



Unique pleuroproctotic taxa of the nudibranch family Aeolidiidae from the Atlantic and Pacific Oceans, with description of a new genus and species

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ABSTRACT

Morphological and molecular data on a deep-sea pleuroproctotic taxon of the family Aeolidiidae from the Barents Sea (subarctic North Atlantic) are presented for the first time. *Zeusia* n. gen. is established for the North Atlantic and North Pacific pleuroproctotic species of the family Aeolidiidae with two species: *Z. hyperborea* n. sp. and *Z. herculea* (Bergh, 1894) n. comb. *Zeusia* was recovered as sister to the genus *Aeolidia* in molecular analyses. The two included species of *Zeusia* share the potential synapomorphies of very large seminal receptacle and long vas deferens. A pleuroproctotic anal opening is an important basal character of the group Nudibranchia and the family Aeolidiidae is discussed in the light of the present discovery.

INTRODUCTION

A pleuroproctotic anal opening on the lateral body side below the notal edge is a well established basal character for Nudibranchia (Odhner, 1939; Gosliner & Kuzirian, 1990; Wägele & Willan, 2000). A group Dexiarchia (Doridoxoidea + Cladobranchia) was defined based on the consideration of the plesiomorphic state of the pleuroproctotic opening of the hindgut (Schrödl, Wägele, Willan, 2001). Recently, it was proposed that the pleuroproctotic taxon *Doridoxa* is a basal member of Nudibranchia s. str. (= Cladobranchia), rather than the sister group of Nudibranchia (Martynov, 2011). This proposal was subsequently confirmed by molecular data (Mahguib & Valdés, 2015). These contributions suggest that the pleuroproctotic anus preceded the cleioproctotic and acleioproctotic states in nudibranch evolution. For the internal phylogeny of Nudibranchia, this predicts a basal position of pleuroproctotic taxa in various families. Further tests of this implication are therefore of special interest.

The nudibranchs of the family Aeolidiidae are good candidates for such a test. In the majority of the aeolidiid genera, the anus is cleioproctotic and placed on the dorsal side within branches of the posterior digestive gland (Marcus, 1961; Gosliner, 1985; Miller, 2001). This family includes mainly the warm-water genera with a graceful narrow body and cleioproctotic anus (Carmona *et al.*, 2014a–e). The pleuroproctotic genus *Protaeolidiella* Baba, 1955 (Rudman, 1990) was recently transferred to the family Facelinidae (Carmona *et al.*, 2015). However, the temperate-water genus *Aeolidia* Cuvier, 1798 does include wide-bodied species (Thompson & Brown, 1984; Schrödl, 2003; Kienberger *et al.*, 2016). While most *Aeolidia* species are cleioproctotic, a deep-sea Pacific species *Aeolidia herculea* Bergh, 1894 is pleuroproctotic (Gosliner & Behrens, 1996; Behrens, 2004; Martynov & Korshunova, 2011). Until the

present study, no pleuroproctotic *Aeolidia*-like taxon from the North Atlantic with a notal edge had ever been described.

As a result of a recent molecular phylogeny of the family Aeolidiidae, the position of the anus was considered to be phylogenetically insignificant (Carmona *et al.*, 2013). This contradicts the consideration of a pleuroproctotic anal opening as one of the key plesiomorphies in nudibranch phylogeny (e.g. Gosliner & Kuzirian, 1990; Wägele & Willan, 2000; Schrödl *et al.*, 2001). Therefore, either this aspect of nudibranch evolution is wrong or some relevant aeolidiid taxa were missing in the recent phylogeny. In the latter case, it is predicted that pleuroproctotic taxa would be in a basal position compared with the cleioproctotic ones, at least within some clades. Because of mosaic evolution, the ancestral pleuroproctotic position is likely to be retained only in some recent clades of Aeolidiidae. In that case a basal phylogenetic position of a pleuroproctotic taxon within a particular aeolidiid clade is expected. To differentiate between that and secondary reversals it is also expected to see other defining features of the pleuroproctotic state (including position of anus under the notal edge outside the dorsum and ceratal rows) similar to *Doridoxa*, Tritoniidae and Flabellinidae. Basal taxa of the pleuroproctotic families Doridoxidae and Tritoniidae also have a wide body. The aeolidacean family Flabellinidae is mostly pleuroproctotic and especially the northern and deep-sea taxa have a wide body with a distinct notal edge (Martynov, 2013). The pleuroproctotic Flabellinidae with a distinct notal edge have been considered as basal (Gosliner & Kuzirian, 1990). By analogy, a basal pleuroproctotic taxon of the family Aeolidiidae would also be expected to possess a wide body and a notal edge.

Here we report a pleuroproctotic aeolidiid with a wide body and a notal edge from relatively deep waters of the North Atlantic

(Barents Sea) for the first time. Both morphological and molecular data are provided for this taxon. Morphological characters reveal external similarities to the genus *Aeolidia*, but differ in the pleuroproctus anus and notal edge. Molecular analyses set this taxon apart from any known genera of the Aeolidiidae and it is therefore described here as a new genus and species. A molecular phylogeny shows this new pleuroproctus taxon to be basal to all recently reviewed (Kienberger *et al.*, 2016) cleioproctus species of *Aeolidia*. Thus this new aeolidiid genus fulfills morphological and molecular predictions that support the hypothesis of the ancestral state of the pleuroproctus anus. The North Pacific bathyal '*Aeolidia*' *herculea* is the only known aeolidiid species that demonstrates morphological similarity to the pleuroproctus aeolidiid from the Barents Sea and is included here in the same genus.

MATERIAL AND METHODS

Collection of material

A single specimen of a pleuroproctus aeolidiid was collected in the subarctic Barents Sea (North Atlantic) (preserved in ethanol) and six specimens in the North Pacific by deep-sea trawling (preserved

in 10% formalin). For molecular phylogenetic analysis, several additional specimens of other aeolidiid species were collected in the North Atlantic by SCUBA diving (Table 1). These localities include Norway, Barents Sea and White Sea and all of these specimens were preserved in 80–95% ethanol. All newly collected previously unregistered specimens were deposited in the Zoological Museum of Moscow State University (ZMMU).

Morphological analysis

The external and internal morphology of the specimens was studied under a stereomicroscope and photographed using digital cameras (Nikon D-90 and D-810) with a set of extension rings. The pharynxes were processed with a weak solution of domestic bleach (NaOCl) or by boiling in KOH solution. The jaws and radulae were mounted, coated with platinum and palladium, and examined under a scanning electron microscope (SEM; CamScan Series II) at the electron microscopy laboratory of the Biological Faculty of Moscow State University.

