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Biodiversity hotspot in cold waters: a review of the genus *Cuthonella* with descriptions of seven new species (Mollusca, Nudibranchia)

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Abstract

Cuthonella Bergh, 1884 is of one of the most neglected nudibranch groups, with a long history of taxonomic confusion with other aeolidacean genera. Owing to its predominantly Arctic distribution with

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cold water, its species are difficult to find and to collect, and thus to describe. In this study we revise the genus by presenting molecular and morphological data for a majority of the species, including the type, *C. abyssicola* Bergh, 1884. The material is based on a broad geographic sampling throughout the Northern Hemisphere. Particular emphasis is placed on the Kuril Islands, a diversity hotspot for the genus. Seven new species and two subspecies of *Cuthonella* are described from the Arctic and North Pacific regions. The number of species of *Cuthonella* is thus increased over threefold and now comprises 15 species plus two subspecies instead of five species. This work is the most substantial update of the genus *Cuthonella* since its description in 1884. To delineate taxonomic and phylogenetic limits of *Cuthonella*-like aeolidaceans, the molecular phylogeny of the wider traditional "tergipedids" is presented and shows that *Cuthonella*-like aeolidaceans form a distinct molecular clade as the family Cuthonellidae Miller, 1977, corroborated by reliable morphological apomorphies.

Keywords

molecular systematics – morphology – Mollusca – phylogenetics – taxonomic revision

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Introduction

Nudibranch molluscs are marine invertebrates that display unique adaptations, like the storage of stinging nematocysts from cnidarian prey in their specialized dorsal outgrowths, i.e., cerata, for defence (Martin et al., 2009). Cold waters are commonly equated with low species richness and diversity, whereas tropical waters are usually noted as biodiversity hotspots for marine animals (e.g., Roberts et al., 2002; Hoeksema, 2007; Barman et al., 2018). It has been concluded that a rise in sea water temperature along a latitudinal gradient from the poles to the equator considerably increases biodiversity (e.g., Bickford et al., 2007). This is generally true for nudibranchs as there are many times the number of species in tropical waters compared to the number of species found in cold polar and temperate waters (e.g., Marshall & Willan, 1999; Martynov & Korshunova, 2012; Papu et al., 2020). However, for some groups of invertebrates biodiversity is higher in northern seas, e.g. in marine isopods (Poore & Bruce, 2012) or nudibranchs of the family Dendronotidae (Korshunova et al., 2020a). Here we report the unexpectedly high diversity of a genus of aeolidacean nudibranch molluscs in the waters of the North Pacific.

In this study, we report the discovery of five new species of nudibranch molluscs of the genus *Cuthonella* Bergh, 1884 among the fauna of a tiny volcanic island, which forms part of the Kuril Islands group. These new species are confirmed with both morphological and molecular data. In addition, we have discovered four more new species and subspecies of the genus *Cuthonella* from adjacent waters of both sides of the North Pacific and the Arctic. To place these new species within a broad phylogenetic and taxonomic framework of 'tergipedid' aeolidaceans, we reviewed the genus *Cuthonella* using various specimens collected in the cold waters of the Northern Hemisphere. We also document that the genus *Cuthonella*, which was originally described from the deep waters of the

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North Atlantic, actually has a wide distribution in the shallow waters of northern Eurasia and northern America. Additionally, based on the broad selection of various aeolidacean taxa, the validity of the family-rank taxon Cuthonellidae Miller, 1977 is confirmed following recent morphological and molecular studies (Korshunova et al., 2017a, 2018a; Martynov et al., 2020a).

Material and methods

Material examined

Material for this study was obtained from various expeditions, and includes specimens belonging to different taxa of aeolidacean nudibranchs. These specimens are deposited in the Zoological Museum of Lomonosov Moscow State University (ZMMU), Gothenburg Natural History Museum (GNM), Natural History Museum, University of Oslo (ZMO), and the NTNU University Museum, Norwegian University of Science and Technology (NTNU-VM) (Bakken et al., 2020). The majority of specimens were collected in various locations in the North Atlantic, including Sweden, Norway, the United Kingdom, in the Arctic Sea (including the Barents Sea), the Russian arctic coasts of the White Sea, the East Siberian Sea, the Chukchi Sea, the North Pacific (including Kamchatka, the Kuril Islands, the Sea of Japan, and the Canadian and the United States Pacific coasts). Some specimens were collected during ship-based research cruises in the North Atlantic and the Arctic Seas.

Morphological analysis

Nudibranch morphology was studied under a stereomicroscope and using digital Nikon D810 and Nikon D600 cameras. For the descriptions of the internal features, both preserved and fresh specimens (when available) were dissected under a stereomicroscope. The buccal mass of each specimen was extracted and processed in 10% sodium hypochlorite solution. The features of the jaws of each species were studied under a stereomicroscope and scanning electron microscope (CamScan, JSM). The platinum-palladium coated radulae were examined and photographed using a scanning electron microscope. The reproductive systems were examined and drawn using a stereomicroscope.

Molecular analysis

Twenty-four specimens of the genus *Cuthonella* were sequenced for the mitochondrial genes cytochrome c oxidase subunit I (COI) and 16S rRNA, and the nuclear genes Histone 3 (H3) and 28S rRNA (C1-C2 domain). Small pieces of tissue were used for DNA extraction with Syntol S-Sorb kit by Syntol Company, according to the manufacturer's protocols. The primers and polymerase chain reaction programs that we used are presented in Appendix (table A1). 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 and H3 sequences were translated into amino acids to verify coding regions and avoid improper base-calling. All new sequences were deposited in GenBank (Appendix, table A2; highlighted in bold). Additional molecular data for *Cuthonella* specimens and several outgroup specimens 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 avoid potential contamination and errors. Original data and publicly available sequences were aligned with the MAFFT algorithm (Katoh et al., 2002). Separate analyses were conducted for COI (657 bp), 16S (445 bp), H3 (327 bp), 28S (333 bp) and four concatenated markers (1762 bp). The GTR+I+G model was chosen for the concatenated datasets using MrModelTest 2.3 (Nylander et al., 2004). Two

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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 500 generations. Analysis was started with random starting trees and 10^7 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. Nodes in the phylogenetic trees with Bayesian posterior values > 0.96% and bootstrap values > 90% were considered 'highly' supported, nodes with 0.90–0.95% and 80–89% accordingly were considered 'moderately' supported (lower support values were considered not significant, Korshunova et al., 2018a). The program MEGA7 (Kumar et al., 2016) was used to calculate the uncorrected p-distances between all the sequences. Automatic Barcode Gap Discovery (ABGD) (Puillandre et al., 2012) was used to estimate the diversity of *Cuthonella* species. An alignment of the COI marker was submitted and processed in ABGD using the Jukes–Cantor (JC69) and Kimura (K80) models and the default settings. To evaluate the genetic distribution of the different haplotypes, a haplotype network for the COI molecular data was reconstructed using Population Analysis with Reticulate Trees (PopART, http://popart.otago.ac.nz) with the TCS network method.

