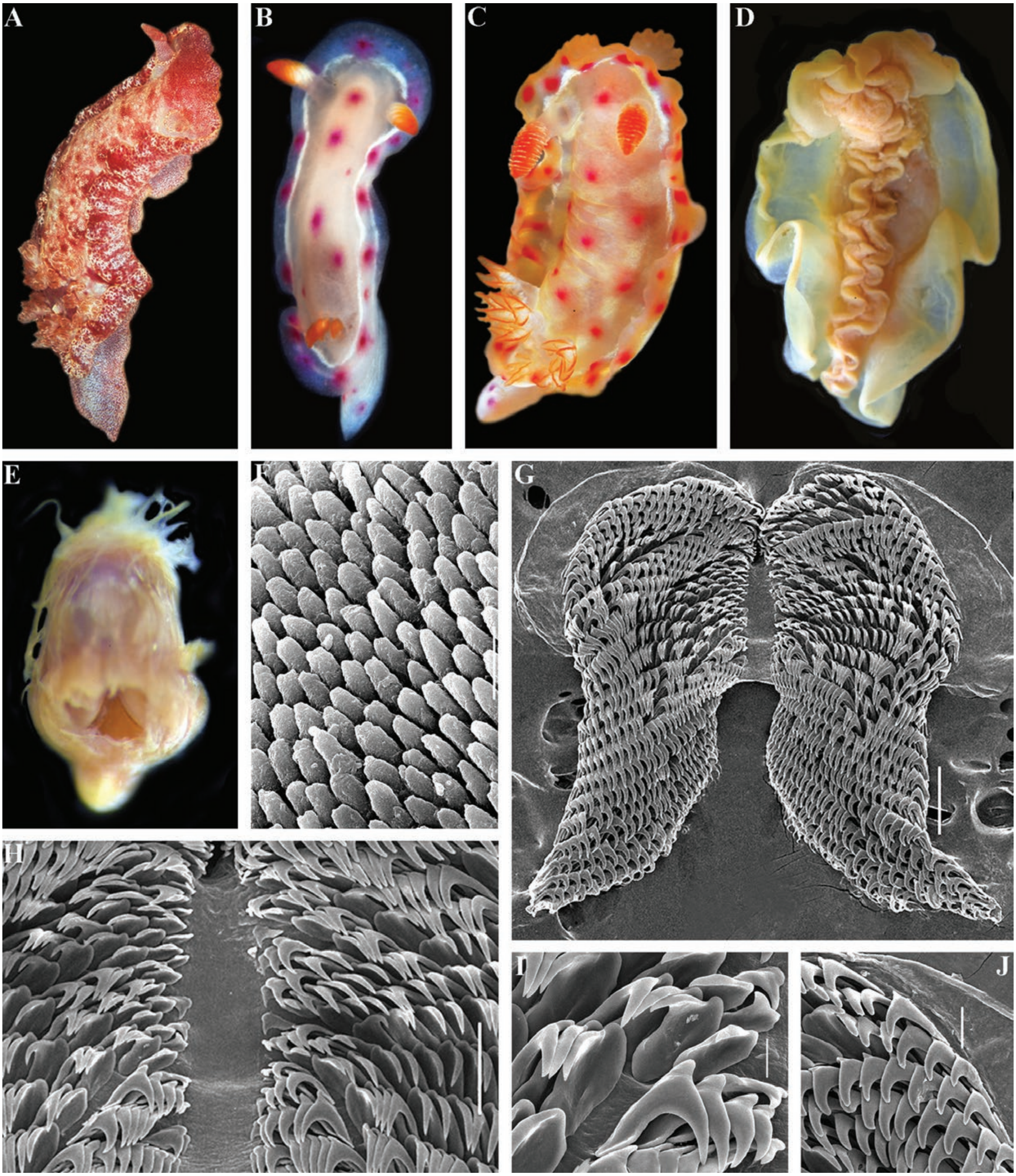

Figure 17. *Hexabranchus sanguineus* (Hexabranchidae), external and internal features. A, adult, 100 mm, Vietnam. B, juvenile, 7 mm (live). C–J, juvenile ZMMU Op-117, 10 mm (preserved), Vietnam. C, dorsal view. D, ventral view. E, buccal bulb. F, elements of labial cuticle, SEM (and following images). G, complete radula (SEM). H, central part of radula. I, central part of radula enlarged to show central and first lateral teeth. J, outer teeth. Scale bars: F, 10 μm; G, 200 μm; H, 100 μm; I, 20 μm; J, 50 μm; Photos: A, C, Oleg Savinkin; B, Alexander Martynov.

Diagnosis: Body relatively narrow, notal edges well defined, covered with strongly protruding, thick, elongated to club-shaped tubercles. Gills are multipinnate, gill cavity well defined. Labial cuticle with bi- to multicuspid elements. Radula broad, central teeth present, elongated with weakly developed cusps, partly directed forward. Vas deferens with narrow ejaculatory duct, penial spines reported to be present. Receptaculum seminis not inserted directly to the base of bursa (semiserial type).

Genera included: Cadlinella Thiele, 1931.

Remarks: In the present study, we additionally investigated *Cadlinella subornatissima* Baba, 1996 from the same locality as *Showajidaia sagamiensis* (see description below). Molecular data for *C. subornatissima* species were obtained for the first time from Osezaki (central Honshu, Pacific side, Japan), which is close to the type locality of this species in Uchiura (Fig. 16). According to the present molecular analysis, *C. subornatissima* clusters together with the type species of the genus *Cadlinella*, *C. ornatissima* Risbec, 1928, and forms a clade that is related to both the cryptobranch family Showajidaiidae and the phanerobranch Hexabranchidae (Fig. 17). Contrary to the results of Johnson (2010), *Cadlinella* is, in our analysis, not part of Chromodorididae. Subfamily Cadlinellinae Odhner, 1934, which is currently considered as a synonym of the family Chromodorididae, is therefore resurrected here in the family status as Cadlinellidae. All known species of Cadlinellidae demonstrate considerable external similarity to various Phyllidiidae (compare Fig. 16A and C, D). Further investigations should clarify if this is a case of mimicry, or if such similarity underlies deeper morphogenetic mechanisms. According to our analysis, Cadlinellidae belong to a large clade (Fig. 1) together with phyllidiids, Cadlinidae, Chromodorididae, Polyceridae and some others. As noted previously (Martynov & Korshunova, 2011) this clade is characterized by predominantly denticulated teeth with a central tooth and a narrow ejaculatory duct, commonly possessing small penial spines (reduced in some taxa). See also the Discussion section.

FAMILY **SHOWAJIDAIIDAE** KORSHUNOVA *ET AL.*, **FAM. NOV.**

LSID: urn:lsid:zoobank.org:act:263BDCE5-88A5-4409-B00A-A66E9CFBE472

Diagnosis: Body broad, notal edges well defined, covered with moderately protruding, conical to rounded tubercles. Gills are multipinnate, gill cavity well defined. Labial cuticle with bicuspid (rarely unicuspid) elements. Radula broad, central teeth present, elongated with massive cusps, which are not directed forward and adpressed to the teeth. Vas deferens with narrow ejaculatory duct, penial spines not evident. Receptaculum seminis is inserted directly to the base of bursa (vaginal type).

Genera included: Showajidaia.

SHOWAJIDAIA KORSHUNOVA *ET AL.*, **GEN. NOV.**

Type species: Cadlina sagamiensis Baba, 1937.
LSID: urn:lsid:zoobank.org:act:55E2348F-A160-47CC-8B38-1671506E1171

Etymology: From the Japanese Shōwa jidai (昭和時代) meaning 'Shōwa era' corresponding to the reign of the Shōwa Emperor Hirohito in reference to the collection of the type material for the type species of this genus *C. sagamiensis* by Hirohito.

Diagnosis: As the family Showajidaiidae.

Remarks: See Discussion.

SHOWAJIDAIA SAGAMIENSIS (BABA, 1937) **COMB. NOV.**

(FIGS 2, 18, 19)

Cadlina sagamiensis: Baba, 1937: 78–80, fig. 2;
Baba, 1949: 58, pl. 21, fig. 78, text fig;
Cadlinella sagamiensis – Nakano, 2018: 275.

Syntype: NSMT-Op R: 59, *L* = 36 mm (preserved), north-western Pacific, Japan, Honshu, Sagami Bay, Amadaiba, 82.3 m depth, 15 January 1937, coll. Household Emperor Laboratory [this specimen was not mentioned in the original description of Baba (1937)].

Additional material: NSMT-Op R: 1140, one spc., *L* = 33 mm (preserved), north-western Pacific, Japan, Honshu, Sagami Bay, Amadaiba, Kannontsuka-dashi, 62–73 m depth, 21 July 1959, coll. Household Emperor Laboratory.

ZMMU Op-690, one spec., *L* = 39 mm (live), dissected, north-western Pacific, Japan, Honshu, Izu Peninsula, Osezaki, stony and soft substrate, *c.* 70 m depth, 11 September 2016, coll. Hiroshi Takashige.

ZMMU Op-691, one spec., *L* = *c.* 20 mm (live), dissected, north-western Pacific, Japan, Honshu, Izu Peninsula, Osezaki, stony and soft substrate,

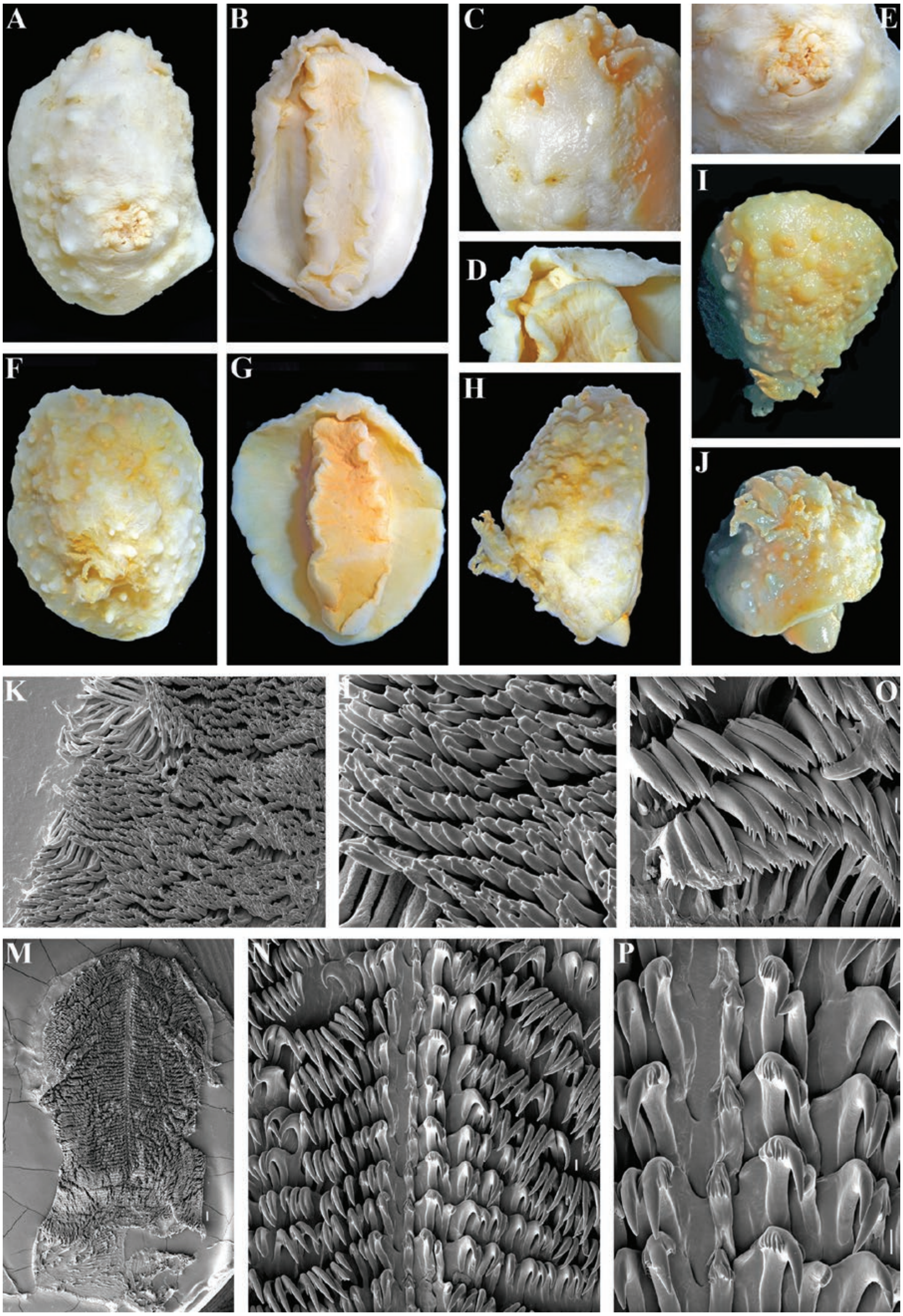

Figure 18. *Showajidaia sagamiensis*, family Showajidaiidae. Japan, external and internal features (Showa Memorial Collection). A–E, syntype NSMT-Op R: 59, 36 mm, Sagami Bay, Japan. F–P, historical topotype NSMT-Op R: 1140, 33 mm, Sagami Bay, Japan. A, F, dorsal view. B, G, ventral view. C, I, dorsal view, anterior part. D, ventral view, anterior part. E, J, dorsal view, posterior part. H, lateral view. K, L, elements of labial cuticle, SEM (and following images). M, complete radula. N, central part of radula. P, enlarged central part of radula to show central teeth and first lateral teeth. O, outer lateral teeth. Scale bars: K, L, 50 µm; M, 100 µm; N, O, 30 µm; P, 20 µm; Photos: Alexander Martynov.