Molecular analysis

All ethanol-preserved specimens were sequenced for part of the cytochrome *c* oxidase subunit I (COI), 16S rRNA (16S) and

Table 1. List of specimens used for molecular phylogenetic analyses.

Species	Locality	COI	16 S	H3
<i>Aeolidia campbellii</i> (Cunningham, 1871)	Chile	KF317849	KF317837	KF317859
<i>Aeolidia filomenae</i> Kienberger <i>et al.</i> (2016)	France	KU160588	KU160562	KU160606
<i>Aeolidia loui</i> Kienberger <i>et al.</i> (2016)	Oregon, USA	KU160591	KU160565	KU160607
<i>Aeolidia papillosa</i> (Linnaeus, 1761)	Barents Sea, Russia (ZMMU Op-558)	KX758258*	KX758253*	KX758262*
<i>Aeolidia papillosa</i> (Linnaeus, 1761)	White Sea, Russia (ZMMU Op-559)	KX758257*	KX758252*	KX758261*
<i>Aeolidia</i> sp. A	France	JX087531	JX087459	JX087593
<i>Aeolidiella alderi</i> (Cocks, 1852)	ZSMML20012341 Italy	HQ616766	HQ616729	HQ616795
<i>Aeolidiella glauca</i> (Alder & Hancock, 1845)	Gulen, Norway (ZMMU Op-560)	KX758255*	KX758254*	KX758259*
<i>Anteaeolidiella cacaotica</i> (Stimpson, 1855)	Line Islands	JQ997030	JQ996825	JQ996926
<i>Anteaeolidiella saldanhensis</i> (Barnard, 1927)	South Africa	JQ997032	JQ996827	JQ996928
<i>Baeolidia moebii</i> Bergh, 1888	Philippines	HQ616770	HQ616733	HQ616799
<i>Baeolidia salaamica</i> (Rudman, 1982)	Philippines	JQ997047	JQ996843	JQ996944
<i>Berghia rissodominguezi</i> Muniain & Ortea, 1999	Cuba	JX087552	JX087484	JX087621
<i>Berghia stephanieae</i> Valdés (2005)	Florida, USA	JQ997044	JQ996839	JQ996940
<i>Berghia verrucicornis</i> (A. Costa, 1864)	Spain	HQ616750	HQ616713	HQ616779
<i>Bulbaeolidia japonica</i> (Eliot, 1913) CASIZ 184527	Japan	JQ997033	JQ996828	JQ996929
<i>Bulbaeolidia</i> sp. B	Hawaii	JQ997022	JQ996817	JQ996916
<i>Cerberilla bernadettae</i> Tardy (1965)	Spain	JX087555	JX087489	JX087625
<i>Flabellina affinis</i> (Gmelin, 1791)	Balearic Is, Spain	HQ616753	HQ616716	HQ616782
<i>Flabellina baetica</i> García-Gómez, 1984	Spain	HQ616755	HQ616718	HQ616784
<i>Flabellina confusa</i> Duarte, Cervera & Poddubetskaia, 2008	France	JX087557	JX087491	JX087627
<i>Flabellina confusa</i> Duarte, Cervera & Poddubetskaia, 2008	France	JX087556	JX087490	JX087626
<i>Flabellina ischitana</i> Hirano & Thompson, 1990	Spain	HQ616757	HQ616720	HQ616786
<i>Flabellina ischitana</i> Hirano & Thompson, 1990	Morocco	HQ616756	HQ616719	HQ616785
<i>Flabellina ischitana</i> Hirano & Thompson, 1990	Spain	–	H1616745	HQ616808
<i>Flabellina pedata</i> (Montagu, 1815)	Spain	HQ616758	HQ616721	HQ616787
<i>Limenandra confusa</i> Carmona, Pola, Gosliner & Cervera, 2014	Philippines	HQ616769	HQ616732	HQ616798
<i>Limenandra nodosa</i> Haefelfinger & Stamm (1958)	Bahamas	JQ997080	JX087527	JQ996991
<i>Piseinotecus gabinieri</i> (Vicente, 1975)	Spain	JX087561	JX087495	JX087631
<i>Piseinotecus gabinieri</i> (Vicente, 1975)	Spain	–	JX087496	JX087632
<i>Piseinotecus gaditanus</i> Cervera, García-Gómez & García, 1987	Spain	HQ616759	HQ616722	HQ616788
<i>Piseinotecus</i> sp.	Philippines	HM162694	HM162604	HM162510
<i>Spurilla neapolitana</i> (Delle Chiaje, 1823)	Portugal	HQ616764	HQ616727	HQ616793
<i>Spurilla sargassicola</i> Bergh, 1871	Bahamas	JQ997098	JQ996901	JQ997010
<i>Zeusia hyperborea</i> n. gen., n. sp.	Barents Sea, Russia (ZMMU Op-557)	KX758256*	KX758251*	KX758260*

*New sequences deposited in GenBank.

histone 3 (H3) genes. Small pieces of tissue were used for DNA extraction with the Diatom™ DNA Prep 100 kit by Isogene Lab, according to the manufacturer's protocols. Partial sequences of COI, 16S and H3 were amplified by PCR using the primers: LCO 1490 (GGTCAACAATCATAAAGATATTGG, Folmer *et al.*, 1994); HCO 2198 (TAAACTTCAGGGTGACCAAAAA TCA, Folmer *et al.*, 1994); 16S arL (CGCCTGTTTAAACAAAA CAT, Palumbi *et al.*, 2002); 16S SR (CCGRTYTGAACCTCA GCTCACG, Puslednik & Serb, 2008); H3 AF (ATGGCTCGTA CCAAGCAGACGG, Colgan *et al.*, 1998) and H3 AR (ATA TCCTTGGGCATGATGGTGAC, Colgan *et al.*, 1998). PCR amplifications were carried out in a 20- μ l reaction volume, which included 4 μ l of 5 \times Screen Mix by Eurogen Lab, 0.5 μ l of each primer (10 μ M stock), 1 μ l of genomic DNA and 14 μ l of sterile water. The amplification of COI was performed with an initial denaturation for 1 min at 95 °C, followed by 35 cycles of 15 s at 95 °C (denaturation), 15 s at 45 °C (annealing temperature) and 30 s at 72 °C, with a final extension of 7 min at 72 °C. The 16S amplification began with an initial denaturation for 1 min at 95 °C, followed by 40 cycles of 15 s at 95 °C (denaturation), 15 s at 52 °C (annealing temperature) and 30 s at 72 °C, with a final extension of 7 min at 72 °C. The amplification of H3 began with an initial denaturation for 1 min at 95 °C, followed by 40 cycles of 15 s at 95 °C (denaturation), 15 s at 50 °C (annealing temperature) and 30 s at 72 °C, with a final extension of 7 min at 72 °C. Sequencing for both strands proceeded with ABI PRISM® BigDye™ Terminator v. 3.1. Sequencing reactions were analysed using an Applied Biosystems 3730 DNA Analyzer. Protein-coding sequences were translated into amino acids for confirmation of the alignment. All sequences were deposited in GenBank (Table 1).