Results

Molecular analysis

In this molecular study, 55 specimens of *Cuthonella* were included, combining 78 novel sequences with 93 sequences from GenBank. Six outgroup specimens (22 sequences) from the genera *Murmania, Xenocratena,* and *Calma* were used according to previous results (Korshunova et al., 2017b, 2018a; Martynov et al., 2019, 2020a). Bayesian Inference (BI) and Maximum Likelihood (ML) analyses based on the combined dataset for the mitochondrial COI and 16S, and the nuclear H3 and 28S genes yielded similar results (figs 1, 2).

All *Cuthonella* species constituted a highly supported clade (PP = 1, BS = 99). The ABGD analysis of the COI dataset run with two different models revealed 14 lineages that could be assigned to morphologically distinct *Cuthonella* species (fig. 1): *Cuthonella osyoro* (Baba, 1940), *C. soboli* Martynov, 1992, *C. georgstelleri* sp. nov., *C. benedykti* sp. nov., *C. ainu* sp. nov., *C. hiemalis* (Roginskaya, 1987), *C. denbei* sp. nov., *C. vasentsovichi* sp. nov., *C. concinna* (Alder & Hancock, 1843) with subspecies *C. concinna bellatula* subsp. nov. and *C. concinna concinna*, *C. sandrae* sp. nov., *C. abyssicola kryos* subsp. nov., *C. punicea* (Millen, 1986), and two potential species in the *C. cocoachroma* (Williams & Gosliner, 1979) group. *Cuthonella soboli* was sister (PP = 1, BS = 100) to *C. osyoro*; *C. benedykti* sp. nov. (PP = 1, BS = 97) was sister (PP = 1, BS = 100) to *C. ainu* sp. nov. and together with *C. georgstelleri* sp. nov. they formed a highly supported lineage (PP = 1, BS = 98). *Cuthonella sandrae* sp. nov. and *C. abyssicola kryos* subsp. nov. clustered in two distinct and separate sister clades (PP = 0.98, BS = 92) that formed the sister group (PP = 1, BS = 98) to the maximally supported (PP = 1, BS = 100) *C. punicea* clade. Unresolved evolutionary ties were revealed for the *C. concinna* clade. All seven *C. concinna* specimens from the NE Pacific formed a separate clade (PP = 0.99, BS = 90) and clustered together with sixteen *C. concinna* individuals from the NE Atlantic (PP = 1, BS = 100).

The maximum intragroup distance for the COI marker in *C. concinna* from the NE Atlantic is 0.91% and in *C. concinna* from the NE Pacific the maximum intragroup distance is 1.67%. The minimum intergroup distance for the COI marker between the NE Atlantic and the NE Pacific *C. concinna* is 1.07%. Thus, the molecular divergence within *C. concinna* from the NE

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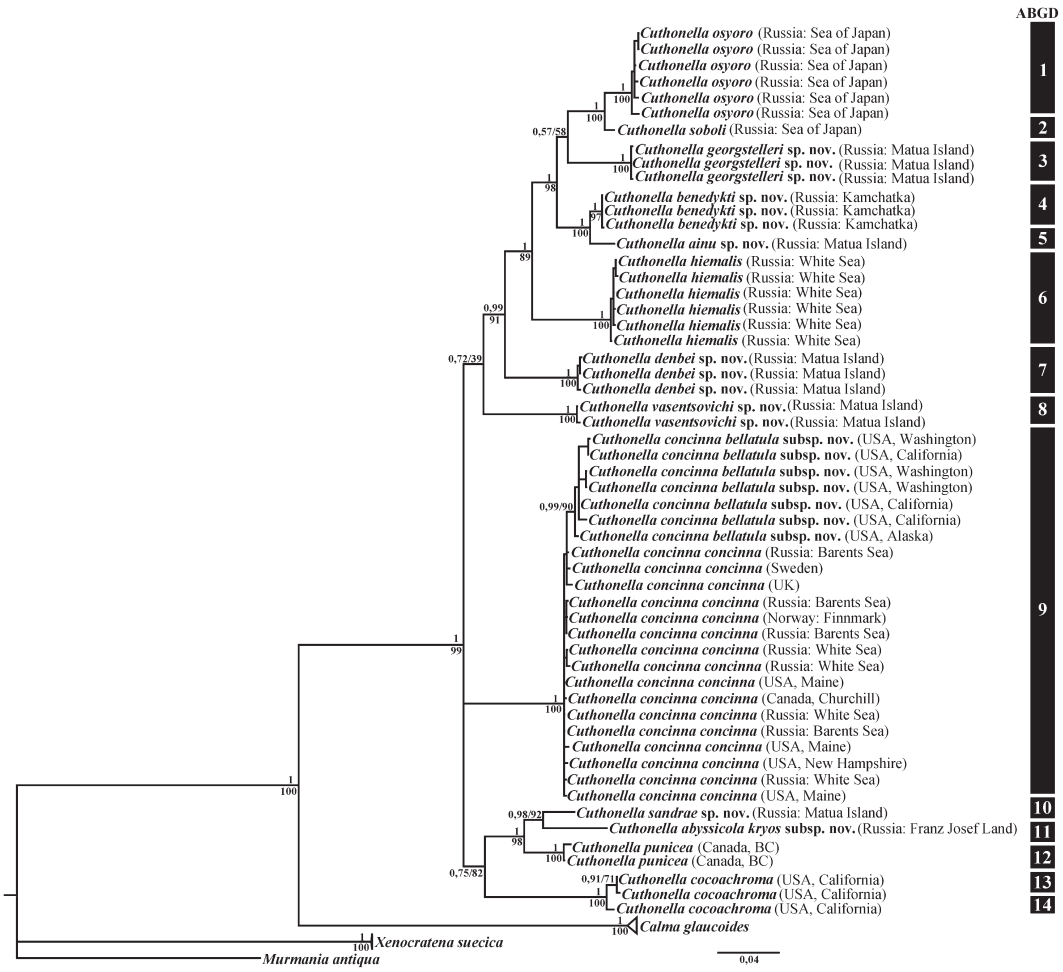

FIGURE 1 Phylogenetic relationships of *Cuthonella* based on COI + 16S + H3 + 28S concatenated dataset inferred by Bayesian inference (BI). Numbers above branches represent posterior probabilities from BI; numbers below branches indicate bootstrap values for Maximum Likelihood. Summary of species delimitation results are noted by numbered clusters from the abgd analyses for the COI dataset.

Pacific group exceeded the molecular divergence between the NE Atlantic and the NE Pacific. The division of *C. concinna* into two subgroups (*C. concinna concinna* and *C. concinna bellatula* subsp. nov.) was also confirmed by the haplotype network based on COI molecular data (fig. 3). Two *C. cocoachroma* (CAS179471 and CAS185193) clustered together (PP = 0.91, BS = 71) and formed the sister group to the *C. cocoachroma* CAS181307b. All three *C. cocoachroma* formed a maximally supported clade (PP = 1, BS = 100). The COI distance of 0.15% is found between *C. cocoachroma* CAS179471 and *C. cocoachroma* CAS185193. The COI distances of 1.37% and 1.52% are found between *C. cocoachroma* CAS181307b and two *C. cocoachroma* (CAS179471 and CAS185193) respectively. The ABGD analysis suggested that two potential species within *C. cocoachroma* may become revealed in future studies. Nevertheless, the three *C. cocoachroma* specimens aligned as the same species in the present analysis according to the integrative molecular results. The maximum intragroup and minimum intergroup genetic distances in *Cuthonella* species for the COI marker are presented in table 1.