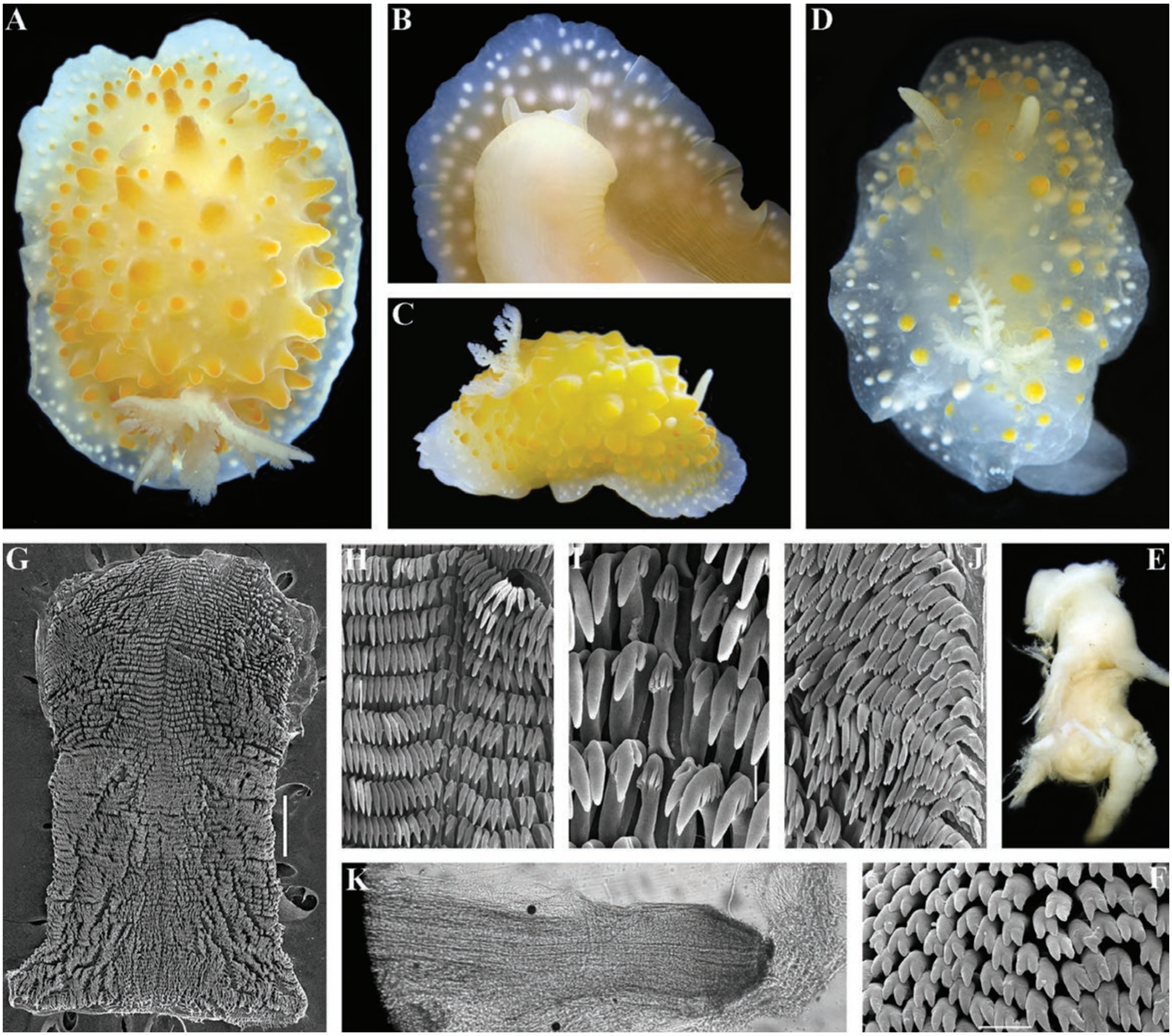

Figure 19. *Showajidaia sagamiensis*, family Showajidaiidae (recent material from Honshu, Osezaki, close to Sagami Bay, the type locality). A–C, E–K, ZMMU Op-690, 39 mm A, dorsal view. D, B, ZMMU Op-691, 20 mm. A, D, dorsal view. B, ventral view, anterior part. C, lateral view. E, buccal bulb, LM. F, elements of labial cuticle, SEM, (and following images). G, complete radula. H, central part of radula. I, enlarged central part of radula to show central teeth and first lateral teeth. J, outer lateral teeth. K, dissected ejaculatory duct without penial spines, LM. Scale bars: F, 10 μm; I, J, 20 μm; H, 50 μm; I, J, 500 μm. Photos: Alexander Martynov and Tatiana Korshunova.

c. 70 m depth, 11 September 2016, coll. Hiroshi Takashige.

External morphology

Notum broad, rounded in front and posteriorly. Rhinophores long and retracted into raised sheaths with smooth (Fig. 19A), soft, sometimes slightly crenulate edges (Fig. 19D), not bearing evident tubercles. Approximately 19–23 rhinophoral lamellae. Notum covered with large, distinct, conical (in adults) (Figs 18A–J, 19A) or conical to rounded (in subadults) (Fig. 19D) tubercles. Five or six multipinnate gills united by common membrane into a circle around the anus (Fig. 19A, D). Gills retractable into common gill cavity. Border of gill cavity moderately raised and furnished with some smaller tubercles (Fig. 19A). Oral veil forms prominent notched oral tentacles (Fig. 19B). Foot broad, anteriorly rounded and slightly thickened to form double edge; it appears as

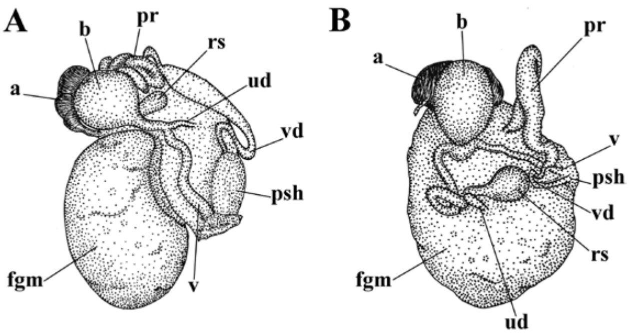

Figure 20. Reproductive systems of *Showajidaia sagamiensis* (A) and *Cadlinella subornatissima* (B). Abbreviations: a, ampulla; b, bursa; fgm, female gland mass; rs, receptaculum seminis; pr, prostate; psh, penial sheath; ud, uterine duct; v, vaginal duct; vd, vas deferens.

entire (Fig. 19B); posteriorly it sometimes projects slightly from notum in crawling animals, forming a rounded tail.

Colour

Living specimens light yellowish in subadults (Fig. 19D) to dark orange-brownish in adults (Fig. 19A). Outer broad edge of notum semitransparent whitish in adults (Fig. 19A). Rhinophores whitish. The gills semitransparent whitish (Fig. 19A, D). Digestive gland barely visible through notum (Fig. 19A), even in subadults (Fig. 19D). Numerous whitish subepidermal glands shine near lateral edges of notum both in adults and subadults (Fig. 19A, D).

Buccal bulb and oral tube

Buccal bulb longer than oral tube (Fig. 19E). Salivary glands relatively long and narrow.

Jaws

Rounded labial disk covered by yellowish to darker brownish cuticle bearing rod-shaped labial elements with commonly double hook-shaped tips (Fig. 19F) or rarely unicuspid (Fig. 18K, L).

Radula

Radular formula approximately 118 × 60.1.60 (Op-690) (Fig. 19G), 120 × 70.1.70 (NSMT-Op R: 1140) (Fig. 18M). Radular teeth slightly yellowish. Central tooth elongate with four to seven (more commonly five to six) distinct but adpressed smaller cusps (Figs 18N, P, 19H, I). Inner lateral tooth hamate with relatively narrow base and long curved cusp; approximately three to seven outer denticles and one or two inner denticles (Fig. 19H). Outer lateral teeth are elongated hook-shaped, bearing up to ten denticles (Figs 18O, 19J).

Reproductive system

Ampulla comprised of a single, slightly constricted, thickened compartment (Fig. 20A, a). Ampulla bifurcates into long vas deferens and oviduct. Uterine duct emerges some distance from female gland mass (Fig. 20A, ud). Prostatic part of vas deferens relatively long, moderately distinct (Fig. 20A, pr). Prostate transits towards penial sheath (Fig. 20A, psh) that encloses a thin and short evertable ejaculatory duct. Penial spines were not found in a big mature specimen (Fig. 19K). Vagina narrow (Fig. 20A, v) and enters relatively large spherical bursa copulatrix (Fig. 20A, b), which is more than two times larger than elongate club-shaped receptaculum seminis, which is inserted directly to the base of bursa (Fig. 20A, rs). Uterine duct short and narrow; it begins from female gland mass and then enters vagina (Fig. 20A, ud).

Habitat

Inhabits stony and soft substrates at depth *c.* 40–100 m.

Distribution

Known only from the central part of the Pacific coast of the Japanese island of Honshu, including Sagami Bay and Suruga Bay.

Remarks

Newly collected specimens and the topotypes in the Showa Memorial Institute studied here agree well with both the original and subsequent descriptions of this species (Baba, 1937, 1949) (Figs 19, 20) in most of the characters, with the exception of the number of radular rows, which somewhat deviated from that indicated in the original description (even with the type material itself). Molecular data for *Showajidaia sagamiensis* were obtained for the first time in the present study (Figs 2, 21, 22). As result, it is shown that '*Cadlinella*' *sagamiensis* neither belongs to the genus *Cadlina* nor *Cadlinella*, but belongs to a separate genus. It is related to both the cryptobranch *Cadlinella* (family Cadlinellidae) and the phanerobranch *Hexabranchus* (family Hexabranchidae), but represents its own family Showajidaiidae (see Discussion for details). Intragroup distances in *S. sagamiensis* are 0% for the *COI* marker and 0% for the 16S marker. The lowest *COI* intergroup distance of 21.94% is found between *S. sagamiensis* and *Cadlinella* sp. from the Republic of Korea; 23.66% between *S. sagamiensis* and *Hexabranchus sanguineus* from Papua New Guinea and 20.03% between *S. sagamiensis* and *Cadlina japonica*. The lowest 16S intergroup distance of 11.37% is found between *S. sagamiensis* and *Cadlinella* sp. from the Philippines and Australia, 8.89% between *S. sagamiensis* and *H. sanguineus* from Hawaii and 11.0% between *S. sagamiensis* and *Cadlina modesta*.

DISCUSSION

THE TAXONOMIC HISTORY OF THE GENUS *CADLINA*

Cadlina is a genus of slow-moving, flattened, often modestly coloured cryptobranchiate dorid nudibranchs. *Cadlina* has a confused taxonomic history fuelled by its still scarcely understood phylogenetic relationship to other dorids. This predominantly cold-water taxon has been traditionally placed in the same family with the colourful tropical chromodoridids (e.g. Rudman, 1984; Schrödl & Millen, 2001), but a molecular phylogenetic study (Johnson, 2010) placed *Cadlina* in a distant clade not only compared to the majority of chromodoridids, but also distinct from the morphologically similar genera *Tyrinna* and *Cadlinella* (Schrödl & Millen, 2001). Initially *Cadlina* had been separated into its own family-level taxon (Bergh, 1879a) based on morphological data, but only a few authors supported this classification (Thompson & Brown, 1984; Roginskaya, 1987).

Species of the genus *Cadlina* are one of the most common dorid nudibranchs in the northern temperate regions, but become significantly scarcer towards tropical waters. For example, in the the shallow tropical Indo-West Pacific, one of the richest regions for marine biodiversity, no *Cadlina* species have been documented (e.g. Cobb & Willan, 2006), whereas in the subtropical and temperate waters of Australia and New Zealand, three species of *Cadlina* have been described (Miller, 1980; Rudman, 1985, 1990; Burn, 2015). In the northern Pacific, eight species of *Cadlina* have been reported (Bergh, 1879a, b; MacFarland, 1905, 1966; Baba, 1937, 1949; Lance, 1962; Behrens, 1991), but two of these are now considered to belong to another genus (Schrödl & Millen, 2001). Four unidentified species of *Cadlina* have been reported from South Africa (Gosliner, 1987). Although five *Cadlina* species have been described from the Antarctic and sub-Antarctic (Thiele, 1912; Odhner, 1926, 1934), some of these are exceedingly rare (Schrödl, 2000). In the North Atlantic, only a single common species, *Cadlina laevis*, has been identified (e.g. Thompson & Brown, 1984; Picton & Morrow, 1997; Martynov & Korshunova, 2011), but a few more putative undescribed species were suggested to inhabit this region (Lemche in: Just & Edmunds, 1985). The single tropical West Atlantic species, *Cadlina rumia* (Marcus, 1955; Marcus & Marcus, 1963; Domínguez *et al.*, 2006), was reported to be uncommon in the Caribbean (Collin *et al.*, 2005), but is relatively common in south-eastern Brazil (Belmonte *et al.*, 2015). The East Atlantic counterpart of *C. rumia* from tropical Africa, *Cadlina dubia* Edmunds, 1981 (and possible synonym as highlighted by the author of this species), was described based on two specimens (Edmunds, 1981). A warm-water species, *Cadlina luarna* from Baja California, is so significantly different both externally and in its radular patterns from the majority of *Cadlina* species (Valdés & Angulo Campillo, 2000) that it is probably better placed in a separate genus, *Inuda*, as was suggested by Marcus & Marcus (1967), and therefore it is not shown in Table 3. Thus, the northern temperate regions are clearly the centre of diversity for the genus *Cadlina*. However, a few *Cadlina* do penetrate tropical waters, which complicates the proposal for an exclusively temperate–polar distribution as an argument for separation from the predominantly warm-water chromodoridids (Johnson, 2010).