Original data and publicly available sequences were aligned with the MUSCLE (Edgar, 2004) algorithm. Gblocks v. 0.91b (Talavera & Castresana, 2007) was applied to discard poorly aligned regions of the 16S dataset (13% of the positions were eliminated). Separate analyses were conducted for the following datasets: resulting alignment for COI (666 bp), 16S (435 bp), H3 (327 bp) and the concatenated dataset. Evolutionary models for each dataset were selected using MrModelTest v. 2.3 (Nylander *et al.*, 2004) under the Akaike information criterion (Akaike, 1974). The General Time Reversal model with invariant sites and gamma distribution (GTR + I + G) was chosen for COI, 16S, H3 and for the full dataset (1428 bp). Two different phylogenetic methods, Bayesian inference (BI) and maximum likelihood (ML), were used to infer evolutionary relationships. BI estimation of posterior probability (PP) was performed in MrBayes v. 3.2. Markov chains were sampled at intervals of 500 generations. Analysis was started with random starting trees and 10⁷ generations. ML phylogeny inference was performed in GARLI v. 2.0 (Zwickl, 2006) with 1000 bootstrap (BS) pseudoreplications. The final phylogenetic tree images were rendered in the FigTree v. 1.4.2. The program Mega7 (Kumar, Stecher & Tamura, 2016) was used to calculate the minimum p-distances among all the sequences.

RESULTS

The single ethanol-fixed specimen *Zeusia hyperborea* n. gen., n. sp. was successfully sequenced for the COI, 16S and H3 genes. Additionally, two specimens of *Aeolidia papillosa* specimens from the White and Barents seas and an *Aeolidiella glauca* specimen from Norway were sequenced for all three genes (Table 1). Other sequences were obtained from GenBank (see Table 1).

The minimum uncorrected p-distances were calculated and compared for the COI, 16S and H3 fragments. The distances between the holotype of *Z. hyperborea* and members of other aeolidiid genera are shown in Table 2. The highest genetic divergences were found for the COI gene, with a range of 17.02–20.82%. The

divergences ranged between 5.94% and 11.93% for 16S and 2.2% and 8.82% for H3. The lowest distances occurred between *Z. hyperborea* and '*Cerberilla*' *bernadettae* (17.02%) for COI, *Z. hyperborea* and *Aeolidia campbellii* (5.94%) for 16S and *Z. hyperborea* and *A. campbellii* (2.2%) for H3. Whereas the distance values occur between *Aeolidia campbellii* and *Aeolidia filomenae* (4.7%) for 16S and (1.5%) for H3.

The molecular phylogenetic relationships were best resolved in the analyses of the combined dataset (Fig. 1) than when COI, 16S or H3 were analysed separately (not shown). In the combined analyses, all *Aeolidia* species clustered together (PP = 1, BS = 97) in a well-supported clade that is sister to the well-supported *Zeusia* clade (PP = 1, BS = 93).

SYSTEMATIC DESCRIPTIONS

AEOLIDIIDAE Gray, 1827

Zeusia new genus

Type species: *Zeusia hyperborea* n. sp.

ZooBank registration: urn:lsid:zoobank.org:act:29669379-2E31-467E-AC7F-E65314 AFB2AA

Etymology: After the Greek god Zeus, father of Hercules, in reference to the binomen *Zeusia herculea* (Bergh, 1894) n. comb. The classical allusion is continued in the specific name of the type species.

Diagnosis: Body elevated, broad. Ceratal rows simple, in oblique rows, directed from centre towards periphery. Rhinophores minutely tuberculated to smooth. Cerata flattened. Anus pleuroproctic, on lateral side of body under reduced notal ridge. Eyes small. Jaws strong, masticatory processes smooth. Radula uniseriate, teeth crescent-shaped. Teeth moderately bilobed or middle indentation absent. Central cusp moderate to well defined, denticulate or absent. Receptaculum seminis very large. Vas deferens long, convoluted. Penis elongated.

Remarks: See below.

Zeusia hyperborea n. gen., n. sp.

(Figs 2, 4A)

Type material: Holotype: ZMMU Op-557, Barents Sea, R/V *G.O. Sars*, stn 278, 74°20.28'N 17°23.95'E, 23.09.2015, depth 176 m, Campelen trawl, leg. O.L. Zimina.

ZooBank registration: urn:lsid:zoobank.org:act:F1018191-9AAB-416 A-A549-F5356CD65BEA

Etymology: After Hyperborea, a northern country in Greek mythology, in reference to the locality of the new species beyond the Arctic Circle.

Diagnosis: Body slightly elevated. Notal edge reduced, but with free border. Teeth moderately bilobed or middle indentation absent. Central cusp moderate to large, smooth or denticulate. Fork-shaped denticles absent. Receptaculum seminis very large, broad. Vas deferens long, convoluted. Penial sheath elongated.

External morphology (Fig. 2A–C): Living holotype 15.5 mm long, 7 mm wide, 5 mm high. Body broad, slightly elevated, slightly narrowed posteriorly. Head about 1.5 times narrower than widest part of foot. Oral tentacles finger-shaped, short. Rhinophores