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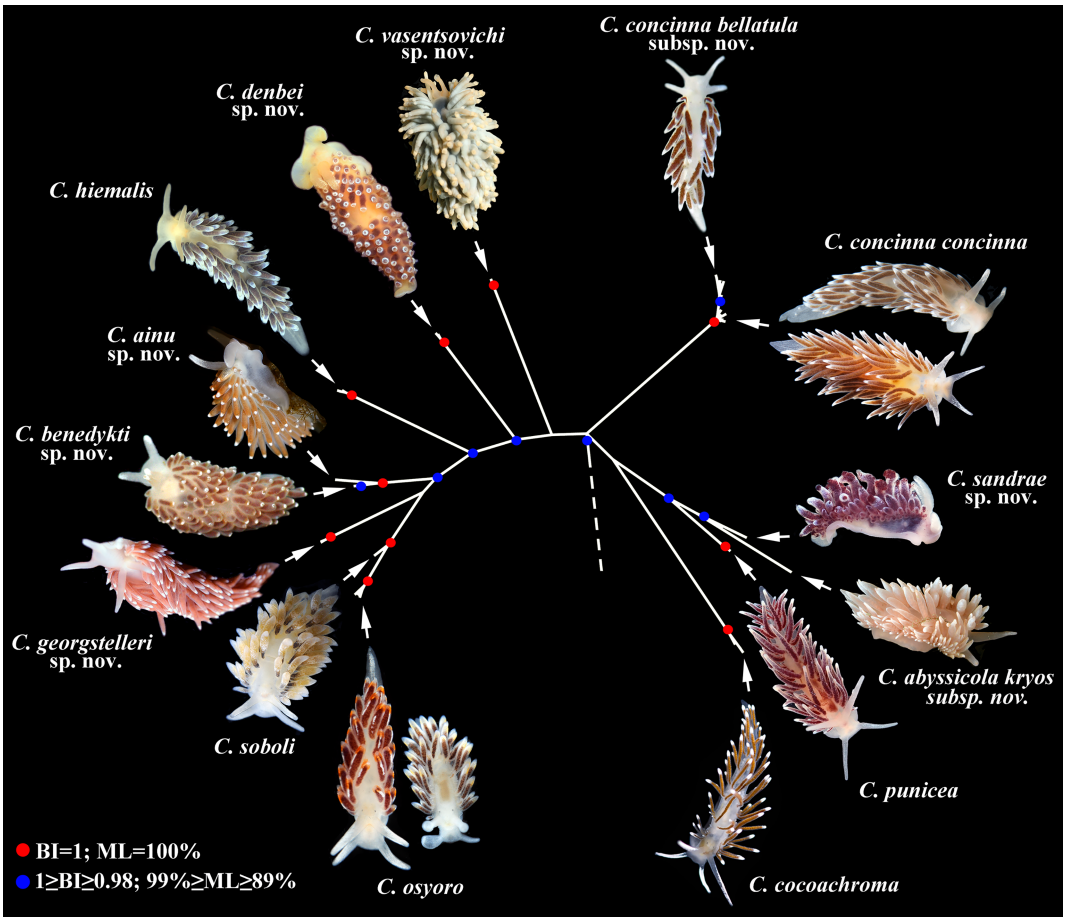

FIGURE 2 Phylogenetic relationships of *Cuthonella* based on COI + 16S + H3 + 28S concatenated dataset inferred by Bayesian inference (BI), radial tree layout. Posterior probabilities from BI and bootstrap values for Maximum Likelihood (ML) are indicated on the figure. *Cuthonella* species are illustrated on the tree.

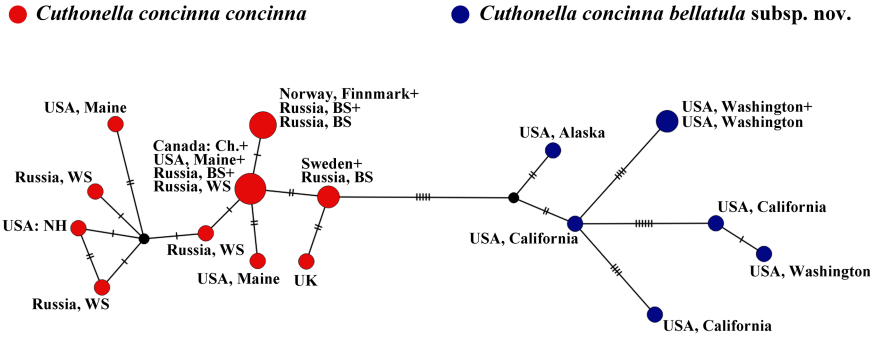

FIGURE 3 Haplotype network based on cytochrome c oxidase subunit I (COI) molecular data showing genetic mutations occurring within *Cuthonella concinna concinna* (red circles) and *Cuthonella concinna bellatula* subsp. nov. (blue circles) species. Abbreviations: BS: Barents Sea; Ch: Churchill (Canada); NH: New Hampshire; UK: United Kingdom; WS: White Sea.

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TABLE 1 Maximum intragroup (highlighted in bold) and minimum intergroup genetic distances (%) for the CO1 marker in *Cuthonella* species

	C. benedykti sp. nov.	*C. ainu* sp. nov.	*C. soboli*	*C. osyoro*	*C. georgstelleri* sp. nov.	*C. hiemalis*	*C. denbei* sp. nov.	*C. concinna concinna*	*C. concinna bellatula* subsp. nov.	*C. vasentsovichi* sp. nov.	*C. abyssicola kryos* subsp. nov.	*C. sandrae* sp. nov.	*C. punicea*	*C. cocoachroma*
***C.benedykti* sp. nov.**	**0.16**	2.65	6.20	7.88	7.75	8.53	9.97	10.44	11.37	10.23	13.08	11.63	11.94	10.85
***C. ainu* sp. nov.**	2.65	-	7.46	8.68	8.22	9.55	10.20	11.11	12.02	11.42	13.09	12.02	12.18	12.33
C. soboli	6.20	7.46	-	2.89	7.91	9.08	9.59	10.81	11.72	10.96	11.72	10.81	10.81	10.35
C. osyoro	7.88	8.68	2.89	**1.15**	8.07	8.37	9.69	10.51	11.82	11.11	11.72	10.65	11.11	10.02
***C. georgstelleri* sp. nov.**	7.75	8.22	7.91	8.07	**0.30**	9.44	10.96	13.09	13.55	12.18	12.63	12.02	10.96	11.57
C. hiemalis	8.53	9.55	9.08	8.37	9.44	**0.31**	9.89	11.78	12.21	9.30	12.52	12.09	11.27	9.77
***C. denbei* sp. nov.**	9.97	10.20	9.59	9.69	10.96	9.89	**0.30**	9.30	9.89	9.74	10.50	11.57	10.81	10.50
C. concinna concinna	10.44	11.11	10.81	10.51	13.09	11.78	9.30	**0.91**	1.07	9.28	12.09	11.78	12.25	11.32
***C. concinna bellatula* subsp. nov.**	11.37	12.02	11.72	11.82	13.55	12.21	9.89	1.07	**1.67**	9.74	11.87	11.87	12.02	12.18
***C. vasentsovichi* sp. nov.**	10.23	11.42	10.96	11.11	12.18	9.30	9.74	9.28	9.74	**0.15**	12.02	10.96	11.26	10.20
***C. abyssicola kryos* subsp. nov.**	13.08	13.09	11.72	11.72	12.63	12.52	10.50	12.09	11.87	12.02	-	7.00	8.52	11.42
***C. sandrae* sp. nov.**	11.63	12.02	10.81	10.65	12.02	12.09	11.57	11.78	11.87	10.96	7.00	-	6.85	11.11
C. punicea	11.94	12.18	10.81	11.11	10.96	11.27	10.81	12.25	12.02	11.26	8.52	6.85	**0.76**	9.74
C. cocoachroma	10.85	12.33	10.35	10.02	11.57	9.77	10.50	11.32	12.18	10.20	11.42	11.11	9.74	**1.52**