There is still no global revision of the genus *Cadlina*, but there are several significant morphological contributions in which details of several *Cadlina* species are outlined as part of monographic studies on particular faunas (e.g. Bergh, 1879b; Odhner, 1926; Marcus, 1955; MacFarland, 1966; Ortea, 1988; Schrödl, 2000; Valdés, 2001). In an extensive review of the family Chromodorididae, Rudman (1984) presented detailed morphological accounts of four species of the genus *Cadlina* and made comparative remarks on other species. More recently, a revision of the morphologically similar genus *Tyrinna* has been published (Schrödl & Millen, 2001). The latter study suggested that some of the previously described species of the genus *Cadlina* should be transferred to *Tyrinna* and that two insufficiently known Japanese species with broad radula – '*C*'. *japonica* Baba, 1937 and '*C.*' *sagamiensis* Baba, 1937 – do not belong either to *Cadlina* or *Tyrinna*, but rather to the small tropical genus, *Cadlinella*. It was then demonstrated that *Tyrinna* is genetically distant from *Cadlina* and the latter, together with the genus *Aldisa*, were suggested to be placed into the family Cadlinidae (Johnson, 2010).

While establishing the genus *Cadlina*, Bergh (1878) designated the most common North Atlantic species as the type species, first described as *Doris laevis* Linnaeus, 1767 and subsequently described again by Alder & Hancock (1842) as *Doris repanda*. A few more species of *Cadlina* have been described from the North Atlantic [e.g. *C. planulata* (Stimpson, 1853), *C. glabra* (Friele & Hansen, 1876) and *C. boscai* Vilella, 1994] usually considered as synonyms of *C. laevis* (Thompson & Brown, 1984; MolluscaBase, 2019d), although the status of some of them needs to be refined. There is another relatively little known *Cadlina* species infrequently reported from more southern parts of the North Atlantic and the Mediterranean, *C. pellucida* (Risso, 1818), which is universally accepted (Ihering, 1880; García-Gomez, 2002; Trainito, 2005). In the present study, we confirm that a broad selection of *Cadlina laevis* specimens from the UK through Norway to the Arctic White and Barents seas revealed only a single species, *C. laevis* (Fig. 2). On the other hand, in the northern Pacific we discovered a considerable diversity across several clades of *Cadlina*.

INTRASPECIFIC VARIABILITY IS OVERLAPPING WITH INTERSPECIFIC DIVERSITY: THE *CADLINA* CASE

The majority of *Cadlina* species have white to creamy ground coloration coupled with scattered yellow spots, marginal epidermal glands and, commonly, a thin yellow line along the notal border. In several species, dark coloration of gills and rhinophores also occurs (including in the eastern Pacific *C. flavomaculata*, *C. limbaughorum*, *C. nigrobranchiata*, the North Atlantic and Mediterranean *C. pellucida* and the tropical western Atlantic *C. rumia*). An otherwise bizarre species, *Cadlina luarna*, from the East Pacific also has unusual uniformly dark-brown ground coloration (Valdés & Angulo Campillo, 2000). In the eastern Pacific, several *Cadlina* species (e.g. *C. luteomarginata* and *C. modesta*) have previously been described using only morphological data (MacFarland, 1966; Behrens, 1991, Behrens & Hermosillo, 2005), but the cold western Pacific *Cadlina* were never investigated in detail and usually have been identified as amphiboreal *Cadlina laevis*. Uniform white and yellow *Cadlina* specimens without any trace of darker pigmentation can commonly be found throughout the temperate, subarctic and Arctic waters of the Northern Hemisphere from British waters in the north-eastern Atlantic to the Sea of Japan in the north-western Pacific. However, the taxonomic status of all these externally similar forms of one of the most abundant genera of northern nudibranchs remains almost unexplored using modern integrative morphological and molecular approaches, even in the well-studied European North Atlantic fauna. The usefulness of the modern integrative morphological and molecular approach (e.g. Schlick-Steiner *et al.*, 2010; Yeates *et al.*, 2010) has been shown using taxa from various animal phyla (Heethoff *et al.*, 2011; Huelsken *et al.*, 2011; Jansen *et al.*, 2011; Degerlund *et al.*, 2012; Ahmadzadeh *et al.*, 2013; Korshunova *et al.*, 2016a, b, 2017a, b, c, 2018a, b, 2019). Johnson (2010) presented molecular data on several *Cadlina* species from different regions showing significant diversity. Here we use an integrative morphological and molecular approach and employ a broad geographic sampling of North Atlantic British and Norwegian waters, the Arctic Barents and White seas, north-eastern Pacific waters of the USA and Canada and western Pacific waters of Kamchatka and the Sea of Japan to address the question of how many white-and-yellow species of the genus *Cadlina* inhabit cold Northern Hemisphere waters. An important part of such a study is to test whether the North Atlantic type species of the genus *Cadlina*, *C. laevis*, represents a single species or is an example of hidden diversity. We have uncovered a pattern where intraspecific morphological variability in the North Atlantic *C. laevis* is overlaid with the diagnostics for particular species patterns from the North Pacific, such as *C. jannanicholsae*, *C. klasmalmbergi*, *C. luteomarginata*, *C. sylviaearleae* and *C. umiushi*. All five species have whitish ground coloration with a yellow line that borders the notal edge, similar to rarer variations of *C. laevis* occuring in Ireland and in the White Sea (see Fig. 2). *Cadlina kamchatica*, which is commonly dark yellow to brownish, is similar to some rarer *C. laevis* variations, for example from Sweden (see Fig. 3F). Previously a pattern had been shown for similar and closely related polychromic species of chromodoridid nudibranchs, suggesting different mimicry circles (Padula *et al.*, 2016). In this study, we show that some variation in one species (*C. laevis*) may correspond to diagnostic features in other species. While north-eastern Pacific *C. jannanicholsae*, *C. klasmalmbergi*, *C. luteomarginata* and *C. sylviaearleae*, although having the yellow notal line, still have some features (e.g. more distinct dorsal tubercles, the notal yellow line itself is thicker, etc.) that make it possible to relatively easily distinguish them from *C. laevis* using external characters (radular and internal features in these species are substantially different from *C. laevis*), the north-western Pacific species *C. umiushi* is hardly distinguishable from *C. laevis* variations with a yellow notal line (compare Figs 3G, I and 7A–E) also because, compared to the north-eastern Atlantic species, *C. umiushi* belongs to the same clade as *C. laevis* (Fig. 2) and shares similar radular features. However, *C. umiushi* and *C. laevis* can be distinguished by some minor but reliable external and internal features like a greater number of radular rows and a more distinct and always present yellow notal line in *C. umiushi*. We, therefore, hypothesize a mechanism of speciation, when a feature that existed in one species as a variation becomes a dominant distinguishing character in another species.

GENERIC AND FAMILY PLACEMENT OF *CADLINA SAGAMIENSIS* BABA, 1937 AND ITS RELATIONSHIP TO THE PHANEROBRANCH FAMILY HEXABRANCHIDAE

Kikutaro Baba (1937, 1949) described two Japanese species in the genus *Cadlina*, *C. japonica* and *C. sagamiensis*, but did not comment that the latter species has significant morphological (both external and internal) differences from other *Cadlina* species. These features include a highly elevated dorsum with large conspicuous tubercles, long gills with numerous branched pinnulae, elongate central teeth with an umbrella-like pattern of denticles and the pattern of insertion of the receptaculum seminis directly to the base of the bursa. While the radular pattern is partly similar to *C. japonica* and several north-eastern Pacific species described above, the pattern of the receptaculum–bursa arrangement is radically different from any Cadlinidae and similar to those in several Chromodorididae (e.g. Rudman, 1984; Johnson, 2010).

Schrödl & Millen, (2001) were the first to highlight the morphological discrepancy between '*C.*' *sagamiensis* and other species of the genera *Cadlina* and *Tyrinna*, and transferred it to the genus *Cadlinella* with a reservation that for '*C.*' *sagamiensis* the reproductive system is unknown and its arrangement in the genus *Cadlinella* needed to be confirmed. In our study, we investigated the reproductive system of '*C.*' *sagamiensis* and presented molecular data for this enigmatic dorid taxon, and integrated it into the dorid phylogeny (Figs 2, 21, 22). According to the present integrative data, '*C.*' *sagamiensis* neither belongs to Cadlinidae, nor to *Cadlinella*. Instead, it is phylogenetically (Figs 2, 21, 22) related to both *Cadlinella* and Hexabranchidae. The latter has the typical phanerobranch gill condition of a total absence of a gill cavity and at the same time possesses a multiserial radula with hamate teeth, a common characteristic for the true cryptobranchs. We also show that *Cadlinella s.s.* is not placed within the Chromodorididae as was suggested previously (Johnson, 2010) and we, therefore, resurrect the family Cadlinellidae Odhner, 1934 for this genus. Thus, the integrative data presented here on the taxon '*Cadlinella*' *sagamiensis* has a general importance for dorid phylogeny, because it directly contributes to that crucial problem of dorid evolution of the relation of phanerobranch and cryptobranch modes of gill organizations. Furthermore, according to morphological data, the reproductive system of '*C.*' *sagamiensis* is not similar to the genus *Cadlinella* (and hence, to the family Cadlinellidae) nor to the genus *Cadlina* (and hence, to the family Cadlinidae) (compare Fig. 20A and B). While numerous genera of Chromodorididae have a predominantly vaginal type of seminal reservoir arrangement where the receptaculum inserts close or directly to the base of the bursa (Fig. 20A) (terminology according to: Odhner, 1926; Schrödl, 2000, 2003); instead Johnson (2010) called that type a 'semiserial' one, Cadlinidae and Cadlinellidae instead have a semiserial type ['serial' according to Johnson (2010)], where the receptaculum is placed distantly from the bursa via a separate duct (Figs 15, 20B). The arrangement of the seminal reservoirs of '*C.*' *sagamiensis* perfectly fits the vaginal type arrangement (Fig. 20A), common in Chromodorididae, but not the semiserial/pseudo-semiserial as is typical in Cadlinidae and Cadlinellidae (Figs 15 and 20).

Thus, while the reproductive system of '*C.*' *sagamiensis* demonstrates morphological similarity to the phylogenetically distantly related families Chromodorididae and Dorididae *s.s.*, the pattern of the reproductive system of the phylogenetically more closely related family Cadlinellidae is substantially different. We additionally investigated a representative of the true genus *Cadlinella*, '*C.*' *subornatisima* Baba, 1996 from Japan (see Figs 16, 20B) and the semiserial type of the reproductive system [terminology according to Schrödl (2003) not Johnson (2010)]; in the latter reference the vaginal type is termed a 'semiserial' one, whereas 'semiserial' is called a 'serial' one. The reproductive system of *C. subornatisima* agrees with the type species of the genus *Cadlinella*, *C. ornatissima* Risbec, 1928, as depicted in Rudman (1984), with the exception that Rudman called it 'pseudo semiserial' because of the potential presence of a thin duct from the receptaculum to the bursa. We cannot exactly confirm (Fig. 20B) such an arrangement for *C. subornatissima*, which is placed in the same clade with the type species of *Cadlinella*, *C. ornatissima* (Figs 2, 21, 22) according to our molecular data. In any case, the arrangement of the receptaculum and bursa in '*C.*' *sagamiensis* has nothing in common with either *C. ornatissima* or *C. subornatissima*, because in the former the receptaculum is directly inserted into the base of bursa, without any long ducts. In the only other described species of *Cadlinella*, *C. hirsuta* Rudman, 1995, the arrangement of the bursa and receptaculum (according to fig. 7 in Rudman, 1995) can be considered a semiserial type, and not a vaginal one. Thus, the enigmatic taxon, '*C.*' *sagamiensis* is phylogenetically related to the morphologically extremely disparate family Hexabranchidae (no gill cavity, dorid-like smooth hamate teeth) and to the family Cadlinellidae with which it does not share similarities in the reproductive system. Instead, the reproductive system of '*C.*' *sagamiensis* is similar to the phylogenetically distantly related (Fig. 20A) family Chromodorididae. Therefore, the partial similarity of the radulae (with the presence of distinct central teeth with several cusps and denticulated outer lateral teeth) between '*C.*' *sagamiensis* and families Cadlinidae, Cadlinellidae and some Chromodorididae (particularly, the genus *Tyrinna*) is likely due to a plesiomorphic condition, because Cadlinidae, Cadlinellidae and the chromodorid *Tyrinna* with considerably similar radula are phylogenetically distantly related (Johnson, 2010; present study, Figs 2, 21, 22). In such a situation, if we taxonomically place '*C.*' *sagamiensis* in the phylogenetically related but morphologically strongly disparate Hexabranchidae, we may produce an artificial group that will be united merely by molecular data, while patterns of the gill apparatus and reproductive systems will be fundamentally different. If we instead try to place '*C.*' *sagamiensis* in Cadlinellidae, we would need to accept that any morphologically diagnosable features of the reproductive system, as outlined by Schrödl (2003) and Johnson (2010), are not taxonomically informative and on a large scale if morphological characters were disregarded it would defeat the purpose of an 'integrative' taxonomy. Although radulae between '*C.*' *sagamiensis* and *Cadlinella s.s.* are superficially similar due to the plesiomorphic condition, the details of the central and lateral teeth are considerably different (compare Figs 16I and 19I), thus not allowing '*C.*' *sagamiensis* to be maintained in *Cadlinella*. The type species of *Cadlinella* was originally described in *Cadlina* (Risbec, 1928; Thiele, 1931; Yonow, 2012) and the decision to separate that taxon was also influenced by the similarity of the radula. Therefore, to accommodate this morphological and molecular disparity we proposed the new genus *Showajidaia* into a new family Showajidaiidae for '*C.*' *sagamiensis*. According to morphological and molecular information presented here, Showajidaiidae represents one of the earlier offshoots of major basal dorid radiation, when the various taxa with plesiomorphic denticulate central teeth of the radula were not yet as distinctly differentiated as they are now (Figs 2, 21, 22).