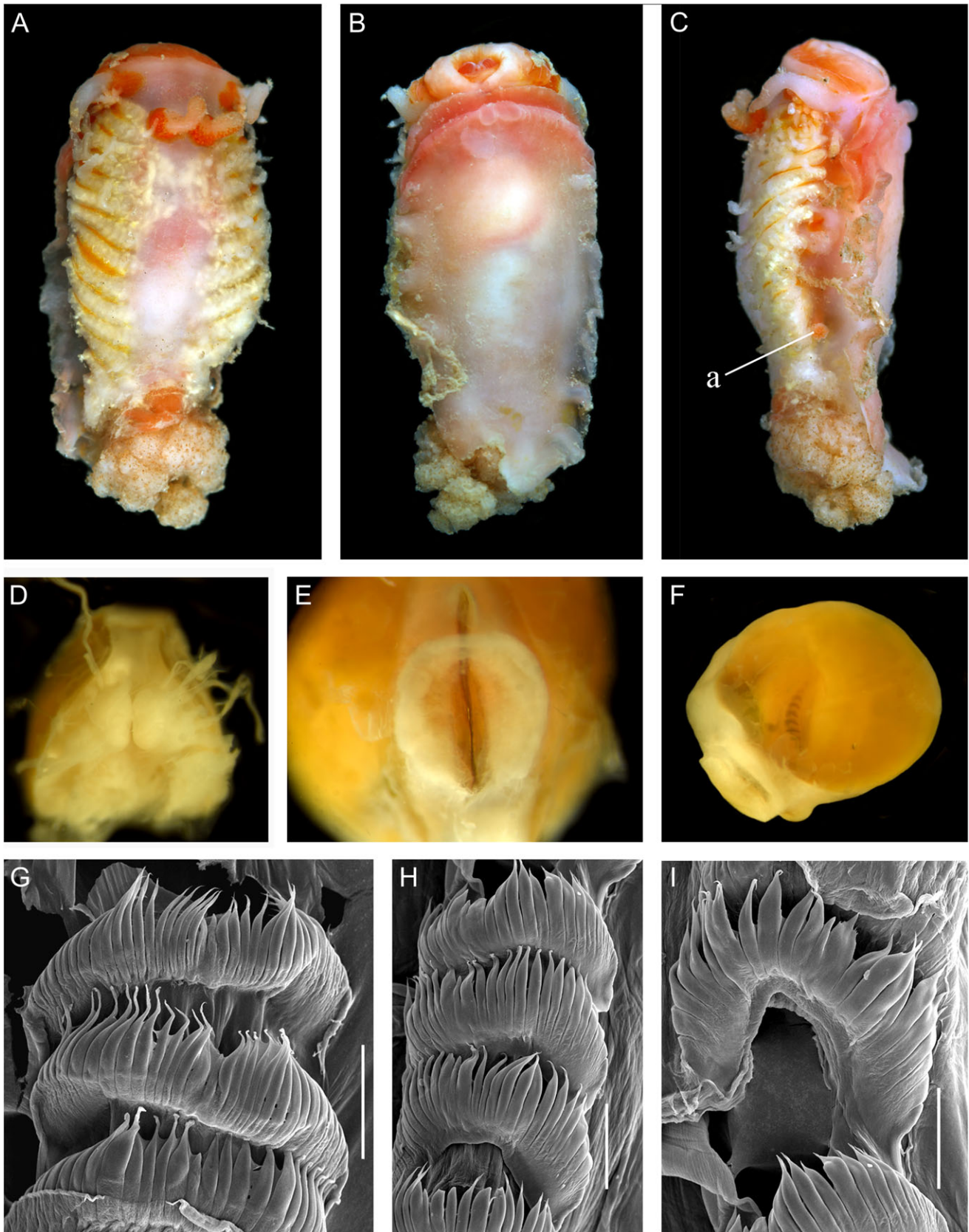


Figure 2. *Zeusia hyperborea* n. gen., n. sp., holotype (ZMMU Op-557), Barents Sea, North Atlantic. **A.** Dorsal view. **B.** Ventral view. **C.** Lateral view, right side. **D.** Central nervous system and pharynx. **E.** Pharynx, anterior view showing masticatory processes of jaws. **F.** Pharynx with jaws and translucent brown radula, lateral view. **G.** Three anterior radula teeth. **H.** Four posterior radula teeth. **I.** Two middle radula teeth. Abbreviation: a, anus. Scale bars: **G–I** = 100 μ m. Colour photographs (**A–C**) by O. Zimina; light microscopy (**D–F**) and SEM images (**G–I**) by A. Martynov.