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Systematic account

Family Cuthonellidae Miller, 1977

Diagnosis. Aeolidaceans with a wide to moderately broad body. Notal edges fully reduced. Cerata non elevated, several per row. Ceratal rows branched or simple. Rhinophores smooth to wrinkled, without distinct lamellae. Anus acleioproctic or cleioproctic, in anterior to middle part of dorsal side. Radula formula 0.1.0. Rachidian teeth usually with strong cusp, not compressed by adjacent lateral denticles. Distal receptaculum seminis present. Vas deferens usually moderate, with indistinct prostate. Massive external permanent penial collar absent. Penis internal, unarmed. Supplementary gland present, commonly inserts to vas deferens.

Type genus *Cuthonella* Bergh, 1884.

Genus *Cuthonella* Bergh, 1884

(Figs 1–22)

Cuthonella Bergh, 1884: 23–24.

Cuthonella Martynov, 1992, revision: 23.

Non *Cuthona* sensu Millen (1986)

Type species: Cuthonella abyssicola Bergh, 1884. Recent, North Atlantic Ocean. Gender feminine.

Diagnosis. Body wide to moderately broad (rarely more narrow). Cerata numerous, continuous. Rhinophores smooth to wrinkled, longer or similar in size to oral tentacles. Anterior foot corners never tentaculate. Anus acleioproctic (rarely cleioproctic). Central teeth with strong cusp and distinct denticles. Distal receptaculum seminis. Long vas deferens without separate granulated prostate. Supplementary gland (= "penial gland") inserts into vas deferens. Penis commonly elongated conical, unarmed.

Contained species: Cuthonella abyssicola abyssicola Bergh, 1884 (fig. 4), *C. abyssicola kryos* subsp. nov. (fig. 5), *C. ainu* sp. nov. (fig. 6), *C. benedykti* sp nov. (fig. 7), *C. cocoachroma* (Williams & Gosliner, 1979), *C. concinna concinna* (Alder & Hancock, 1843) (fig. 8), *C. concinna bellatula* subsp. nov. (fig. 9), *C. denbei* sp. nov. (fig. 10), *C. elenae* Martynov, 2000, *C. georgstelleri* sp. nov. (fig. 11), *C. hiemalis* (Roginskaya, 1987) (fig. 12), *C. orientosiberica* sp. nov. (fig. 13), *C. osyoro* (Baba, 1940) (fig. 14), *C. punicea* (Millen, 1986) (fig. 15), *C. sandrae* sp. nov. (fig. 16), *C. soboli* Martynov, 1992 (fig. 17), *C. vasentsovichi* sp. nov. (fig. 18).

Remarks. Until 1992, the genus *Cuthonella* was rarely used to refer just to the deep-sea species, *C. abyssicola*, and its two synonymous taxa (e.g., Odhner in Franc, 1968; Miller, 1977), or more often it was considered invalid (Millen, 1986). Other species that demonstrate morphological similarities to the type species *C. abyssicola* were never considered as belonging to the genus *Cuthonella* in faunal lists and guides (e.g., Odhner, 1907, 1939; Thompson & Brown, 1984; Behrens, 1980; Behrens & Hermosillo, 2005). Martynov (1992) initially revised the composition of the genus *Cuthonella* to include six species – *C. abyssicola* (Bergh, 1884), *C. concinna* (Alder & Hancock, 1843), *C. distans* (Odhner, 1922), *C. hiemalis* (Roginskaya, 1987), *C. marisalbi* (Roginskaya, 1963), *C. punicea* (Millen, 1986) and to describe a new one, *C. soboli* Martynov, 1992.

Thus, a future monophyletic molecular clade (fig. 1) was predicted using only morphological data. This is a clear indication that morphological data (ontogenetic in a broad sense) should have value independent of molecular data (Korshunova et al., 2017a, b) instead of being considered merely an inferior auxiliary addition, a view commonly held in the current use of molecular techniques to delineate species (e.g., Carmona et al., 2013).

In the present study, five of the seven species that were included in the genus *Cuthonella* by Martynov (1992) are confirmed to belong to the monophyletic molecular clade that includes *Cuthonella abyssicola* s.l. Moreover, *Cuthonella concinna* s.l., *C. hiemalis* (Roginskaya, 1987), *C. punicea* (Millen, 1986)

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and *C. soboli* Martynov, 1992 are confirmed to be valid species (figs 1–3, 4, 8, 12, 15, 17), whereas *C. distans* (Odhner, 1922) and *C. marisalbi* (Roginskaya, 1963) – while still *Cuthonella* as predicted by Martynov (1992) – are now both considered to be junior synonyms of *Cuthonella concinna concinna* (see below and fig. 8).

Previously, a few Antarctic species were described under the genus *Cuthonella*, i.e. *Cuthonella antarctica* Eliot, 1907 (currently is known under a replacement name *Cuthonella elioti* (Odhner, 1944)), *Cuthonella modesta* Eliot, 1907 and *Cuthonella paradoxa* Eliot, 1907. Since *C. elioti* is known to have supplementary gland that inserts into the penial base and possibly a penial stylet, and *C. modesta* is also described as having supplementary gland that inserts into the penial base and jaws without denticles (Eliot, 1907; Valdés et al., 2012), they are definitely not considered to be *Cuthonella*. The taxonomic placement of these taxa should be addressed in a separate study.