EVOLUTIONARY PATHWAYS OF DORID NUDIBRANCHS AND THE PLESIOMORPHIC STATE OF THE GILL CAVITY

Dorids have usually been divided into the widely accepted, monophyletic groups Cryptobranchia (gill cavity present) and Phanerobranchia (gill cavity absent) (e.g. Odhner, 1934; Schmekel & Portmann, 1982; Thompson & Brown, 1984; Rudman, 1998; Wägele & Willan, 2000). There were also other classification schemes of dorids that did not consider this cryptobranch–phanerobrach dichotomy, but were based on some details of the reproductive systems (e.g. Minichev & Starobogarov, 1979; Golikov & Starobogatov, 1988). These reproductive system-based dorid and opisthobranch classifications turned out to be factually and logically inaccurate (Willan, 1987; Martynov, 1995).

Recently, Hallas *et al.* (2017: 17) mentioned that their study 'reinforces the conclusion from previous studies that traditional phanerobranch and cryptobranch groupings are not monophyletic'. Under 'previous studies' they mentioned three works – Valdés (2002), Wägele & Willan (2000) and Hallas *et al.* (2015). However, among cited works, Wägele & Willan (2000: 165) clearly reached a completely opposite conclusion: 'The Cryptobranchia and the Phanerobranchia seem to be monophyletic groups.' Hallas *et al.* (2017) did not mention the work where independent loss of the gill cavity, and hence a non-monophyletic origin of the phanerobranch dorids, had been explicitly stated for the first time (Martynov, 1999a: 13–14). The first molecular phylogeny that included data for the unambiguously 'cryptobranch phanerobanch', *Onchimira*, was presented at the Opisthobranch Workshop in Porto, Portugal, (Martynov *et al.*, 2015c) and confirmed placement of the genus *Onchimira* in Onchidorididae. Two years later the molecular results on the placement of *Onchimira* in Onchidorididae were repeated in Hallas *et al.* (2017).

Penney *et al.* (2018: 1) mentioned that recent works 'questioned the monophyly of the Cryptobranchia', and cited, among others, the paper by Martynov & Schrödl (2011). In this respect, we need to indicate that in this paper the monophyly of the traditional taxon Cryptobranchia was tested and evidence was provided that the cryptobranch gill cavity is a plesiomorphic condition and that other types of gill patterns in Onchidorididae and Corambidae have originated by secondary modifications of the ancestral gill cavity. A large corpus of integrative data provides evidence for the primacy of cryptobranch dorids in nudibranch evolution, and hence, their monophyly in an expanded concept, i.e. including phanerobranchs (Martynov & Schrödl, 2011; Martynov & Korshunova, 2015; Martynov *et al.*, 2016). Despite this, the main conclusion of the Hallas *et al.* (2017: 17) study was that 'it is unclear how or under what conditions the gill pocket might have evolved or was lost throughout the Doridina because of the lack of resolution at the base of the tree'.

In the present study, analysis of a carefully checked dataset of a representative taxon selection encompassing most of the dorid families, including several key taxa such as *Showajidaia sagamiensis* and several taxa of Cadlinidae, results in a revised dorid phylogeny (Figs 1, 21, 22). There are still several problems with some clades, but the major pattern did not change in our obtained trees; for example, the more basal

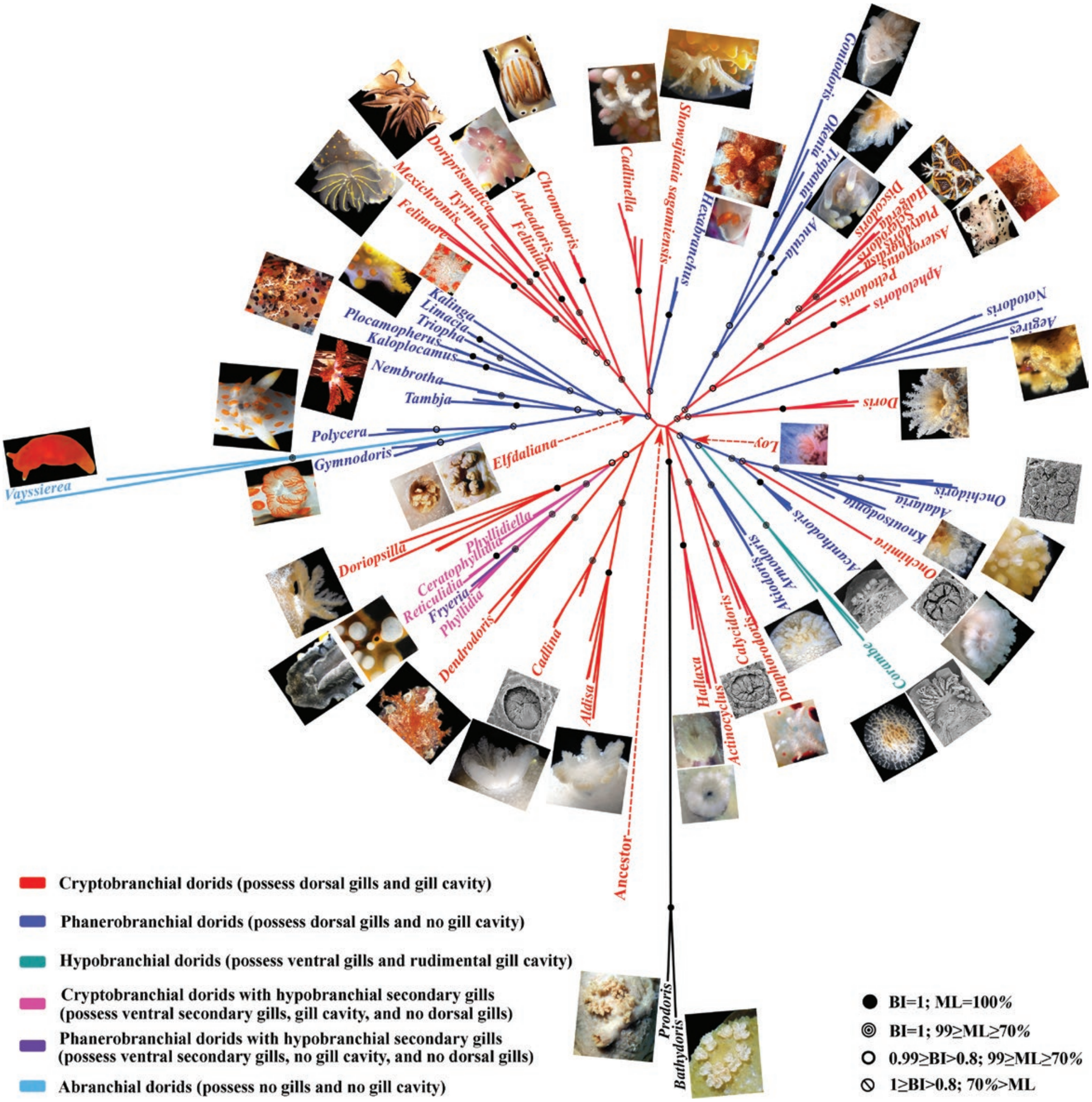

Figure 21. Phylogenetic tree of the dorids based on concatenated molecular data (*COI* + 16S + 28S + 18S) represented by Bayesian inference (BI), represented in a radial tree layout and integrated with the several types of adult gill organization (indicated by different colours, excluding outgroup Bathydorididae, see explanations on the figure).

position of cryptobranch groups like Actinocyclidae, Cadlinidae, Chromodorididae, Dendrodorididae, Phyllidiidae and others. Instead, phanerobranch groups are nested mosaic-like among cryptobranchs (Figs 1, 21, 22). Importantly, some phanerobranch groups, which were unstable in previous analyses (e.g. Hallas *et al.*, 2017), were recovered with considerable node support. For example, Aegiridae was recovered as sister to the cryptobranch family Dorididae and not basal to all dorids (Figs 1, 21, 22). The entire group of true dorids (i.e. without Bathydorididae) has high support in our analysis (Figs 1, 21, 22). Several traditional phanerobranch families either contain true cryptobranch taxa or are sister to well-recognized cryptobranchs, including Calycidorididae (close to Actinocyclidae in some

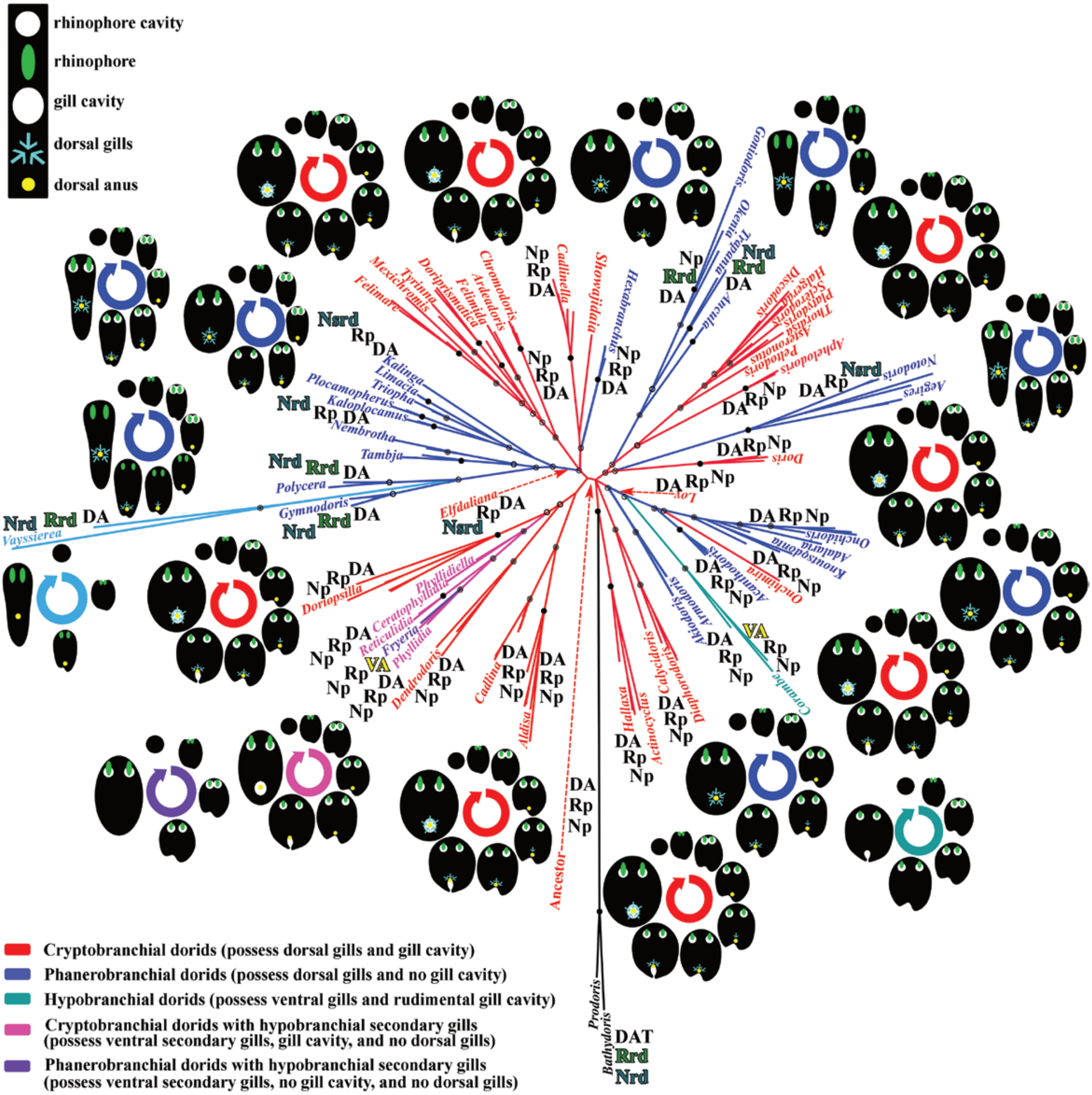

Figure 22. Phylogenetic tree of the dorids based on concatenated molecular data (*COI* + 16S + 28S + 18S) represented by Bayesian inference (BI), represented in a radial tree layout and integrated with ontogenetic information (every icon within the ontogenetic cycle indicates a particular developmental stage). See explanations on the figure and in the Discussion section for the main types of dorid organization.

trees, but most commonly placed basal-most to the phanerobranch Akiodorididae and Onchidorididae and hypobranchs Corambidae), Hexabranchidae (sister to Cadlinellidae) and the phanerobranch family Onchidorididae contains a true cryptobranch genus *Onchimira* (Figs 1, 21, 22).