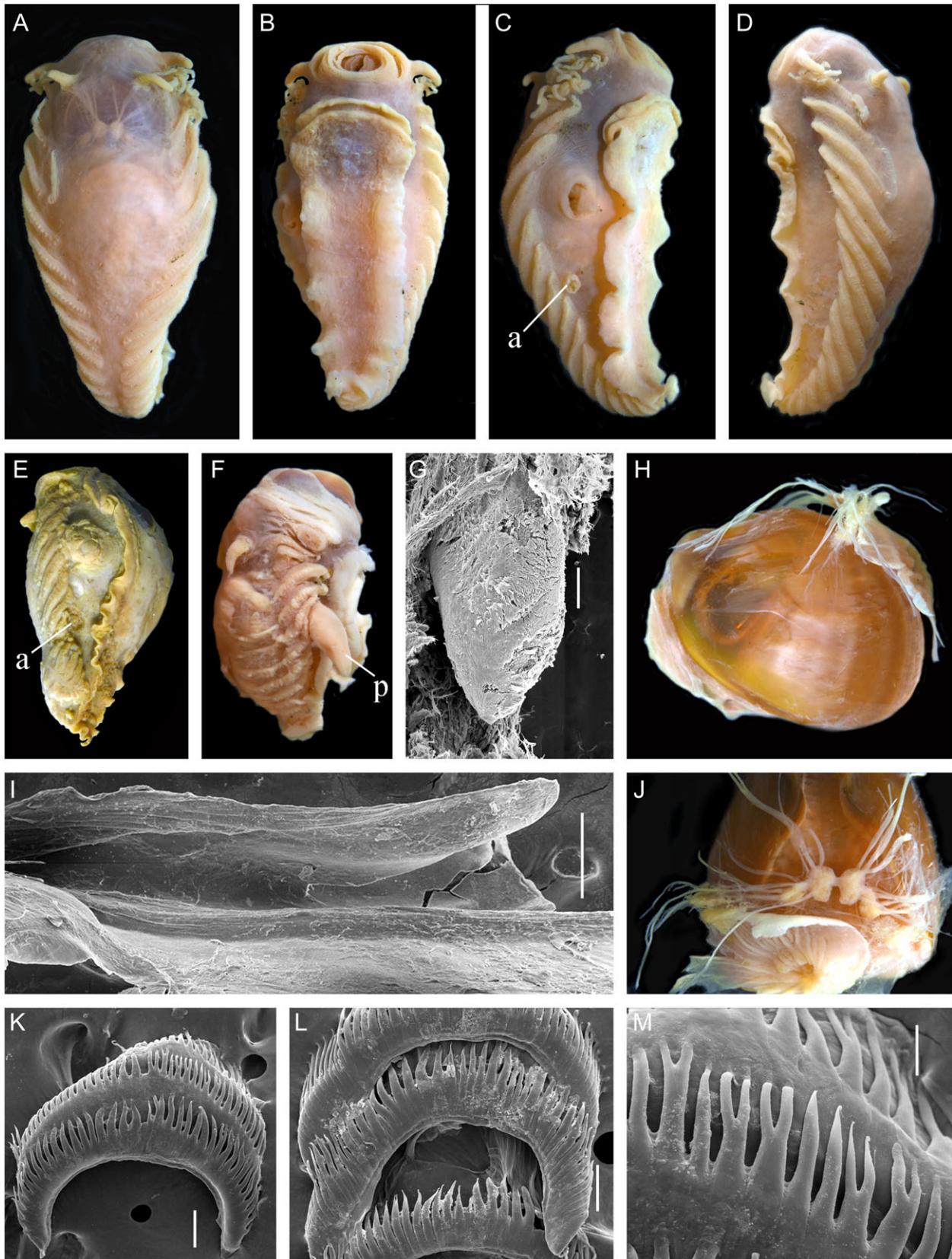


Figure 3. *Zeusia herculea* (Bergh, 1894) n. comb. **A–D, F–M**, fixed specimen, 31 mm long (ZIN N 3), Bering Sea. **A**. Dorsal view. **B**. Ventral view. **C**. Lateral view, right side. **D**. Lateral view, left side. **G**. Penis. **H**. Jaws and central nervous system on pharynx, lateral view. **I**. Masticatory process of jaws. **J**. Central nervous system and pharynx. **K**. Three anterior radula teeth. **L**. Three posterior radula teeth. **M**. Details of anterior radula teeth. **E**. Syntype of ‘*Aeolidia*’ *grandis* (ZIN N 1; synonym or congener of *Z. herculea*, see text), Okhotsk Sea, 25 mm long. **F**. Lateral view of fixed specimen 15 mm long (ZIN N 3), Bering Sea; penis everted. Abbreviations: a, anus; p, penis. Scale bars: **G, I** = 300 μ m; **K, L** = 100 μ m; **M** = 30 μ m. Photos and SEM images: A. Martynov.

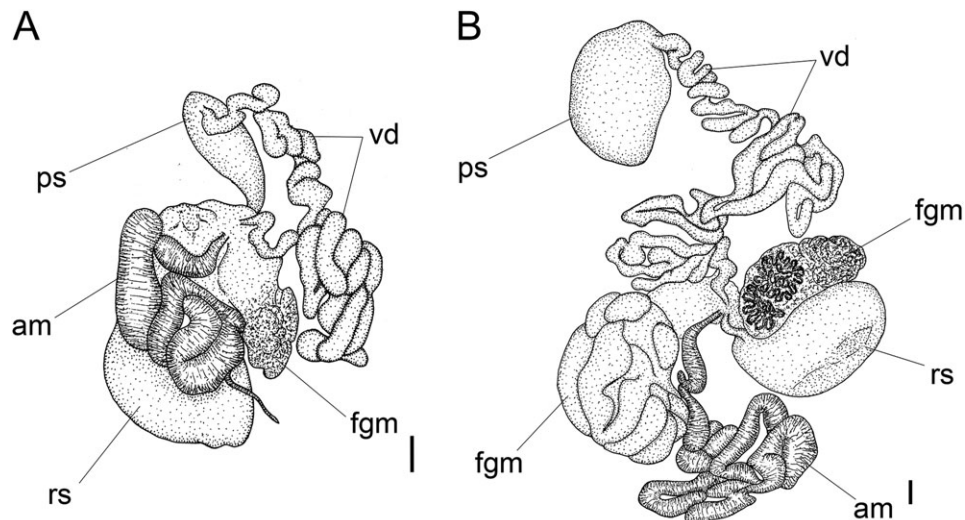


Figure 4. Reproductive systems of *Zeusia hyperborea* n. gen., n. sp. (A) and *Z. herculea* (Bergh, 1894) n. comb. (B). Abbreviations: am, ampulla; fgm, female gland mass; rs, receptaculum seminis; ps, penial sheath; vd, vas deferens. Scale bars = 1 mm.

opening, which is situated below the reduced but distinct notal ridge (Fig. 2C). Some species of the genus *Cerberilla* have a pleuroproctic anus (e.g. Carmona *et al.*, 2013); however, in that genus the opening of the hindgut represents rather a mixture of pleuroproctic and cleioproctic states without a distinct notal edge (see figures by e.g. Baba, 1976; Hermosillo & Valdés, 2007). Thus, there is a smooth transition between the sides of the body and the dorsum in *Cerberilla*. A similar pleuroproctic anus in a higher cleioproctic position, without a reduced notal edge, has been reported for *Anteaeolidiella* cf. *takanosimensis* (Baba, 1930) (Baba, 1979; Carmona *et al.*, 2014a). In *Zeusia* the body sides and dorsum are distinctly separated, a similar condition to that in the most basal taxa of the Flabellinidae (Gosliner & Kuzirian, 1990).

For several species of *Cerberilla*, e.g. *C. albopunctata* Baba, 1976, *C. misyuki* Martynov *et al.*, 2015a true cleioproctic anus has been reported (Baba, 1976; Martynov, Sanamyan & Korshunova, 2015a, b). According to the first description of the common tropical West Pacific species *C. affinis* Bergh, 1888, “Die kleine Analpapille im äussersten Theile des Interstitiums zwischen der dritten und vierten Papillenreihe (hinter dem Hufeisen)” [“The small anal papilla is in the outermost part of the space between the third and fourth rows of the cerata (behind the horseshoe-like ceratal rows)”] (Bergh, 1888a: 686). This implies that the cleioproctic position is between the third and fourth ceratal rows. On the contrary, the description of the type species of *Cerberilla*, *C. longicirra* Bergh, 1873, indicates that “An den Hinterrand des äussersten Theiles des fünften Papillenkissens stützt sich die kurze (klaffende) Anal Papille...” [“The short anal papilla is placed at the posterior margin of the outermost part of the fifth ceratal row”] (Bergh, 1873: 90). This can be interpreted as rather high pleuroproctic position tending towards the cleioproctic one. Thus, *Cerberilla* is characterized by an unstable position of the anus, but it never demonstrates a true pleuroproctic state with a reduced notal edge. The morphological heterogeneity within *Cerberilla* can be considered in the light of the proposed paraphyly of this genus according to molecular data (Carmona *et al.*, 2013). In addition, apparently all species of *Cerberilla* have very long oral tentacles together with a broad foot and a narrower dorsal side. This also distinguishes *Zeusia* from *Cerberilla*. The majority of the other genera of Aeolidiidae (Table 3) have a cleioproctic anus, by which *Zeusia* is readily distinguished from most of the aeolidiid genera.