It has also subsequently been shown that *Cuthonella paradoxa* belongs to a valid Antarctic genus *Guyvalvoria* Vayssière, 1906, and has been synonymised with the type species of the genus *Guyvalvoria*, *G. francaisi* Vayssière, 1906 because of the high morphological similarity (Martynov, 2006a). However, *Guyvalvoria paradoxa* sensu Valdés et al. (2012: 1171–1173) does not match the original description of *Cuthonella paradoxa* in Eliot (1907: 24–25) and considerably differs in the radular morphology. There are seven distinct, "fairly stout and long" lateral denticles of the central teeth in the original description of *Cuthonella paradoxa* (Eliot 1907: 25, 11 mm preserved length) and 13–15 small denticles in *Guyvalvoria "paradoxa"* sensu Valdés et al. (2012: 1172, 15 mm preserved length). Notably, a fewer number (ca. 5–11) of distinct, long lateral denticles is well attested for the type species of *Guyvalvoria, G. francaisi* Vayssière, 1906 with similar body size (up to 14.5 mm preserved length), whereas another Antarctic species *Guyvalvoria gruzovi* Martynov, 2006 has a clearly larger number (11–15) of less distinct lateral denticles in specimens with smaller (8–9 mm) preserved body length (Martynov, 2006a: 78–84). In addition, *Cuthona schraderi* (Pfeffer in Martens & Pfeffer, 1886) was considered as a potential synonym of *G. "paradoxa"* sensu Valdés et al. (2012: 1173). Nonetheless, *Cuthona schraderi* differs significantly from any species of the genus *Guyvalvoria* by the presence of distinct ceratal rows and from *G. "paradoxa"* sensu Valdés et al. (2012) also by considerably fewer lateral denticles (Odhner, 1926). Thus, *Cuthona schraderi* is not a potential synonym of *G. francaisi* Vayssière, 1906 or *G. "paradoxa"* sensu Valdés et al. (2012: 1173). According to the morphology of the radular teeth and reproductive system, *Guyvalvoria "paradoxa"* sensu Valdés et al. (2012) is the most similar to *G. gruzovi* (Martynov, 2006a), but not to *G. francaisi* Vayssière, 1906 (= "*Cuthonella" paradoxa* Eliot, 1907).

The genus *Guyvalvoria* is a well-defined taxon by the very specific combination of a posterior anus, laterally compressed branched rows of cerata, uniserial radula and a supplementary gland that inserts into the penial base. These features were already described in detail elsewhere (Martynov, 2006a) and by those characters *Guyvalvoria* is not only clearly different from the genus *Cuthonella*, but also from the majority of other aeolidacean families (Korshunova et al, 2017b; Martynov et al., 2020a). Some morphological similarity in presence of the posterior anus *Guyvalvoria* shares only with the family Murmaniidae (Martynov, 2006a; Martynov et al., 2020a). Therefore, *Guyvalvoria* recently was transferred with

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reservation to the family Murmaniidae (Korshunova et al., 2017b: Supplementary material 1, Synopsis of the families of suborder Aeolidacea). The current status of the genus *Guyvalvoria* as "taxon inquirendum" of the "family Eubranchidae" (MolluscaBase, 2020) should therefore be corrected to fully valid status and, pending the availability of molecular data, to the family Murmaniidae. The family Murmaniidae, on one hand, is morphologically consistent with the characters of *Guyvalvoria*, but on the other hand, is related to the families Cuthonellidae and Xenocratenidae according to the most recent phylogenetic analysis (Martynov et al., 2020a). Therefore a future phylogenetic analysis will show if *Guyvalvoria* can be retained in the family Murmaniidae or should be placed in its own family.

In the original diagnosis of the genus *Cuthonella*, Bergh (1884) did not mention the key feature that has proven to be present in all species of the genus *Cuthonella* studied so far (except for uncertainties in the species *C. cocoachroma* Williams & Gosliner, 1979, see below), which is that the supplementary gland is inserted into the vas deferens instead of the penis (Martynov, 1992; present study). From the characters initially mentioned by Bergh (1884), the dorso-lateral position of the anus cannot be considered specific for the genus *Cuthonella*, and the absence of cnidosacs in the type species of the genus *Cuthonella* was disproved by Millen (1986).

So, at this time the genus *Cuthonella* should be defined by the following features: relatively abundant anterior pre-anal rows of cerata, either branched or unbranched (the majority of species have at least five to six, or more, pre-anal ceratal rows in the adult state), a predominantly acleioproctic anus (the type species and a few other species may have a cleioproctic one), relatively broad jaws with usually a single row of distinct denticles (the type species apparently may also have a few additional indistinct rows), an exclusively uniserial radula with a central cusp always protruding (except for the few anteriormost eroded teeth), either with lateral denticles closely adhering to the central cusp (as in the type species) or usually distinct from the central cusp. In the reproductive system, so far only a single receptaculum seminis is reported (with a tendency to be more proximal in *Cuthonella concinna* s.l., otherwise in the majority of species it is distal) and the receptaculum seminis is usually oval, but it can also be a rather tubular one (e.g., *C. abyssicola* s.l., *C. punicea*). The penis is unarmed.

The most specific feature of the genus – the insertion of the supplementary gland into the vas deferens instead of the penis – was evident in all the *Cuthonella* species that we were able to examine (figs 4–20). *Cuthona norvegica* was originally described by Odhner (1929) within the genus "*Cuthonella*". However, *C. norvegica* has a supplementary gland inserted into the penial base (Millen, 1986) and was transferred to the genus *Cuthona* s.str. by Martynov (1992). There are no new specimens of *Cuthona norvegica* available, and after a future clarification of its phylogenetic position, it may be necessary to transfer this species to a different genus.

The insertion of the supplementary gland into the vas deferens is likely a plesiomorphic feature because it is also present in at least one very different taxon with a triserial radula – *Eubranchus tricolor* – within the family Eubranchidae (Korshunova et al., 2017a, b). Potentially, this feature may occur within some other basal 'tergipedids'. However, among genera and families with a uniserial radula it has so far been confirmed only for *Cuthonella* and Cuthonellidae. Therefore, the insertion of the supplementary gland into the vas deferens should be used in combination with the other characters mentioned above to identify future

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members of Cuthonellidae. Notably, within the family Cuthonidae (genera *Cuthona* and *Bohuslania*) this feature has so far never been observed (Korshunova et al., 2017a, 2018a).

The family Cuthonellidae Miller, 1977 has been resurrected recently, including a morphological diagnosis and molecular phylogenetic data (Korshunova et al., 2017a, b, 2018a). Miller (1977: 200) proposed the subfamily name Cuthonellinae based on the valid genus name *Cuthonella* and provided a brief morphological diagnosis "digestive ducts unbranched". This diagnosis meets the requirements of the relevant ICZN (1999) articles (i.e., 11.7, 13, 29) for the availability of a family group name. Miller (1977: 200) also mentioned that the name Cuthonellinae "replaced" the name Precuthoninae introduced by Odhner in Franc (1968: 885). Miller did not provide explanations of his reasons and did not make a special indication why this is a "replacement" name. Bouchet & Rocroi (2005: 59) commented that Cuthonellinae Miller (1977) was invalid; they said in their remarks that it was "Introduced presumably (and thus in violation of Art. 40.1)