UPDATED ONTOGENETIC MODEL OF DORID EVOLUTION AND NEW MOLECULAR DATA

The phylogenetic tree in the present analysis is rooted with *Bathydoris*, the gills of which are not retractable into a (lacking) gill pocket. This is one reason the phanerobranch condition was considered a primary

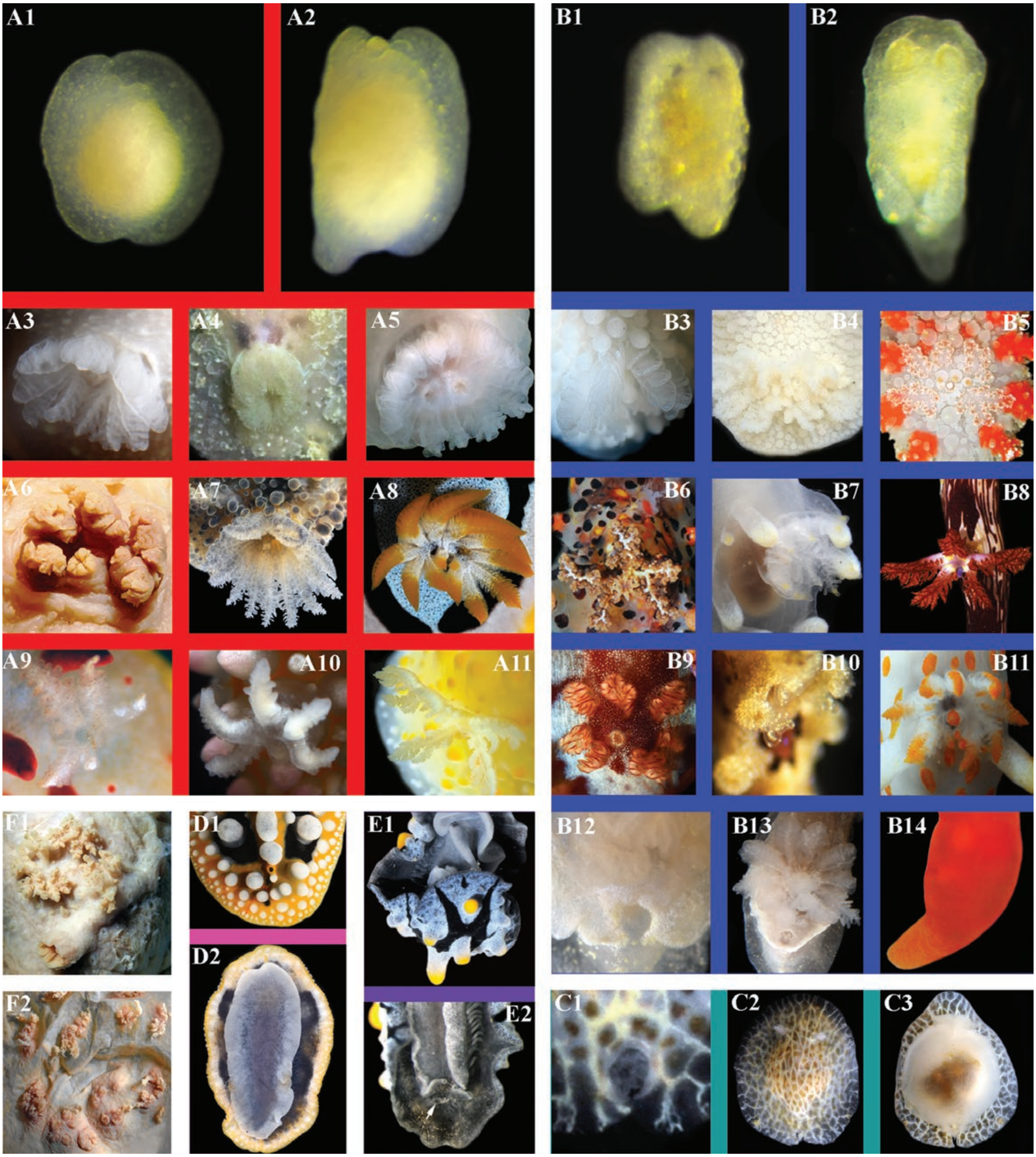

Figure 23. Comparison of early dorid juvenile phylotypic stages [(A1–B2) see Martynov & Korshunova (2015) for details] with adult dorid gill organization. Note essential similarity of the early juveniles of adult cryptobranchs (A1, A2, *C. laevis*) and early juveniles of adult phanerobranchs (in the latter there are rudiments of the gill cavity formation, as in the early juveniles of *Onchidoris muricata*, B1, and *Palio dubia*, B2). Panels coloured in red (A3–A11) represent adult crybrobranch dorids across various families (the formula Np, Rp, G, GC, DA is the same for all species; see text): A3, *Cadlina laevis* (Cadlinidae); A4, *Hallaxa chani* (Actinocyclidae); A5, *Onchimira cavifera* (Onchidorididae); A6, *Elfdaliana profundimontana* (Polyceridae); A7, *Doris verrucosa* (Dorididae); A8, *Chromodoris michaeli* (Chromodorididae); A9, *Diaphorodoris lutescens* (Calycidorididae, Np, Rp, G, GC, DA); A10, *Cadlinella subornatissima*; A11, *Showajidaia sagamiensis* (Showajidaiidae).

one for dorids for a long time and apparently found support in previous morphological cladistic studies (Wägele & Willan, 2000). Using ontogeny-based arguments, a model of dorid evolution has been developed by Martynov *et al.* (2011) and Martynov & Korshunova (2015). Here we update the model with both morphological and molecular data. Particularly, we have selected five key characters of external dorid organization (see Figs 21–23). They are not arbitrarily chosen, but encompass major features of dorid organization, i.e. notum, rhinophores, gills, gill cavity and the position of the anal opening. Exploring these key characters throughout all dorid families we can detect the following states: Np – notal edge present, Nrd – notal edge completely absent (Nsrd – partly reduced, a rare condition, e.g. in *Kalinga* and *Aegires*), Rp – rhinophoral sheaths present, Rrd – rhinophoral sheaths fully reduced, G – gill present, Grd – gills fully reduced, GC – gill cavity present (gill cavity present, additionally coloured red in Figs 21, 22), GCrd – gill cavity fully reduced (coloured blue in Figs 21, 22), DA – dorsal anus (DAT, variant with strongly protruding, more terminally shifted dorsal anus in Bathydorididae only), VA – ventral anus. In most families (16 of 20), gills and gill cavities are present at least in some taxa, whereas a gill cavity is completely absent (i.e. not present even in some included taxa) only in five families. The rhinophoral sheaths were found in an overwhelming majority of families (18), whereas they are absent just in three families. Gills are present also in a majority of families and absent only in two.

Aligning these key external morphological patterns to the molecular phylogeny (Fig. 1), we have found that *Bathydoris* (root) species have a reduced combination of the characters, i.e. Nrd, Rrd, G and GCrd. Thus, only gills (G) are present; other key external characters are reduced. Such a combination appears in full only in two other dorid families (Goniodorididae and Gymnodorididae), which are distantly related to Bathydorididae according to all existing molecular data (Fig. 1). Thus, it is not possible to suggest that within true dorids there are phanerobranch families that are directly related to the phanerobranch Bathydorididae. In the family Polyceridae, most genera have rhinophoral sheaths and in only a few genera (e.g. *Palio* and *Polycera*) are they absent. Such character distribution clearly suggests that reduction of the rhinophoral sheaths evolved secondarily in the largest dorid clade, which has the highest bootstrap support both in Bayesian and maximum likelihood inferences (Fig. 1).

The formation of the gill cavity is ontogenetically similar to the rhinophoral sheaths, as invaginations of early juvenile notal (mantle) edges (Martynov, 2011; Martynov & Korshunova, 2015). The updated ontogenetic scheme that also integrates new molecular data is presented here in Figure 22 (with an ontogenetic cycle for every family, which includes stages where rudiments of the gill cavity and rhinophoral sheaths appear during ontogeny of the phanerobranch or hypobranchs dorids). Therefore, the evolutionary reduction of the gill cavity is a reliable and expected process. The supposedly most basal Bathydorididae has one of the most maximally reduced combinations (except for the family Okadaiidae) of these key external characters, i.e. Nrd, Rrd and GCrd. According to strictly phylogenetic logic (e.g. Hallas *et al.*, 2017), Bathydorididae must have a plesiomorphic phanerobranch condition for all dorids, but according to integrative, ontogenetic and phylogenetic data this is most likely the result of an earlier reduction of the notal edge, rhinophoral sheaths and, ultimately, the gill cavity. There is the following evidence for that: (1) the majority of *Bathydoris* species have fully reduced (absent) notal edges and rhinophoral sheaths, which is definitely not a primary, but a secondary modified feature in nudibranch; (2) only *Bathydoris spiralis* Valdés, 2002 has remnants of the notal edge (but still no rhinophoral sheaths and gill

Panels coloured in blue (B3–B14) represent adult phanerobranch dorids across various families: B3, *Adalaria slavi* (family Onchidorididae, formula Np, Rp, G, GCrd, DA); B4, *Akiodoris lutescens* (Akiodorididae, Np, Rp, G, GCrd, DA); B5, *Kalinga ornata* (Polyceridae, Nsrd, Rp, G, GCrd, DA); B6, *Plocamopherus tilesii* (Polyceridae, Nsrd, Rp, G, GC, DA); B7, *Ancula gibbosa* (Goniodorididae, Nrd, Rrd, G, GCrd, DA); B8, *Nembrotha rutilans* (Polyceridae, Nrd, Rp, G, GCrd, DA); B9, *Hexabranchus sanguineus* (Hexabranchidae, Np, Rp, G, GCrd, DA); B10, *Aegires punctilucens* (Aegiridae, Nsrd, Rp, G, GCrd, DA); B11, *Polycera quadrilienata* (Polyceridae, Nrd, Rrd, G, GCrd, DA); B12, B13, *Goniodoris nodosa* (Goniodorididae, Nrd, Rrd, G, GCrd, DA, with clear rudiments of a semiclosed juvenile gill cavity, as in hypobranchial *Corambe obscura*, family Corambidae (C1–C3, Np, Rp, G, GC, DA). Notably, 'phanerobranch dorids' do not form a consistent morphological unit, e.g. *Onchimira* (A5) ontogenetically belongs to the cryptobranchs (Np, Rp, G, GC, DA), but phylogenetically is a member of phanerobranch Onchidorididae (e.g. B3, Figs 1, 21, 22). The same is true for the cryptobranch *Elfdaliana* (A6) placed among the phanerobranch family Polyceridae (B1), which phylogenetically ended up with a maximally reduced abranchial family Okadaiidae with a formula Nrd, Rrd, Grd, GCrd, DA (B14, *Vayssierea elegans*). Within the family Phyllidiidae the anus became ventral in few species, e.g. *Fryeria picta* (E1, E2, indicated by arrow), but phylogenetically *Fryeria* is nested among cryptobranch genus *Phyllidia* (D1, D2, *P. ocellata*, Np, Rp, Grd, GC, DA), proving that complex ancestral cryptobranch organization underwent independent reduction. In this light, the outgroup for the true dorids, the predominantly deep-sea family Bathydorididae represents a highly reduced external formula Nrd, Rrd, G, GCrd, DAT (F1, *Prodoris clavigera*, F2, *Bathydoris* (s.str.) spp.) that is highly likely to have been evolutionarily derived from more complex ancestors. Not to scale.

cavity); (3) there are no special morphological similarities between other characters of Bathydorididae (such as the radula and reproductive systems) and the few phanerobranch families that have the same combination Nrd-Rrd-GCrd; (4) genera with a highly reduced combination of Nrd-Rrd are nested in some families (e.g. Polyceridae), which otherwise have well-defined rhinophoral sheaths and in some cases also traces of defined notal edges; (5) the gills of Bathydorididae are different from those with superficially similar gills in other phanerobrach families (e.g. *Hexabranchus* and *Kalinga*; Figs 17A, C, 21); (6) *Bathydoris spiralis*, with a non-fully reduced notal edge, has a compact gill corolla, whereas other *Bathydoris* with a fully reduced notal edge have separate gill tufts; (7) during ontogeny, the few compactly placed gills within a cavity-like depression (revealed for the first time in the present study; Fig. 17B) are preceded in the adult stage with separate gills, e.g. in *Hexabranchus* (Figs 17A, 23B9), and at the same time the separate gills of *Hexabranchus* adults are different from any *Bathydoris* by the position of the anus and incomplete symmetry (Figs 21, 23); (8) the existing data on the ontogeny of Bathydorididae show that *Bathydoris* has extremely modified direct development with huge intracapsular 'postlarvae' up to approximately 30 mm in length and estimated duration of egg development approximately 10 years (!) (Moles *et al.*, 2017) – this fact clearly implies that ancestors of recent bathydoridids should have much less specialized ontogeny; (9) there is both morphological and molecular unequivocal evidence that taxa with morphologically indistinguishable gills and gill cavity are deeply nested in otherwise phanerobranch families [as the cryptobranch *Onchimira*, Onchidorididae, with gills that are highly similar to the phylogenetically distantly related Actinocyclidae (Fig. 21) and cryptobranch *Elfdaliana* in phanerobranch Polyceridae; see also Martynov & Korshunova (2015)]; (10) adults of fully phanerobranch families, like, for example, in some genera of Onchidorididae or some Polyceridae, have small precursors of a gill cavity at early juvenile stages (Fig. 22; see also: Martynov & Korshunova, 2015); and (11) we here provide molecular phylogenetic evidence that the phanerobranch *Hexabranchus* is sister to the two cryptobranch families, Showajidaiidae (*S. sagamiensis*) and Cadlinellidae (Fig. 1), but does not show any special similarity to the phanerobranch *Bathydoris* either in external or internal characters. Instead, only a superficial similarity occurs between the external appearance of Bathydorididae with spiny but soft dorsal tubercles and the onchidoridid genus *Acanthodoris*. However, even details of these tubercles are different between *Bathydoris* and *Acanthodoris* (the former has somewhat an aeolid-cerata like detachable tubercles, whereas tubercles of *Acanthodoris* are undetachable ones, typical for all true dorids), which only highlights the deep phylogenetic gap within these taxa (Figs 1, 21, 22). At the same time, juvenile specimens of *Hexabranchus* actually do not differ from cryptobranch dorids and possess a cavity-like structure (Fig. 17B).