The ceratal pattern of *Zeusia* is of simple rows directed from the centre towards the front. Such a pattern, in various degrees, is shared by many aeolidiid genera including *Aeolidia*, *Aeolidiella*,

Bulbaeolidia, *Cerberilla* and *Limenandra*. The three last-named, however, differ significantly from *Zeusia* by their external body shape and radular morphology (Table 3). *Aeolidiella* species from the deep sea of the North Atlantic (Valdés *et al.*, 2017) differ considerably from *Z. hyperborea* in anus position, number of radular teeth and absence of the middle cusp. Shallow-water North Atlantic *Aeolidiella* species (including the type species *A. alderi* (Cocks, 1852)) differs considerably from *Z. hyperborea* by the presence of a cleioproctic anus and distinctly bilobed radular teeth (Schmekel & Portmann, 1982; Thompson & Brown, 1984). In turn, evident members of the genus *Aeolidia* (Kienberger *et al.*, 2016) (including its type species *A. papillosa*) never display pleuroproctic anus and large denticulated middle cusps on some teeth of the radula, as described for *Z. hyperborea*. However, there is another deep-sea pleuroproctic species from North Pacific that has been traditionally assigned to the genus *Aeolidia*, *A. herculea* (Bergh, 1894; Gosliner & Behrens, 1996; Martynov & Korshunova 2011), of which the generic position has not yet been tested using morphological or molecular data.

According to the first molecular data presented here for the truly pleuroproctic *Zeusia hyperborea*, it is genetically distant from all known aeolidiid genera, including *Aeolidia*, *Aeolidiella* and *Cerberilla* (Table 2). For example, minimum uncorrected p-distances for COI are 17.02 % from *Cerberilla bemaetatae*, 17.93 % from *Aeolidia papillosa* and 18.23 % from *Aeolidiella alderi* (type species of *Aeolidiella*). All other genera of Aeolidiidae differ from *Z. hyperborea* by more than 18%.

Morphological data show that there is some external similarity between *Z. hyperborea* and ‘*Aeolidia*’ *herculea* Bergh, 1894 (compare Figs 2 and 3). There are significant similarities in the internal characters between two taxa: presence of a very large seminal receptacle and long vas deferens (Fig. 4). This suggests a close phylogenetic relationship between the two and, therefore, we include the latter species in the new genus *Zeusia*.

***Zeusia herculea* (Bergh, 1894) new combination**

(Figs 3, 4B)

Aeolidia herculea Bergh, 1894: 128–129, pl. 1, figs 8–12 (types in Zoological Museum, University of Copenhagen; Santa Barbara Islands, California, depth 757 m); Martynov 2006a: 294, pl. 138, fig. F. (Not *Aeolidia papillosa herculea sensu* MacFarland, 1966)

Aeolidia farallonensis Gosliner & Behrens, 1996: 351–353, figs 3–6 (types in California Academy of Sciences, CASIZ 105718, 105719; Farallon Islands, California, depth 510–1491 m).

Table 3. Comparison of morphological characters of the genera of the family Aeolidiidae.

	Body width	Dorsum/foot ratio	Rhinophoral pattern	Oral tentacleslength	Ceratal pattern	Anus position	Radula teeth	Middle cusp of radular teeth	Masticatory processes of jaws	Receptaculum seminis	Vas deferens /penis	References
<i>Aeolidia</i> Cuvier, 1798	Broad	Similar	Smooth	Moderate	Simple rows, directed from centre to the anterior part	Cleioproctic	Not bilobed, outer and inner denticles similar in size	Absent or rarely very short	Smooth	Narrow	Relatively short/ penis elongated, narrow	Cuvier (1798); Thompson & Brown (1984); Kienberger <i>et al.</i> (2016); own data
<i>Aeolidiella</i> Bergh, 1867	Moderate to narrow	Similar	Smooth	Moderate	Same as previous	Cleioproctic	Bilobed	Short smooth	Smooth	Narrow	Relatively short/ penis elongated, narrow	Bergh (1867); Thompson & Brown (1984); Miller (2001); Carmona <i>et al.</i> (2013); own data
<i>Anteaeolidiella</i> Miller, 2001	Narrow	Similar	Smooth	Moderate	Clusters of rows, directed from centre and arches	Cleioproctic	Strongly bilobed, outer middle denticles considerably longer	Short smooth	Smooth	Narrow	Relatively short/ penis elongated, narrow	Baba (1979); Miller (2001); Carmona <i>et al.</i> (2014a)
<i>Baeolidia</i> Bergh, 1888	Narrow	Similar	Papillate, or rarely smooth or ribbed	Moderate	Arches, rows	Cleioproctic or rarely acleioproctic	Not bilobed or bilobed, outer middle denticles and inner denticles similar in size or considerably longer	Absent	Smooth	Narrow, rarely broad	Relatively short/ penis elongated, narrow	Bergh (1888b); Carmona <i>et al.</i> (2014b)
<i>Berghia</i> Trinchese, 1877	Narrow	Similar	Papillate	Moderate	Arches, few posterior rows	Cleioproctic	Bilobed, middle outer and inner denticles often similar in size	Short smooth or absent	Denticulated or rarely smooth	Narrow	Relatively short/ penis elongate to bulbous	Trinchese (1877); Schmekel & Portmann (1982); Garcia-Gomez & Thompson (1990); Valdés (2005); Domínguez, Troncoso & García <i>et al.</i> (2014c)
<i>Bulbaeolidia</i> Carmona <i>et al.</i> , 2013	Narrow	Similar	Few swellings	Moderate	Rows and arches	Cleioproctic	Strongly bilobed, outer denticles considerably longer than inner ones	Long, smooth	Smooth or denticulated	?Broad	Relatively short/ penis elongate, narrow	Gosliner (1985); Carmona <i>et al.</i> (2013); Caballer & Ortea (2015)