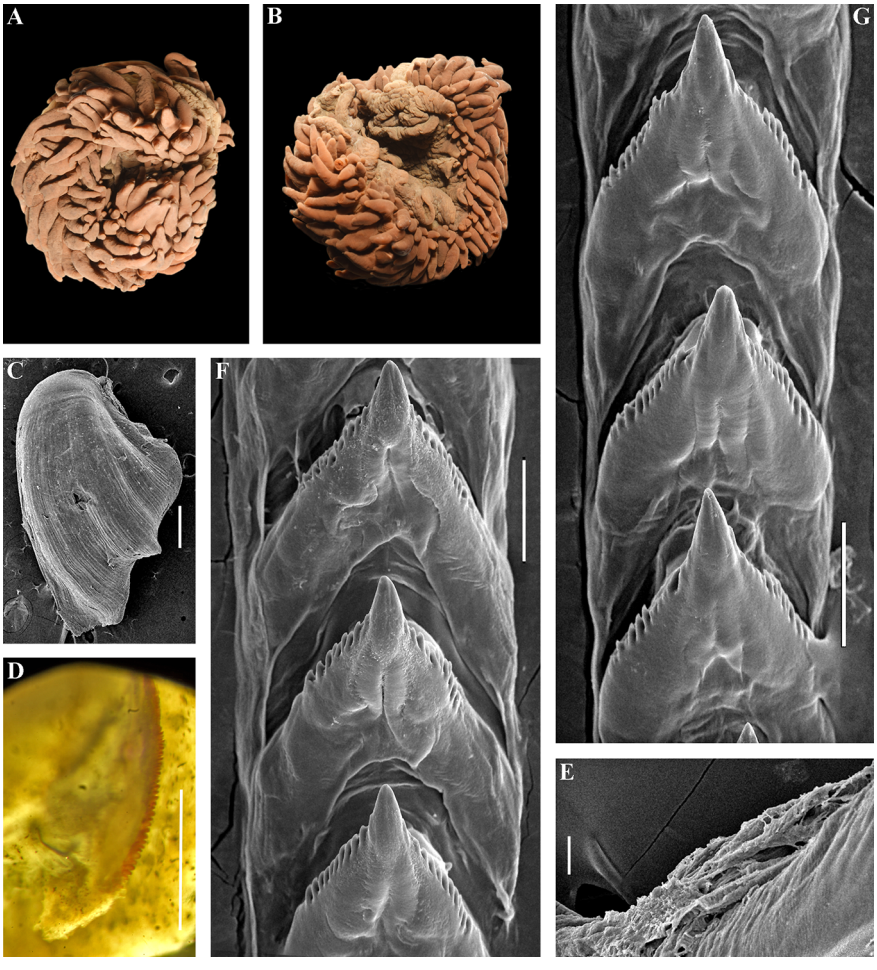

FIGURE 4 *Cuthonella abyssicola abyssicola* Bergh, 1884. A, B, dorsal and ventral views, respectively, of a preserved specimen ZMMU Op-616 from the deep waters of the Barents Sea, 23 mm. C, jaw (SEM). D, jaw, details (light microscopy). E, jaws, details (SEM). F, posterior part of the radula (SEM). G, anterior part of the radula (SEM). Scale bars: C, D, 500 μm; E, 10 μm; F, G, 30 μm; Photos: Alexander Martynov.

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as a replacement name for Precuthoninae, because *Cuthonella* has precedence over *Precuthona* Odhner, 1929." However, *Precuthona* Odhner, 1929 is not a synonym of the genus *Cuthonella* Bergh, 1884 and therefore there is no violation of Article 40.1 of ICZN (1999). The name *Precuthona* Odhner, 1929 is a synonym of the genus *Cuthona* (Brown, 1980), which belongs to the different family Cuthonidae, supported by morphological and molecular data (Korshunova et al., 2017a, 2018a). The name Precuthoninae Odhner in Franc (1968: 885), therefore, is a synonym of the family Cuthonidae Odhner, 1934. The name Cuthonellinae Miller, 1977 is thus an available family group name in full compliance with Article 13 ("to be available, every new family-group name published after 1930 must satisfy the provisions of Article 13.1 and must be formed from an available genus-group name then used as valid by the author in the family-group taxon [Arts. 11.7.1.1, 29]", ICZN 1999). The available family group name Cuthonellinae Miller, 1977 (in a restricted sense compared to the mention in Miller (1977), without "*Precuthona*") with an amended diagnosis was therefore introduced as the valid family Cuthonellidae Miller, 1977 and the (incorrect and unnecessary) term "replaced" should be discounted.

Cuthonellidae is distinct by the morphological and molecular phylogenetic data (Korshunova et al., 2017a, 2018a, this study). In some publications (Korshunova et al., 2017a, b) the year of the original publication of Cuthonellinae was indicated as 'Miller, 1971' due to a typo (the reference 'Miller, 1977' was provided correctly). The correct year of publication is Miller (1977). The type genus of the family Cuthonellidae is *Cuthonella* Bergh, 1884.

In the present revision of the genus *Cuthonella* the number of known species is increased threefold. It is the most substantial update to the knowledge of the genus *Cuthonella* since its description in 1884. All previously known and novel species are presented below in alphabetical order (figs 4–18).

***Cuthonella abyssicola abyssicola* Bergh, 1884**

(figs 1, 2, 4, 19A, 21)

Cuthonella abyssicola Bergh, 1884: 24–26, pl. 10, figs. 1–3, pl. 11, fig. 2, pl. 12, figs. 9–13; Martynov, 1992: 23; Martynov, 2006a: 73; Martynov, 2006b: 290; Martynov & Korshunova, 2011: 195.

Cuthonella berghi Friele, 1903: 11, tab. II, fig. 3–4, tab. III, fig. 7–10.

Cuthonella ferruginea Friele, 1903: 10, tab. II, fig. 1–2, tab. III, fig. 3–5.

Cuthona abyssicola (Bergh, 1884) – Millen, 1986: 1358–1359, figs 8, 9.

Type material. Holotype lost (K. Jensen (ZMUC), personal communication; K. Lundin performed an additional search in ZMUC and confirmed the absence of the type material).

Material. ZMMU Op-616, *L* = 23 mm length (preserved, convoluted, more than 30 mm if unrolled), Arctic Ocean, Barents Sea, 77° 06′ N, 58° 12′ E, 307 m, 07.08.1948. NTNU-VM 73124, 1 spec., L = 31 mm length (preserved), Norwegian Sea, Nyegga, 64° 40.115N 5° 15.702E, 731 m, coll. Hans Tore Rapp, 05.08.2008.

External morphology. Body wide, massive. Foot and tail broad. Oral tentacles moderate. Rhinophores smooth to slightly wrinkled, similar in size to oral tentacles. Dorsal cerata elongate, thick, arranged in continuous rows. Up to 17 pre-anal branched ceratal rows. Anal opening cleioproctic.

Colour (*preserved*). Background colour yellowish white. Digestive gland diverticula in cerata possibly reddish to pinkish. Ceratal tips without distinct spots or bands of opaque white pigment.

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Jaws. Jaws broad, yellowish to brown in colour. Masticatory processes of jaws covered with several rows of denticles (with a few indistinct additional rows) (fig. 4C–E).

Radula. Radula formula 21 × 0.1.0 (specimen 23 mm in length, Barents Sea). Central tooth broad, with a strongly protracted, pointed non-compressed cusp (fig. 4F, G). Central teeth with up to 14 lateral denticles, which are rarely clustered. Cusp quite clearly delineated from the adjacent lateral denticles which do not reach the top of the cusp.

Reproductive system. Diaulic. Hermaphroditic duct leads to a swollen ampulla. Vas deferens long, without a distinct prostate. Supplementary gland long, inserts into the vas deferens at a considerable distance from the elongated penial sheath. Penis conical, strong, unarmed. Oviduct connects through the insemination duct into the female gland complex. Exceedingly long tubular receptaculum seminis placed distally, widened in the middle part with a small oval reservoir (fig. 19A).