We found this series of integrative arguments more reliable for employing ontogenetic data and integrating it with the molecular inferences (Figs 21, 22) and forming the predictive Periodic-like taxonomic Table (see Martynov & Korshunova, 2015), evidently suggesting a primary cryptobranch condition for the highly supported (Fig. 1) clade of true dorids (which includes a majority of the recognized dorid families) and subsequent numerous events of regressive evolution (Figs 21, 22). We also provide substantial evidence that the ancestor of Bathydorididae should possess at least a well-defined notal edge and rhinophoral sheaths, which, in turn, should reliably also predict a gill cavity, but maybe not yet as fully formed as in true dorids. However, in any scenario, if previous common assessments that phanerobranch organization is primary were correct, the pattern of inferred molecular phylogeny should differ considerably from the presently inferred pattern (Fig. 1) and plainly agree with older morphological cladistic analyses when all phanerobranch families were strictly placed in a basal monophyletic clade, and cryptobranchs should appear as a crown group (e.g. Gosliner & Johnson, 1994). However, to the contrary, in all variants of the trees inferred during our study, phanerobrachs dorids never formed a single basal clade or grade, but instead are scattered among true dorids with high bootstrap support, while the most basal dorids are invariably cryptobranchs (Figs 1, 21, 22). The genus *Onchimira*, having the cryptobranch gill apparatus that is indistinguishable from basal cryptobranchs of Actinocyclidae (Figs 21, 23), is nested in Onchidorididae according to molecular phylogenetic data (Martynov *et al.*, 2015c, 2016; present study, Fig. 1) not in the crown group, but close to the genus *Acanthodoris*, which has no gill cavity but a compact corolla of multipinnate gills identical in shape to those in such central cryptobranchs families Dorididae and Discodorididae (Fig. 21). Such a pattern clearly suggests that the gill apparatus of *Onchimira* was not formed *de novo* in Onchidorididae, but instead represents a relic of basal onchidoridid radiation, when earlier cryptobranch taxa, which combined true cryptobranch organization with the onchidoridid special features, existed. The surviving *Onchimira*-like taxa from one side preserved ancestral plesiomoprhic cryptobranch patterns (including corresponding early embryonal *Homeobox* gene properties) and at the same time had already acquired apomorphic onchidoridid characters in the radula and buccal apparatus. *Onchidoris*, which is phanerobranch at the adult state but cryptobranch in juvenile states (Fig. 22), definitely originated by a reduction of the cryprobranch gill cavity of *Onchimira*-like ancestors, as unequivocally implied by previous integrative evidence and our molecular phylogeny (Fig. 1). In all our obtained trees, *Onchidoris* has been invariably placed as a crown phanerobranch group compared to the more basal cryptobranch *Onchimira* (Figs 1, 21), thus fully fulfilling the criteria of even the strictest followers of molecular phylogenies. Therefore, the previous assessment of *Onchimira* being a 'missing link' (see Martynov *et al.*, 2009) between cryptobranchs and phanerobranchs is fully confirmed by the present integrative analysis.

Furthermore, the formerly most enigmatic dorid family, Corambidae, also possessing a cryptobranch-like retractable gill cavity that is fully closed in the genus *Loy* (Martynov *et al.*, 2011), represents a paedomorphic offshoot of early divergence of the onchidoridid from cryptobranch dorids, because corambids never appeared basal to the all dorids (as was incorrectly assessed previously using morphological ontogenetic-free arguments, e.g. Odhner in Franc, 1968; Thompson & Brown, 1984; Rudman, 1998) on any molecular tree, but instead is basal to Onchidorididae, including in the present analysis (Fig. 1). The ontogenetic arguments regarding paedomorphosis in Corambidae were included in the most comprehensive morphological cladistic study on the nudibranchs by Wägele & Willan (2000). Despite that, our previous morphological cladistic analysis of the Corambidae (Martynov & Schrödl, 2011) placed it in a higher position, close to the genus *Adalaria*, compared to the more basal position according to the molecular phylogeny (Fig. 1), we accurately predicted its generally derived position, and not a basal one as was invariably considered in previous morphology-based classifications. The ontogenetic- and molecular-based reconstruction of the major features of evolution among Doridida presented here show that the most reduced variant of the main dorid external features formula, Nrd-Rrd-Grd-GCrd (which implies a complete reduction in gills, see Fig. 22), manifested in Okadaiidae appeared as a definitely secondary clade in Gymnodorididae, which is in turn nested in the traditional Polyceridae. Remarkably, the molecular phylogenetic pattern inferred here was predicted with high accuracy using solely morphological data in an ontogenetic framework, before any molecular data on Okadaiidae (= Vayssiereidae) was available (see Martynov & Korshunova, 2011: 116, 'Based on the radular features, vayssiereids can be descendants of the widely distributed tropical family Gymnodorididae… from which they can have originated by paedomorphosis'). Gymnodorididae, which has the pattern Nrd-Rrd-G-GCrd (both notal edge and gill cavity reduced and no rhinophoral sheaths), is deeply nested in the family Polyceridae (Figs 1, 22), most of which also have a reduced notal edge-gill cavity combination Nrd-Rp-G-GCrd, but with rhinophoral sheaths present. Some polycerid genera, i.e. *Holoplocamus*, have the pattern Nsrd-Rp-G-GCrd (somewhat reduced, but still evident, notal edge and rhinophoral sheaths present), and ultimately, the polycerid genus *Elfdaliana* has a cryptobranch gill cavity (Martynov & Korshunova, 2015) and the fully cryptobranch formula Np-Rp-G-GC (notal edge, gill cavity and rhinophoral sheaths all present).

Nevertheless, the presence of a true cryptobranch genus in the otherwise phanerobranch Polyceridae (Martynov & Korshunova, 2015) was not mentioned in Hallas *et al.* (2017). This is of crucial importance, because if we conditionally consider a maximal lumping system of Polyceridae (e.g. Bouchet *et al.*, 2017, with the family Gymnodorididae as a synonym of Polyceridae, which we are not supporting here) and take into consideration the highly derived position of the families Gymnodorididae and Okadaiidae according to molecular phylogenetic data (Palomar *et al.*, 2014; Hallas *et al.*, 2017; present study), the apparent pan-lumping Polyceridae *s.l.* would include almost all possible stages of reductions of the gill apparatus. For example, such a large family would encompass dramatically different taxa, both externally and internally, such as the true cryptobranch in the basal polycerid *Elfdaliana* (for which there is as yet no molecular data, but we do provide molecular data for the first time here for the similar genus *Kalinga*, which also possesses a multiserial radula, and this genus appears to be one of the most basal among Polyceridae; see Figs 1, 21) and the highly aberrant gill- and cavity-less turbellarian-like *Vayssierea*, which is definitely in a most-derived phylogenetic position (Figs 1, 21). Despite the implication that a family-level classification of the family Polyceridae needs to be revised in a future study (with the potential resurrection of several existing names such as Triophidae and Nembrothidae and the separation of some new ones), there are no doubts that all these morphologically disparate taxa, such as the cryptobranch-looking *Kalinga* with a broad body and multiserial cryptobrach-type radula and the tiny vermiform *Vayssierea*, are all phylogenetically related with evidence for the reduction of the gill cavity and gills in the course of evolution of the true dorids (Figs 21, 22, 23) and not vice versa. Otherwise, several polycerid genera such as *Polycera* and *Palio* with a highly reduced external formula Nrd-Rrd-G-GCrd and the most extremely reduced dorid family Okadaiidae (with formula Nrd-Rrd-Grd-GCrd) would not occupy the most-derived crown position (Fig. 1), but a basal one close to Bathydorididae. On the contrary, there is no morphological- or molecular-based evidence for this. Instead, the presence of the almost full cryptobranch formula Nsrd-Rp-G-GC in the polycerid *Elfdaliana* (with only the notum starting to be reduced) and at the same time a multiserial radula with denticulated teeth and reduced (but still evident) central teeth, makes the linkage to such cryptobranch families as Cadlinidae, Showajidaiidae and Cadlinellidae correspond more to the morphological and molecular data than their linkage to the phanerobranch Bathydorididae. As additional evidence in the present study, we detected not yet cuspidated central teeth (Fig. 6H, I) in the late juvenile specimen of the common North Atlantic cadlinid *Cadlina laevis*, which thus further reinforces the possibility of reduction-based evolution towards smooth central teeth in many phanerobranchs, such as Polyceridae, Akiodorididae and Onchidorididae. Therefore, the solid data obtained in the present study that the cryptobranch family Cadlinellidae is sister to the phanerobranch family Hexabranchidae, which has the formula Np-Rp-G-GCrd (i.e. majority of features, except the gill cavity is not reduced, compared to the different formula of the Nrd-Rrd-G-GCrd in the putatively externally similar Bathydorididae, Fig. 21) is in line with multiple examples of previously outlined evidence for the reliability of multiple independent reduction of the gill cavity in the course of dorid evolution. Thus, further developing an integrative ontogenetic and molecular model of dorid evolution using newly obtained data from previously enigmatic members of the cryptobranch families Cadlinidae and Cadlinellidae we can objectively infer, with a high degree of probability, that the ancestral organization of the Doridoidea, i.e. the largest dorid clade that includes the majority of dorid families, true dorids (Fig. 1), was a cryptobranch one. Further ontogeny-based integration of the molecular data presented in this study will contribute to developing an updated classification of gastropod molluscs.

ACKNOWLEDGEMENTS

Hiroshi Saito (National Museum of Nature and Science, Tsukuba) and Hiroshi Takashige (Tokyo) are warmly thanked for the help during our collecting trip in Japan in September 2016. Special thanks to Kazunori Hasegawa (National Museum of Nature and Science, Tsukuba) for the loan of type materials from the Showa Memorial Institute. Torkild Bakken (NTNU University Museum) and the team of Gulen Dive Resort (Christian Skauge, Ørjan Sandnes, Monica Bakkeli and Guido Schmitz) are thanked for their generous help and support during fieldwork in Norway, as some of these specimens were used for comparative purposes in this study. Electron Microscopy Laboratory MSU is thanked for support with electron microscopy. Molecular work was supported by the German Research Foundation (DFG SCHR667/13, 15 to MS). This study was supported by research project of MSU Zoological Museum (AAAA-A16-116021660077-3), National Council for Scientific and Technological Development (CNPq-Brazil) to VP, in frame of Moscow University Project 'Noah's Ark', and RFBR grant №17-04-01827a (molecular study).

REFERENCES

Ahmadzadeh F, **Flecks M**, **Carretero MA**, **Mozaffari O**, **Böhme W**, **Harris DJ**, **Freitas S**, **Rödder D. 2013.** Cryptic speciation patterns in Iranian rock lizards uncovered by integrative taxonomy. *PLoS ONE* **8:** e80563.

Alder J, **Hancock A. 1842.** Descriptions of several new species of nudibranchous Mollusca found on the coast of Northumberland. *Annals & Magazine of Natural History* **9:** 31–36.

Alder J, Hancock A. 1845–1855. *A monograph of the British nudibranchiate Mollusca: with figures of all the species.* Pt. 1–7. London: Ray Society.

Baba K. 1937. Two new species of the nudibranchiate genus *Cadlina* from Sagami Bay, Japan. *Venus, Japanese Journal of Malacology* **7:** 75–80.

Baba K. 1949. *Opisthobranchia of Sagami Bay collected by His Majesty the Emperor of Japan.* Tokyo: Iwanami Shoten.

Baba K. 1996. Description of a new species of *Cadlinella* (Nudibranchia: Chromodorididae) from Japan. *Venus, Japanese Journal of Malacology* **55:** 265–271.

Behrens DW. 1991. *Pacific coast nudibranchs: a guide to the opisthobranchs, Alaska to Baja California, 2nd edn*. Monterey: Sea Challengers.

Behrens DW, **Hermosillo A. 2005.** *Eastern Pacific nudibranchs, a guide to the opisthobranchs from Alaska to Central America.* Monterey: Sea Challengers.

Belmonte T, **Alvim J**, **Padula V**, **Muricy G. 2015.** Spongivory by nudibranchs on the coast of Rio de Janeiro state, southeastern Brazil (Mollusca, Gastropoda). *Spixiana* **38:** 187–195.

Bergh R. 1879a. Gattungen nordische Doriden. *Archiv für Naturgeschichte* **45:** 340–369.

Bergh R. 1879b. On the nudibranchiate gasteropod Mollusca of the North Pacific Ocean, with special reference to those of Alaska, part 1. *Proceedings of the Academy of Natural Sciences Philadelphia***31:** 71–132.

Bergh R. 1890. Report on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–1878), and in the Caribbean Sea (1879–1880). Report on the nudibranchs. *Bulletin of the Museum of Comparative Zoology, Harvard* **19:** 155–181.

Bergh R. 1892. System der Nudibranchiaten Gasteropoden. Malacologische Untersuchungen. Reisen im Archipel der Philippinen von Dr. Carl Gottfried Semper. Zweiter Theil. *Wissenschaftliche Resultate, Band* **2:** 995–1165.

Bertsch H. 1969. *Cadlina modesta*: a range extension, with notes on habitat and a color variation. *Veliger* **12:** 231–232.

Bertsch H. 1975. Additional data for two dorid nudibranchs from the southern Caribbean seas. *Veliger* **17:** 416–417.

Bouchet P, **Tardy J. 1976.** Faunistique et biogéographie des nudibranches des côtes Françaises de l'Atlantique et de la Manche. *Annales de l'Institut Océanographique, Monaco*, **52:** 205–213.

Bouchet P, **Rocroi J-P**, **Hausdorf B**, **Kaim A**, **Kano Y**, **Nützel A**, **Parkhaev P**, **Schrödl M**, **Strong EE. 2017.** Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* **61:** 1–526.

Burn R. 2015. *Nudibranchs and related molluscs.* Melbourne: Museum Victoria.

Calado G, **Urgorri V**, **Gaspar R**, **Cristobo FJ. 1999.** Catálogo de los moluscos opistobranquios bentónicos de las costas de Setúbal-Espichel (Portugal). *Nova Acta Científica Compostelana (Bioloxía)* **9:** 285–294.

Calado GP, **Malaquias M**, **Gavaia C**, **Cervera L**, **Megina C**, **Dayrat B**, **Camacho Y**, **Pola M**, **Grande C. 2005.** New data on opisthobranchs (Mollusca: Gastropoda) from the southwestern coast of Portugal. *Boletin Instituto Espanol de Oceanografia* **19:** 199–204.