<i>Cerberilla</i> Bergh, 1873	Moderately broad	Foot significantly broader	Smooth	Very long	Rows or clusters	Mixture of cleioproctic and highly placed pleuroproctic, immediately below rows of cerata or proper cleioproctic, no reduced notal ridge	Not bilobed, middle outer and inner denticles similar in size or outer are longer, but in most species characteristic intercalated smaller denticles present	Absent in most species, rarely present, smooth	Smooth or denticulated	Narrow	Relatively short/ penis elongate to bulbous	Bergh (1873, 1888a, b); Tardy (1965); Bum (1966); McDonald & Nybakken (1975); Baba (1976); Hermosillo & Valdés (2007); Padula & Delgado (2010); Martynov <i>et al.</i> (2015a, b)
<i>Limenandra</i> Haefelfinger & Stamm, 1958	Narrow, extremely elongated	Similar	Papillate	Moderate	Rows	Cleioproctic	Not bilobed, middle outer and inner denticles similar in size	Absent	Smooth or denticulated	Broad	Short/ penis elongate to bulbous	Haefelfinger & Stamm (1958); Schmekel & Portmann (1982); Carmona <i>et al.</i> (2014d)
<i>Spurilla</i> Bergh, 1864	Narrow	Similar	Perfoliate	Moderate	Arches	Cleioproctic	Moderately to strongly bilobed	Short smooth	Smooth or rarely denticulated	Narrow or rarely broad	Relatively short/ penis elongate to bulbous	Bergh (1864); Schmekel & Portmann (1982); Carmona <i>et al.</i> (2014e)
<i>Zeusia</i> n. gen.	Broad	Similar	Smooth to small tubercles	Moderate	Simple rows, directed from centre to anterior part	Pleuroproctic, distinct from ceratal rows, below reduced notal edge	Not bilobed or moderately bilobed, middle outer denticles longer or similar to inner ones	Short, long or absent	Smooth	Broad	Long/ penis elongated to broad	Present study; Bergh (1894); Gosliner & Behrens (1996); Martynov & Korshunova (2011)

Material examined: 4 specs (ZIN N 3, Zoological Institute, Russian Academy of Sciences, St Petersburg), Unimak Strait, Bering Sea, R/V *Akademik Oparin*, cruise 14, stn 32, 54°35.8'N 165°51.6'E, 16 August 1991, depth 422 m, Sigsbee trawl, Leg. A.V. Smirnov. 2 syntypes of *Aeolidia grandis* Volodchenko, 1941 (ZIN N 1), Okhotsk Sea, R/V *Gagara*, stn 217, 51°35.6'N 154°46'E, 10 July 1932, depth 418 m, beam trawl, leg. P.V. Ushakov (see Remarks below). All specimens formalin fixed.

Diagnosis: Body high, elevated. Notal edge considerably reduced, its free edge almost imperceptible. Radula teeth with reduced central cusp, forked denticles may be present. Receptaculum seminis large, broad. Penial sheath and penis large, broad.

External morphology (Fig. 3A–D, F–M): 15–31 mm long, 9–18 mm wide, 7–14 mm high. Body wide, high, narrowed posteriorly. Oral tentacles conical. Rhinophores covered with minute sparse tubercles, similar in size and length to oral tentacles. Cerata shed in all specimens, except for some of smallest cerata in a few rows. Up to 17 ceratal rows. Ceratal rows simple, placed in oblique rows directed from midline to anterior. Ceratal rows ending with rounded strongly reduced notal edge. Ceratal formula of 31-mm length spec.: left (19,21,28,24,20,27,25,27,18,24,21,20,14,11,10,7), right (20,27,18,20,17,17,16,15; anus; 12,12,12,13,11,9,6); of 15-mm length spec.: left (17,19,38,35,25,21,27,23,15,14,20,12,11,10,5,2,1,1), right (21,26,39,29,38,43,32,37; anus; 28,15,10,12,7,4). Anterior and posterior ceratal rows not clearly separated. Foot wide, gradually narrowed toward tail. Anterior part of foot with massive lobes ('labium') and distinct foot corners. Anus pleuroproctoc, placed in posterior part of body, near midline, under reduced notal edge, distinct from ceratal rows (Fig. 2C). Genital openings on right side of body in its first quarter length.

Anatomy (Fig. 3, 4B): Jaws broadly oval (Fig. 3H). Masticatory edges smooth (Fig. 3I). Oral glands absent. Cerebral and pleural ganglia fused, rounded, pedal ganglia elongated (Fig. 3A). Optic nerves short, eyes small, black pigment present. About 5 pairs of cerebropleural nerves and three pairs of pedal nerves. Radula formula 29–32 × 0.1.0. Teeth of radula wide, crescent-shaped, not bilobed (Fig. 3K–M). About 36–52 denticles on posterior teeth (Fig. 3L); *c.* 30–40 on anterior teeth; forked denticles may be present. Ampulla convoluted (Fig. 4B). Vas deferens prostatic, long, entangled (Fig. 4B). Penial sheath and penis very large, broad, unarmed (Fig. 3F). Receptaculum seminis large, oval (Fig. 4B).

Remarks: Bergh (1894: 129) described '*Aeolidia herculea*' from the deep sea off California and indicated the pleuroproctoc position of the anus: "der Anus dicht am Rande des Endes der 7–8 Papillenreihe" ["the anus close to the edge of the ends of 7–8 rows of cerata]. Just on the previous page of the same publication, Bergh (1894: 128) described the anus position of the shallow-water *Aeolidia papillosa* *s. l.* as "Der Anus etwas hinten der Mitte der Lange des Ruckens ganz oben zwischen zwei Papillenreihen liegend" ["the anus behind the middle part of the dorsum between two ceratal rows"], in other words a cleioproctoc position. Unfortunately, the pleuroproctoc deep-sea species '*A. herculea*' has not been redescribed since this first description. This neglect can partly be ascribed to the incorrect usage of the epithet '*herculea*' by MacFarland (1966) for a shallow-water Californian species from the *A. papillosa* complex (Martynov, 2006a; Kienberger *et al.*, 2016). A pleuroproctoc deep-sea aeolidiid from off the Californian coast was again described only in 1996, under the name '*Aeolidia farallonensis*' (Gosliner & Behrens, 1996). This was formally synonymized with '*A. herculea*' for the first time by Martynov (2006a), but details were not provided. '*Aeolidia herculea*' and '*A. farallonensis*' were described from the same geographical region, their type localities in California being separated by distance

of *c.* 620 km. Both species were discovered at similar depths (see synonymy above) and demonstrate very similar morphological features of a high body with a pleuroproctoc anus. Therefore, '*A. farallonensis*' is confirmed as a synonym of '*A. herculea*'.

In the present study, it is shown that the anal opening of '*A. herculea*' is placed separately from the end of the ceratal rows under the reduced notal edge (Fig. 3C). This is similar to the condition in *Zeusia hyperborea* (Fig. 1C), rather than to the cleioproctoc/pleuroproctoc position in *Cerberilla* (see above). Among all known taxa of the family Aeolidiidae, only *Z. hyperborea* and '*A. herculea*' share the presence of a true flabellinid-like pleuroproctoc anus, a long and entangled vas deferens and a large, broad receptaculum seminis (Figs 2–4). This suggests that *Z. hyperborea* and '*A. herculea*' may be more closely related to each other rather than to any other aeolidiid genera. The nudibranch fauna of the North Atlantic and North Pacific often demonstrate allopatric pairs of similar but distinct species, including deep-sea taxa. For example there is the species pair of North Atlantic '*Coryphella salmonacea*' (Couthoy, 1838) and North Pacific '*C. japonica*' Volodchenko, 1941 (see Martynov, 2013). According to the morphological evidence we therefore include '*A. herculea*' in the genus *Zeusia*.