Ecology. Lives on soft bottoms with stones, commonly at bathyal and shelf depths of *c.* 300–1112 m. A record from the shallow waters of the Laptev Sea (Martynov & Korshunova, 2011) (49 m depth) needs verification.

Distribution. Faroe Islands in the North Atlantic; Norwegian Sea; Barents Sea, possibly the Laptev Sea (Millen, 1986; Martynov & Korshunova, 2011; present study).

Remarks. Cuthonella abyssicola differs from the majority of other *Cuthonella* species by the substantial number of anterior ceratal rows (up to 17), radular teeth with small denticles which are not always clearly delineated from the cusp, long vas deferens and distal seminal receptacle on a very long stalk.

In the present study, we give for the first time both morphological and molecular data for a relatively shallow-water specimen from Franz Joseph Land in the Arctic (see description below). Morphologically, this specimen showed closely similar features with the deeper-water specimens (300 m) from the Barents Sea in the presence of up to 17 pre-anal branched ceratal rows, a long vas deferens and a receptaculum seminis on a long stalk. In the original description (Bergh, 1884), a type specimen from deeper waters of the Faroe Channel (*c.* 1000 m) shows closely similar external and reproductive features with the shallow-water specimen from Franz Joseph Land, but the radular teeth have a significantly fewer number of lateral denticles (10–14 vs. 13–36). Notably, in the Franz Joseph Land specimen the lateral denticles are usually clustered and extend to the top of the central cusp (fig. 5I, J), compared to the deep-sea *C. abyssicola* (fig. 4F, G). Millen (1986) performed a detailed investigation of the surviving type material of the nominal species *Cuthonella berghi* Friele, 1903 and *C. ferruginea* Friele, 1903, which have been considered synonymous with *C. abyssicola*. Both of these synonymous species come from similar geographic regions (NE Atlantic, Norwegian Sea) and also from similar depths (from deeper waters of 590–1098 m) as *C. abyssicola*. The radulae of *C. berghi* and *C. ferruginea* are similar to the original description of *C. abyssicola* (Bergh 1884): the central teeth possess only a few lateral denticles (*c.* 6–10), and the cusp is more clearly delineated. This agrees well with our specimens from the deep waters of the Barents Sea (*c.* 6–14) (fig. 4F, G). The number of teeth of the radula of the deeper water specimen from the Barents Sea (21 teeth) also corresponds well with the first description of Bergh (1884) and also to those described by Friele (1903) and Grieg (1913) (18–21 teeth), but not to the shallow-water specimen from Franz Joseph Land (27 teeth). Thus, the radular characters (which are reliably based on several deep-sea specimens collected in various locations) are different

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FIGURE 5 *Cuthonella abyssicola kryos* subsp. nov. A, dorsal view of living holotype ZMMU Op-727, shallow water of Franz Josef Archipelago, 25 mm (preserved length). B–E, dorsal, lateral, latero-ventral and ventral views respectively of the same preserved specimen. F, jaw (SEM). G, jaw, details (light microscopy). H, jaws, details (SEM). I, anterior part of the radula (SEM). J, posterior part of the radula (SEM). Scale bars: F, G, 500 μm; H, 50 μm; I, J, 100 μm; Photos: A, Oleg Savinkin, B–J, Alexander Martynov.

from the shallow-water specimen from Franz Joseph Land, which by other features are similar to the real *C. abyssicola*. Therefore, these differences cannot be ignored while making a taxonomic decision. Because only a single shallow-water specimen was available, we preferred in this case to separate it here as a subspecies; *Cuthonella abyssicola kryos* subsp. nov. (see description below).

It was previously shown (Korshunova et al., 2017b; Martynov & Korshunova, 2017) that the waters of Franz Josef Land demonstrate considerable endemism in other various nudibranch taxa, such as in the genera *Adalaria*, *Microchlamylla*, and *Ziminella*. We have also studied a single specimen from the Laptev Sea, from a relatively shallow-water locality at *c.* 50 m. Remarkably, compared to the specimen from Franz Joseph Land, the Laptev Sea specimen possesses no more than 14–15 lateral denticles on the central tooth (23 teeth in total), and thus more closely matches the real deep-sea *C. abyssicola* than the Franz Joseph Land specimen. Thus, the distributional data for *C. abyssicola abyssicola* and *C. abyssicola kryos* subsp. nov.

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implies that the nominative subspecies can be found in shallow depths, but not in the high latitude Franz Joseph Land. It should also be taken into consideration that the shallow-water record from the Laptev Sea needs further verification. *C. abyssicola* s.l. potentially feeds on athecate hydroids. We have studied few deep-sea specimens of *C. abyssicola abyssicola*, but none of them were suitable for molecular investigation due to the considerable age of collection and primary fixation in formaldehyde. We made additional inquiries to obtain recent deep-sea specimens, but none were available. Therefore, though details of the radular features and distributional patterns may potentially imply that we are dealing with two sister species rather than with two subspecies, we need more data to confirm this. However, because the shallow-water subspecies (see below) shows substantially similar major features in both external and internal morphology, including the reproductive system, we can confirm that it represents a form that is close to the original *Cuthonella abyssicola* and therefore can be used here for defining the genus *Cuthonella*. For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella abyssicola kryos* subsp. nov.**
(Figs 1, 2, 5, 19B, 21)
ZooBank: http://urn:lsid:zoobank.org:act:9F7FA1E7-3326-4009-9F9B-ADFFC10E7F82

Type material. Holotype, ZMMU Op-727, *L* = 25 mm length (preserved), Arctic Ocean, Franz Josef Land, Wiltona Island, 18–33 m depth, collected by O.V. Savinkin, 23.08.2013.

Etymology. From Ancient Greek *κρύος* (kryos), "icy cold" in reference to the Arctic, high latitude type locality.

External morphology. Body wide, massive. Foot and tail broad. Oral tentacles moderate. Rhinophores similar in size to oral tentacles, smooth to slightly wrinkled. Dorsal cerata elongate, thick, arranged in continuous rows. Up to 17 pre-anal branched ceratal rows. Anal opening cleioproctic.

Colour (*live*). Background colour light pinkish to whitish. Digestive gland diverticula in cerata light pinkish to whitish. Ceratal tips with dispersed white pigment. Rhinophores light yellowish with indistinct white pigment towards the top (fig. 5A).

Jaws. Jaws broad, yellowish to brown in colour. Masticatory processes of jaws covered with a few rows of denticles (with a few indistinct additional rows) (fig. 5F, G, H).

Radula. Radula formula 27 × 0.1.0. Central tooth broad, with a strongly protracted, pointed non-compressed cusp (fig. 5I, J). Central teeth with up to 36 lateral denticles (often clustered and increasingly irregular towards the cusps). Cusp is not clearly delineated from the adjacent lateral denticles which may reach the top of the cusp.

Reproductive system. Diaulic. Hermaphroditic duct leads to a long, moderately swollen convoluted ampulla. Vas deferens long, without a distinct prostate. Supplementary gland long, inserts into the vas a considerable distance from the elongated penial sheath. Penial sheath elongated. Penis conical, strong, unarmed. Oviduct connects through the insemination duct into the female gland complex. Very long tubular receptaculum seminis in a distal position, with a widened base and small pear-shaped reservoir (fig. 19B).