Cattaneo-Vietti R. 1986. Alcune considerazioni sui molluschi opistobranchi del Mar Ligure. *Lavori Società Italiana di Malacologia* **22:** 85–96.

Cervera JL, **Calado G**, **Gavaia C**, **Malaquias M**, **Templado J**, **Ballesteros M**, **Garcia-Gomez JC**, **Megina C. 2004.** An annotated and updated checklist of the opisthobranchs (Mollusca: Gastropoda) from Spain and Portugal (including islands and archipelagos). *Boletin Instituto Espanol de Oceanografia* **20:** 1–122.

Chichvarkhin A. 2016. Shallow water sea slugs (Gastropoda: Heterobranchia) from the northwestern coast of the Sea of Japan, north of Peter the Great Bay, Russia. *PeerJ* **4:** e2774.

Cobb G, **Willan RC. 2006.** *Undersea jewels. A colour guide to nudibranchs.* Canberra: Australian Biological Resources Study.

Collin R, **Díaz MC**, **Norenburg J**, **Rocha RM**, **Sánchez JA**, **Schulze A**, **Schwartz M**, **Valdés A. 2005.** Photographic identification guide to some common marine invertebrates of bocas Del Toro, Panama. *Caribbean Journal of Science* **41:** 638–707.

Degerlund M, **Huseby S**, **Zingone A**, **Sarno D**, **Landfald B. 2012.** Functional diversity in cryptic species of *Chaetoceros socialis* Lauder (Bacillariophyceae). *Journal of Plankton Research* **34:** 416–431.

Domínguez M, **Garcia FJ**, **Troncoso JS. 2006.** Some aspects of the family Chromodorididae (Opisthobranchia: Nudibranchia) from Brazil, with description of a new species. *Scientia Marina* **70:** 621–634.

Edmunds M. 1981. Opisthobranchiate Mollusca from Ghana: Chromodorididae. *Zoological Journal of the Linnean Society* **72:** 175–201.

Eliot CNE. 1906. Report upon a collection of Nudibranchiata from the Cape Verd Islands, with notes by C. Crossland. *Proceedings of the Malacological Society of London* **7:** 131–159.

Eliot CNE. 1910. *A monograph of the British nudibranchiate Mollusca: with figures of the species, pt. VIII (supplementary).* London: Ray Society, 1–198.

Friele H, **Hansen GA. 1876.** Bidrag til kundskaben om de norske Nudibranchier. *Forhandlinger i Videnskabs-Selskabet, Christiania* **1875:** 69–80.

García García FJ. Domínguez Álvarez M. Troncoso JS. 2008. *Opistobranquios de Brasil: Descripción y distribución de opistobranquios del litoral de Brasil y del Archipiélago Fernando de Noronha.* Vigo: Feito, S.L.

García Gómez JC. 2002. *Paradigmas de una fauna insólita. Los moluscos opistobranquios del estrecho de Gibraltar (Serie Ciencias) 20.* Algeciras: Instituto de Estudios Gibraltareños.

García Goméz JC, **Cervera JL**, **García FJ**, **López de la Cuadra CM. 1989.** Resultados de la Campaña Internacional de Biologia Marina 'Ceuta-86': moluscos opistobranquios. *Bollettino Malacologico (Pubblicazione Mensile Edita dalla Societa Italiana di Malacologia)* **25:** 223–232.

Golikov AN, **Starobogatov YaI. 1988.** Questions of phylogeny and system of prosobranch gastropods. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR* **176:** 4–77.

Gosliner TM. 1987. *Nudibranchs of southern Africa, a guide to opisthobranch molluscs of southern Africa.* Monterey: Sea Challengers.

Gosliner TM, **Johnson S. 1994.** Review of the genus *Hallaxa* (Nudibranchia: Actinocyclidae) with descriptions of nine new species. *Veliger* **37:** 155–191.

Hallas JM, **Gosliner TM. 2015.** Family matters: the first molecular phylogeny of the Onchidorididae Gray, 1827 (Mollusca, Gastropoda, Nudibranchia). *Molecular Phylogenetics and Evolution* **88:** 16–27.

Hallas JM, **Chichvarkhin A**, **Gosliner TM. 2017.** Aligning evidence: concerns regarding multiple sequence alignments in estimating the phylogeny of the Nudibranchia suborder Doridina. *Royal Society Open Science* **4:** 171095.

Heethoff M, **Laumann M**, **Weigmann G**, **Raspotnig G. 2011.** Integrative taxonomy: combining morphological, molecular and chemical data for species delineation in the parthenogenetic *Trhypochthonius tectorum* complex (Acari, Oribatida, Trhypochthoniidae). *Frontiers in Zoology* **8:** 2.

Huelsken T, **Dahlmann TA**, **Tapken D**, **Wägele H. 2011.** Systematics and phylogenetic species delimitation within *Polinices* s.l. (Caenogastropoda: Naticidae) based on molecular data and shell morphology. *Organisms Diversity and Evolution* **12:** 349–375.

Ihering HV. 1880. Beiträge zur Kenntniss der Nudibranchien des Mittelmeeres. I. (1. *Chromodoris*, 2. *Doriopsis*, 3. *Cadlina*.). *Malakozoologische Blätter, Neue Følge* **2:** 57–112.

Imajima M. 2003. Polychaetous annelids from Sagami Bay and Sagami Sea collected by the Emperor Showa of Japan and deposited at the Showa Memorial Institute, National Science Museum, Tokyo (II): orders included within the Phyllodocida, Amphinomida, Spintherida and Eunicida. *National Science Museum Monographs* **23:** 1–221.

Iredale T, **O'Donoghue CH. 1923.** List of British nudibranchiate Mollusc. *Proceedings of the Malacological Society of London* **15:** 201–233.

Jansen M, **Bloch R**, **Schulze A**, **Pfenninger M. 2011.** Integrative inventory of Bolivia's lowland anurans reveals hidden diversity. *Zoologica Scripta* **40:** 567–583.

Johnson RF. 2010. Breaking family ties: taxon sampling and molecular phylogeny of chromodorid nudibranchs (Mollusca, Gastropoda). *Zoologica Scripta* **40:** 137–157.

Just H, **Edmunds M. 1985.** North Atlantic nudibranchs (Mollusca) seen by Henning Lemche, with additional species from the Mediterranean and the north east Pacific. *Ophelia, Supplement* **2:** 1–170.

Katoh K, **Misawa K**, **Kuma K**, **Miyata T. 2002.** MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* **30:** 3059–3066.

Korshunova TA, **Sanamyan N**, **Zimina O**, **Fletcher K**, **Martynov AV. 2016a.** Two new species and a remarkable record of the genus *Dendronotus* from the North Pacific and Arctic oceans (Nudibranchia). *ZooKeys* **630:** 19–42.

Korshunova TA, **Sanamyan NP**, **Martynov AV. 2016b.** Morphological and molecular evidence indicate *Dendronotus primorjensis* is a valid species that has priority over *D. dudkai* (Nudibranchia). *ZooKeys* **634:** 15–28.

Korshunova TA, **Martynov AV**, **Bakken T**, **Evertsen J**, **Fletcher K**, **Mudianta WI**, **Lundin K**, **Schrödl M**, **Picton B. 2017a.** Polyphyly of the traditional family Flabellinidae affects a major group of Nudibranchia: aeolidacean taxonomic reassessment with descriptions of several new families, genera, and species (Mollusca, Gastropoda). *ZooKeys* **717:** 1–139.

Korshunova TA, **Zimina O**, **Martynov AV. 2017b.** Unique pleuroproctic taxa of the nudibranch family Aeolidiidae from the Atlantic and Pacific Oceans, with description of a new genus and species. *Journal of Molluscan Studies* **83:** 409–421.

Korshunova TA, **Martynov AV**, **Picton B. 2017c.** Ontogeny as an important part of integrative taxonomy in tergipedid aeolidaceans (Gastropoda: Nudibranchia) with a description of a new genus and species from the Barents Sea. *Zootaxa* **4324:** 1–22.

Korshunova TA, **Lundin K**, **Malmberg K**, **Picton B**, **Martynov AV. 2018a.** First true brackish-water nudibranch mollusc provides new insights for phylogeny and biogeography and reveals paedomorphosis-driven evolution. *PLoS ONE* **13:** e0192177.

Korshunova TA, **Fletcher K**, **Lundin K**, **Picton B**, **Martynov AV. 2018b.** The genus *Zelentia* is an amphi-boreal taxon expanded to include three new species from the North Pacific and Atlantic oceans (Gastropoda: Nudibranchia: Trinchesiidae). *Zootaxa* **4482:** 297–321.

Korshunova TA, **Picton B**, **Furfaro G**, **Mariottini P**, **Pontes M**, **Prkić J**, **Fletcher K**, **Malmberg K**, **Lundin K**, **Martynov AV. 2019.** Multilevel fine-scale diversity challenges the 'cryptic species' concept. *Scientific Reports* **9:** 6732.

Kumar S, **Stecher G**, **Tamura K. 2016.** MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* **33:** 1870–1874.

Lance JR. 1962. Two new opisthobranch mollusks from southern California. *Veliger* **4:** 155–159.

Linnaeus C. 1767. *Systema naturae per regna tria naturae. Edito duodecima, reformata. Vol. 1, Regnum animale. Pt. 2.* Stockholm: L. Salvius, 533–1327.

MacFarland FM. 1905. A preliminary account of the Dorididae of Monterey Bay, California. *Proceedings of the Biological Society, Washington* **18:** 35–54.

MacFarland FM. 1906. Opisthobranchiate Mollusca from Monterey Bay, California, and vicinity. *Bulletin of the United States Bureau of Fisheries* **25:** 109–151.

MacFarland FM. 1966. Studies of opisthobranchiate mollusks of the Pacific coast of North Americ. *Memoirs of the California Academy of Sciences* **6:** 1–546.

Marcus ER. 1955. Opisthobranchia from Brazil. *Boletim da Faculdade de Filosofia, Ciências e Letras, Universidade de São Paulo, Zoology* **207:** 89–261.

Marcus ER. 1958. On western Atlantic opisthobranchiate gastropods. *American Museum Novitates* **1906:** 1–82.

Marcus ER. 1959. Reports from the Lund University Chile Expedition 1948–49, No. 36. Lamellariacea und Opisthobranchia. *Lunds Universitets Årsskrift (Ny Följd), Avd. 2* **55:** 1–133.

Marcus ER. 1961. Opisthobranch mollusks from California. *Veliger* **3:** 1–85.

Marcus EV, **Marcus ER. 1963.** Opisthobranchs from the Lesser Antilles. *Studies on the Fauna of Curaçao and other Caribbean Islands* **19:** 1–76.

Marcus EV, **Marcus ER. 1967.** American opisthobranch mollusks. Part I, tropical American opisthobranchs. Part II, opisthobranchs from the Gulf of California. *Studies in Tropical Oceanography, Miami* **6:** 1–256.

Martynov AV. 1994a. Materials for the revision of the nudibranch molluscs of the family Corambidae (Gastropoda, Opisthobranchia) Part 1. Taxonomy. *Zoologichesky Zhurnal* **73:** 1–15.

Martynov AV. 1994b. Materials for the revision of the nudibranch molluscs of the family Corambidae (Gastropoda, Opisthobranchia). Part II. Origin. *Zoologichesky Zhurnal* **73:** 36–43.

Martynov AV. 1995. Materials for the revision of the nudibranch family Corambidae (Gastropoda, Opisthobranchia). 2. Origin of the Corambidae. *Hydrobiological Journal* **31:** 59–66.

Martynov AV. 1999a. Buccal pumps, gills pockets and new understanding of the suctorial phanerobranchial dorids. In: Rotolo VG, ed. *Proceedings of the 2nd International Workshop of Malacology: systematics, phylogeny and biology of opisthobranch molluscs. 10–14 June 1999.* Menfi: Istituzione Culturale Federico II, 13–14.

Martynov AV. 1999b. *Nudibranch molluscs of North-West part of the Sea of Japan with discussion on taxonomy and phylogeny of the order Nudibranchia.* Unpublished Ph. D. Thesis. St. Petersburg: Zoological Institute RAS, 424.

Martynov AV. 2011. From 'tree-thinking' to 'cycle-thinking': ontogenetic systematics of nudibranch molluscs. *Thalassas* **27:** 193–224.

Martynov AV, **Korshunova TA. 2011.** *Opisthobranch molluscs of the seas of Russia. A colour guide to their taxonomy and biology.* Moscow: Fiton Press.

Martynov AV, **Korshunova TA. 2012.** *Opisthobranch molluscs of Vietnam (Gastropoda: Opisthobranchia). Benthic fauna of the Bay of Nhatrang, southern Vietnam, Vol.* **2**. Moscow: KMK Scientific Press Ltd., 142–257.

Martynov AV, **Korshunova TA. 2015.** A new deep-sea genus of the family Polyceridae (Nudibranchia) possesses a gill cavity, with implications for the cryptobranch condition and a 'Periodic Table' approach to taxonomy. *Journal of Molluscan Studies* **81:** 365–379.

Martynov AV, **Schrödl M. 2011.** Phylogeny and evolution of corambid nudibranchs (Mollusca: Gastropoda). *Zoological Journal of the Linnean Society* **163:** 585–604.

Martynov AV, **Korshunova TA**, **Sanamyan P**, **Sanamyan K. 2009.** Description of the first cryptobranch onchidoridid *Onchimira cavifera* gen. et sp. nov., and of three new species of the genera *Adalaria* Bergh, 1879 and *Onchidoris* Blainville, 1816 (Nudibranchia: Onchidorididae) from Kamchatka waters. *Zootaxa* **2159:** 1–43.