Another North Pacific pleuroproctoc species, '*A. grandis*' Volodchenko, 1941 (syntype Fig. 2E) also shows external and internal features that essentially similar to those of *Z. herculea* (see Volodchenko, 1941). Indeed, '*A. grandis*' has been already synonymized with '*A. herculea*' (Martynov, 2006a). The type locality of '*A. grandis*' is the deep sea (450–1000 m) off Kamchatka. Thus the bathymetric distribution is the same as that of *Z. herculea*, but there is a considerable geographical gap between their localities. We have also presented here a somewhat intermediate record of several specimens identified as *Z. herculea* off Unimak Strait close to Alaska (Fig. 3A–D, G–M), which show basic external and internal similarity to *Z. herculea* from California. Therefore, it is possible that *Z. herculea* represents a single species with a transpacific distribution. Many other deep-sea species in various invertebrate phyla show similarly broad ranges (McClain & Hardy, 2010). Nevertheless, until molecular data are available from both northeastern and northwestern Pacific specimens (the present specimens were fixed in formalin), we prefer to retain *Zeusia grandis* as a potentially separate northeastern Pacific species.

Another species, *Baeolidia cryoporos* Bouchet, 1977, was described from the bathyal zone (2110 m) of the North Atlantic. This differs considerably both externally and internally from other *Baeolidia* species and is also the single supposed species of this genus known from the North Atlantic (Carmona *et al.*, 2014b). It has a very long vas deferens and the position of the anus is rather intermediate between pleuroproctoc and cleioproctoc, without any trace of the notal ridge (Bouchet, 1977: fig. 26). Therefore, although '*B. cryoporos*' is clearly distinct from the *Zeusia* species considered here, it may represent either another member of this genus or a closely related undescribed genus.

DISCUSSION

Zeusia hyperborea has a wide body and pleuroproctoc anus situated below a reduced notal ridge (Fig. 2A–C). This pattern is similar to that of the basal nudibranchs *Doridoxa* and Flabellinidae. Our molecular phylogeny (Fig. 1) places *Z. hyperborea* as the sister to all cleioproctoc wide-bodied *Aeolidia* species. A possible case of secondary reversal could be considered if a pleuroproctoc-like anus is found without any traces of a notal edge in a species of morphologically derived aeolidiids (e.g. *Limnandra*) and if a molecular analysis supports such a derived position of a hypothetical pleuroproctoc species (currently no pleuroproctoc species of *Limnandra* are known). However, in the case when an aeolidiid taxon is found to retain a morphological pattern similar to the other evidently basal family

(Flabellinidae) and molecular data support its basal placement within a particular clade, this should be interpreted as evidence for a true ancestral condition. The combined evidence presented here suggest that the pleuroproct state of *Z. hyperborea* is truly ancestral, rather than a secondary reversal.

The morphological and molecular evidence for *Z. hyperborea* provides an evolutionary link between the predominantly cleio-proct Aeolidiidae and mostly pleuroproct Flabellinidae. A hypothetical ancestral aeolidiid taxon probably had a pleuroproct anus similar in position to that of the genus *Zeusia*, but it was likely placed under a more distinct notal edge. This prediction is concordant with the morphological data for the acleioproct family Tergipedidae, a family that includes mostly small shallow-water species with few ceratal rows and acleioproct anus. However, a decade ago a large-sized tergipedid genus, *Murmania*, was described from the deep sea of the Arctic Ocean (Martynov, 2006b) and molecular data obtained in 2013 have confirmed its placement within the Tergipedidae near the genus *Cuthonella* (A. Martynov, unpublished data). *Murmania* has numerous ceratal rows, a reduced notal edge and a cleioproct or occasionally a pleuroproct anus. According to its radula pattern and reproductive system, *Murmania* is an evident member of the Tergipedidae *sensu lato*. However, this large tergipedid genus strongly resembles externally the aeolidiid genera *Aeolidia* and *Zeusia* (see Martynov, 2006b: fig. 1C–F). This is additional evidence for the reliability of the proposition of the pleuroproct anus as an ancestral nudibranch state.

The type species of the new genus *Zeusia* from the deep-sea North Atlantic shows significant morphological similarity to the deep-sea pleuroproct aeolidiids (here *Z. herculea* and *Z. grandis*) from the North Pacific. These similarities include a true pleuroproct anus, long entangled vas deferens and very large receptaculum seminis (Figs 2–4). While the first feature can be considered as a shared plesiomorphy, the combination of all three characters is here interpreted as evidence for a systematic relationship. This needs to be confirmed by future molecular data for North Pacific pleuroproct aeolidiids.

Carmona *et al.* (2013: 9) proposed that “...the position of the anus does not have any phylogenetic significance within Aeolidiidae”. The discovery of *Z. hyperborea* partially challenges this suggestion and agrees with the concept that the pleuroproct state for any internal cladobranch subgroup is ancestral (Wägele & Willan, 2000; Schrödl *et al.*, 2001; Martynov, 2011). Another aeolidiid genus, *Cerberilla*, with a modified pleuroproct or cleio-proct anus was considered as a paraphyletic taxon by Carmona *et al.* (2013). This conclusion stretches the morphological disparity of this genus and potentially suggests that a separate genus may be required for pleuroproct *Cerberilla* species. However, for the majority of Aeolidiidae, pleuroproct species are unknown. The pleuroproct *Zeusia* is in fact not a sister genus to all Aeolidiidae according to our phylogenetic analyses, but a fully resolved aeolidiid phylogeny remains a future goal. *Zeusia* may retain an ancestral pleuroproct state, but other characters have already evolved towards conditions found in the extant cleioproct *Aeolidia* clade. Therefore, additional pleuroproct taxa are to be expected in various otherwise cleioproct clades of Aeolidiidae. Some genera may have become extinct, while other taxa are yet undiscovered, like the newly described *Z. hyperborea*. This in turn has morphological and ontogenetic implications (e.g. Martynov & Korshunova, 2015). Therefore, we suggest that Carmona *et al.* (2013) were too ready to discount available morphological data when discussing the results of their three-gene molecular phylogeny for the Aeolidiidae. The future of taxonomy and phylogenetics lies in an integrative approach, because the expression of morphology during ontogeny is determined by multiple genes and their epigenetic interactions (e.g. Holland, 2013; Danchin *et al.*, 2011; Laland *et al.*, 2015).

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