Martynov AV, **Brenzinger B**, **Hooker Y**, **Schrödl M. 2011.** 3D-anatomy of a new tropical Peruvian nudibranch gastropod species, *Corambe mancorensis*, and novel hypotheses on dorid gill ontogeny and evolution. *Journal of Molluscan Studies* **77:** 129–141.

Martynov AV, **Sanamyan NP**, **Korshunova TA. 2015a.** New data on the opisthobranch molluscs (Gastropoda: Opisthobranchia) of waters of Commander Islands and far-eastern seas of Russia. In: *Conservation of biodiversity of Kamchatka and coastal waters. Proceedings of XV international scientific conference Petropavlovsk-Kamchatsky*. Petropavlovsk-Kamchatsky: Kamchat Press, 55–69.

Martynov AV, **Sanamyan NP**, **Korshunova TA. 2015b.** Review of the opisthobranch mollusc fauna of Russian Far Eastern seas: Pleurobranchomorpha, Doridida and Nudibranchia. *Bulletin of Kamchatka State Technical University* **34:** 62–87.

Martynov AV, **Korshunova TA**, **Padula V**, **Picton B**, **Schrödl M. 2015c**. Was the common ancestor of dorids cryptobranchiate or phanerobranchiate? Re-reorganizing onchidoridid systematics. In: *5th International Workshop on Opisthobranchs, Abel Salazar Institute of Biomedical Sciences University of Porto, Porto, Portugal, book of abstracts.* Porto: 32–33.

Martynov AV, **Korshunova TA**, **Padula V**, **Picton B**, **Schrödl M. 2016.** Evolution of dorid nudibranchs: a call for integration of molecular, morphological and developmental data. In: *World Congress of Malacology, Penang, Malaysia, book of abstracts.* Penang: 69.

McDonald GR, **Nybakken JW. 1997.** *List of the worldwide food habits of nudibranchs.* Santa Cruz: University of California.

Miller MC. 1980. *Cadlina willani*, a new dorid nudibranch (Gastropoda: Opisthobranchia) from New Zealand. *New Zealand Journal of Zoology* **7:** 165–171.

Minichev Yu S. 1970. On the origin and system of nudibranchiate molluscs (Gastropoda, Opisthobranchia). *Monitore Zoologico Italiano* **4:** 169–182.

Minichev Yu S, **Starobogatov Ya I. 1979.** *Pecularities of the evolution of the reproductive system and systematics of Opisthobranchia. Molluscs: main results of its investigation.* Leningrad: Nauka, 16–21.

Moles J, **Wägele H**, **Cutignano A**, **Fontana A**, **Ballesteros M**, **Avila C. 2017.** Giant embryos and hatchlings of Antarctic nudibranchs (Mollusca: Gastropoda: Heterobranchia). *Marine Biology* **164:** 114.

MolluscaBase. **2019a.** Infraorder Doridoidei. *World Register of Marine Species.* Available at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=246038 (accessed 15 January 2019).

MolluscaBase. **2019b.** *Cadlinella sagamiensis* (Baba, 1937). *World Register of Marine Species.* Available at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=536917 (accessed 15 January 2019).

MolluscaBase. **2019c.** Infraorder Bathydoridoidei. *World Register of Marine Species.* Available at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=1056908 (accessed 15 January 2019).

MolluscaBase. **2019d.** *Cadlina* Bergh, 1879. *World Register of Marine Species.* Available at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=137781 (accessed 15 January 2019).

Montagu G. 1804. Description of several marine animals found on the south coast of Devonshire. *Transactions of the Linnean Society of London* **7:** 61–85.

Müller OF. 1776. *Zoologiae Danicae. Prodromus seu animalium Daniae et Norvegiae ingenarum characteres, nomina, et synonyma imprimis popularium.* Copenhagen: Hallager.

Nakano R. 2018. *Field guide to sea slugs and nudibranchs of Japan.* Tokyo: Bun-ichi Co.

Nylander JA, **Ronquist F**, **Huelsenbeck JP**, **Nieves-Aldrey JL. 2004.** Bayesian phylogenetic analysis of combined data. *Systematic Biology* **53:** 47–67.

Odhner NH. 1907. Northern and Arctic invertebrates in the collection of the Swedish State Museum (Riksmuseum). III. Opisthobranchia and Pteropoda. *Kungliga Svenska Vetenskaps Akademiens Handlingar, Neue Følge* **41:** 1–113.

Odhner NH. 1921. Mollusca from Juan Fernandez and Easter Island. In: Skottsberg C, ed. *Natural History of Juan Fernandez and Easter Island* **3:** 219–254.

Odhner NH. 1926. Die Opisthobranchien. Further Zoological Results of the Swedish Antarctic Expedition 1901–1903. **2:** 1–100.

Odhner NH. 1934. The Nudibranchiata. British Antarctic ('Terra Nova') Expedition, 1910. *British Museum (Natural History) Natural History Report, Zoology* **7:** 229–310.

Odhner NH. 1968. Sous-classe des opisthobranches. In: Fischer E, Franc A, Martoja M, Termier G, Termier H, eds. *Traité de zoologie. Anatomie, systématique, biologie. Tome V, mollusques gasteropodes et scaphopodes.* Lisboa: Sociedade Portuguesa de Malacologia. 608–893.

Ortea JA. 1988. Opistobranquios nuevos para el litoral iberico colectados en Galicia. I. *Boletin del Instituto Español de Oceanografia* **6:** 49–60.

Ortea JA, **Urgorri V. 1981.** Opistobranquios nuevos para el litoral iberico colectados en Galicia. *I. Boletin del Instituto Español de Oceanografia* **6:** 49–60.

Pabst EA, **Kocot KM. 2018.** Phylogenomics confirms monophyly of Nudipleura (Gastropoda: Heterobranchia). *Journal of Molluscan Studies* **84:** 259–265.

Padula V, **Bahia J**, **Stöger I**, **Camacho-García Y**, **Malaquias MA**, **Cervera JL**, **Schrödl M. 2016.** A test of color-based taxonomy in nudibranchs: molecular phylogeny and species delimitation of the *Felimida clenchi* (Mollusca: Chromodorididae) species complex. *Molecular Phylogenetics and Evolution* **103:** 215–229.

Palomar G, **Pola M**, **Garcia-Vazquez E. 2014.** First molecular phylogeny of the subfamily Polycerinae (Mollusca, Nudibranchia, Polyceridae). *Helgolander Marine Research* **68:** 143–153.

Penney BK, **Ehresmann KR**, **Jordan KJ**, **Rufo G. 2018.** Micro-computed tomography of spicule networks in three genera of dorid sea-slugs (Gastropoda: Nudipleura: Doridina) shows patterns of phylogenetic significance. *Acta Zoologica*: 1–19. Available at: https://doi.org/10.1111/azo.12266 (accessed 20 January 2019).

Picton BE, **Morrow C. 1994.** *A field guide to the nudibranchs of the British Isles.* London: Immel Publishing.

Pruvot-Fol A. 1936a. Note préliminaire sur les nudibranches de Risso. *Revue Suisse de Zoologie* **43:** 531–533.

Pruvot-Fol A. 1936b. Essai d'identification des nudibranches de Risso. *Revue Suisse de Zoologie* **43:** 631–639.

Pruvot-Fol A. 1951. Études des nudibranches de la Méditerranée (2e partie). *Archives de Zoologie Expérimentale et Générale* **88:** 1–80.

Pruvot-Fol A. 1954. Mollusques Opisthobranches. *Faune de France, Paris* **58:** 1–460.

Puillandre N, **Lambert A**, **Brouillet S**, **Achaz G. 2012.** ABGD, Automatic barcode gap discovery for primary species delimitation. *Molecular Ecology* **21:** 1864–1877.

Risbec J. 1928. Contribution a l'étude des nudibranches Néo-Calédoniens. *Faune des Colonies Française* **2:** 1–328.

Risso A. 1826. *Histoire naturelle des principales productions de l'Europe Méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes, Vol.* **4**. Paris: F. G. Levrault.

Roginskaya IS. 1987. Order Nudibranchia Blainville, 1814. In: *Molluscs of the White Sea. Keys to Fauna of SSSR, 151*, Leningrad: Nauka. 155–202.

Ronquist F, **Teslenko M**, **van der Mark P**, **Ayres DL**, **Darling A**, **Höhna S**, **Larget B**, **Liu L**, **Suchard MA**, **Huelsenbeck JP. 2012.** MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61:** 539–542.

Rudman WB. 1984. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: a review of the genera. *Zoological Journal of the Linnean Society* **81:** 115–273.

Rudman WB. 1985. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: *Chromodoris aureomarginata*, *C. verrieri* and *C. fidelis* colour groups. *Zoological Journal of the Linnean Society* **83:** 241–299.

Rudman WB. 1990. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: further species of *Glossodoris*, *Thorunna*, and the *Chromodoris aureomarginata* colour group. *Zoological Journal of the Linnean Society* **100:** 263–326.

Rudman WB. 1995. The Chromodorididae (Opisthobranchia: Mollusca) of the Indo-West Pacific: further species from New Caledonia and the *Noumea romeri* colour group. *Molluscan Research* **16:** 1–43.

Rudman WB. 1998. Suborder Doridina. In: Beesley PL, Ross GJB, Wells A, eds. *Mollusca: the southern synthesis. Fauna of Australia, Vol. 5, part B, Chapter 16.* Melbourne: CSIRO Publishing, 990–1001.

Rudman WB. 2010. Cadlina tasmanica Rudman, 1990. In: *Sea Slug Forum.* Australian Museum, Sydney. Available at: http://www.seaslugforum.net/factsheet/cadltasm (accessed 20 January 2019).

Schlick-Steiner BC, **Steiner FM**, **Seifert B**, **Stauffer C**, **Christian E**, **Crozier RH. 2010.** Integrative taxonomy: a multisource approach to exploring biodiversity. *Annual Review of Entomology* **55:** 421–438.

Schmekel RL, **Portmann A. 1982.** *Opisthobranchia des Mittelmeeres, Nudibranchia und Saccoglossa. Fauna e flora del Golfo di Napoli 40, Monografia della Stazione Zoologica di Napoli.* Berlin+: Springer-Verlag. i–viii, 1–410.

Schrödl M. 2000. Revision of the nudibranch genus *Cadlina* (Gastropoda: Opisthobranchia) from the Southern Ocean. *Journal of the Marine Biological Association of the United Kingdom* **80:** 299–309.

Schrödl M. 2003. *Sea slugs of southern South America*. Hackenheim: ConchBooks.

Schrödl M, **Millen SV. 2001.** Revision of the nudibranch gastropod genus *Tyrinna* Bergh, 1898 (Doridoidea: Chromodorididae). *Journal of Natural History* **35:** 1143–1171.

Stamatakis A, **Hoover P**, **Rougemont J. 2008.** A rapid bootstrap algorithm for the RAxML web-servers. *Systematic Biology* **75:** 758–771.

Stimpson W. 1853. Synopsis of the marine Invertebrata of Grand Manan: or the region about the mouth of the Bay of Fundy, New Brunswick. *Smithsonian Contributions to Knowledge* **6:** 1–66.

Talavera G, **Castresana J. 2007.** Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* **56:** 564–577.

Thiele J. 1912. Die antarktischen Schnecken und Muscheln. *Deutsche Südpolar-Expedition 1901–1903. Zoologie* **5:** 183–285.

Thiele J. 1931. *Handbuch der Systematischen Weichtierkunde. Band 1.* Stuttgart: Gustav Fischer.

Thompson TE, **Brown GH. 1984.** *Biology of opisthobranch molluscs, Vol. 2*. London: Ray Society.

Trainito E. 2005. *Nudibranchi del Mediterraneo guida al riconoscimento dei mollluschi opistobranchi.* Milano: Il Castello.

Valdés Á. 2001. Deep-sea cryptobranch dorid nudibranchs (Mollusca, Opisthobranchia) from the tropical West Pacific, with descriptions of two new genera and eighteen new species. *Malacologia* **43:** 237–311.

Valdés Á, **Angulo Campillo O. 2000.** Redescription and reassessment of *Cadlina luarna* (Ev. Marcus and Er. Marcus, 1967), comb. nov. (Mollusca, Opisthobranchia, Doridina). *Proceedings of the California Academy of Sciences series 4* **52:** 77–85.

Valdés A, **Hamann J**, **Behrens DW**, **Dupont A. 2006.** *Caribbean sea slugs, a field guide to the opisthobranch mollusks from the tropical northwestern Atlantic.* Monterey: Sea Challengers.

Vilella M. 1994. Tres nuevas especies de doridáceos (Gastropoda: Nudibranchia) en la costa del Mediterráneo catalán. *Butlletí del Centre d'Estudis de la Natura del Barcelonès-Nord* **3**: 63 –72.

Wägele H, **Willan RC. 2000.** Phylogeny of the Nudibranchia. *Zoological Journal of the Linnean Society* **130:** 83–181.

Willan RC. 1987. Phylogenetic systematics of the Notaspidea (Opisthobranchia) with reappraisal of families and genera. *American Malacological Bulletin* **5:** 215–241.

Willan RC. 1998. Order Nudibranchia. In: Beesley PL, Ross GJB, Wells A, eds. *Mollusca: the southern synthesis. Fauna of Australia, Vol. 5, part B, Chapter 16.* Melbourne: CSIRO Publishing, 990.

Yeates DK, **Seago A**, **Nelson L**, **Cameron SL**, **Joseph L**, **Trueman JWH. 2010.** Integrative taxonomy, or iterative taxonomy? *Systematic Entomology* **36:** 209–217.

Yonow N. 2012. Opisthobranchs from the western Indian Ocean, with descriptions of two new species and ten new records (Mollusca, Gastropoda). *Zookeys* **197:** 1–129.

SUPPORTING INFORMATION

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

Table S1. Primers.
Table S2. GenBank accession numbers and references for all sequences used in this study.