Ecology. Lives on soft bottom with stones at depths of 18–33 m.

Distribution. High latitude arctic region of Franz Josef Land.

Remarks. See remarks for *C. abyssicola abyssicola*. The lowest CO1 intergroup distance of 7.00% is found between *C. abyssicola kryos* subsp. nov. and *C. sandrae* sp. nov. (table 1). For a morphological comparison with other *Cuthonella* species, see table 2.

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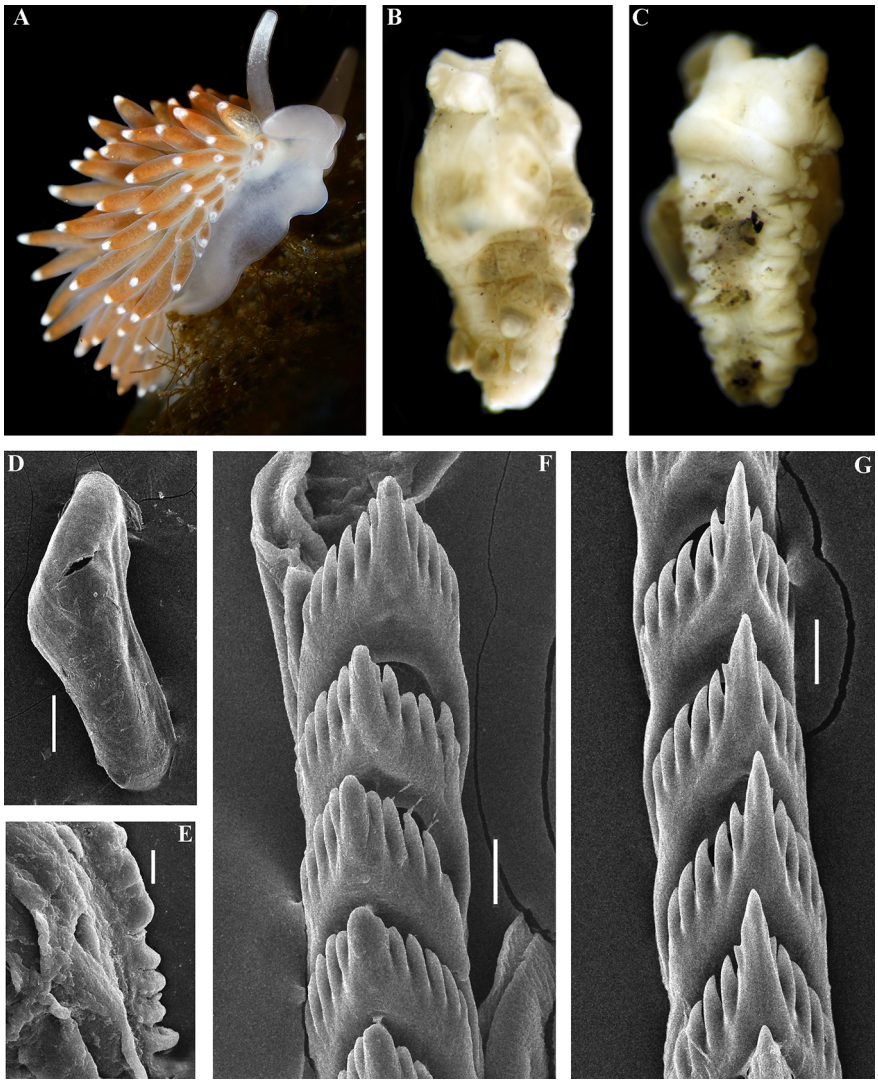

FIGURE 6 *Cuthonella ainu* sp. nov. A, dorsolateral view of living holotype ZMMU Op-618, Matua Island. B, C, dorsolateral and ventral views of preserved holotype, 4 mm. D, jaw (SEM). E, jaws, details (SEM). F, anterior part of the radula (SEM). G, posterior part of the radula (SEM). Scale bars: D, 200 μm; E, 10 μm; F, G, 20 μm. Photos: A, Nadezhda Sanamyan, B–J, Alexander Martynov.

***Cuthonella ainu* sp. nov.**

(Figs 1, 2, 6, 19C, 21)

ZooBank: http://urn:lsid:zoobank.org:act:29DB6C94-45E8-4826-907D-2F5B53B85413

Type material. Holotype. ZMMU Op-618, 1 spec., *L* = 4 mm length (preserved), Pacific Ocean, Middle Kuril Islands, Matua Island, Klyuv Cape, 14 m, collected by N.P. Sanamyan, 04.08.2017.

Etymology. Named in honour of the Ainu, the indigenous people of the Kuril Islands (type locality of this new species), southern Kamchatka, Sakhalin, Hokkaido and northern Honshu (Tohoku). The Ainu speak a highly isolated language, which is now critically endangered. The Ainu were forced to leave their original lands both by Japanese and Russian authorities. Ainu *de facto* was extinct in Russia since the early 70s, but attempts to

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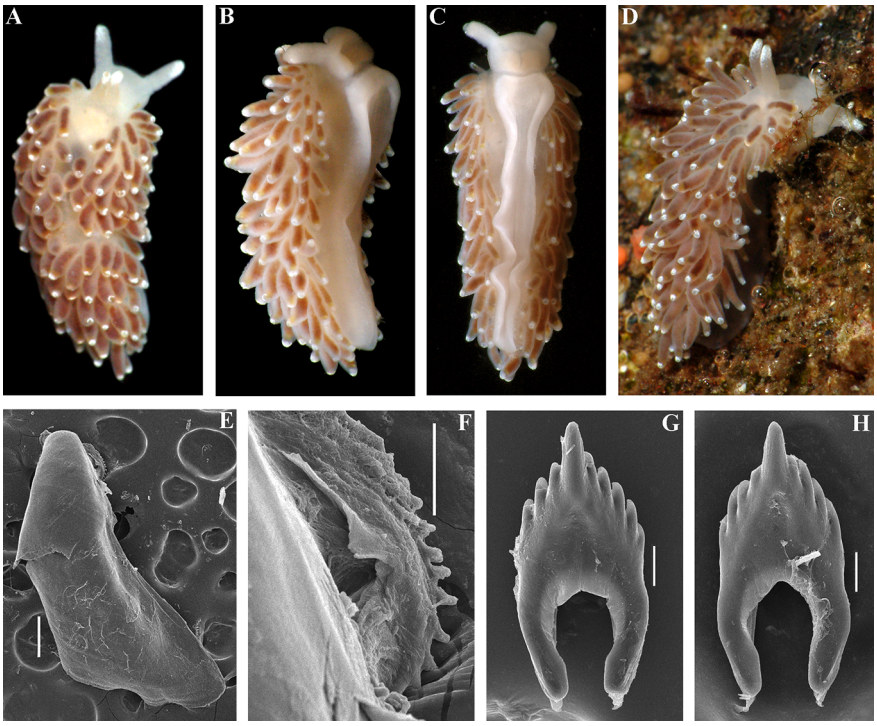

FIGURE 7 *Cuthonella benedykti* sp. nov. A–D, dorsal, lateral, ventral and dorsolateral views of living holotype ZMMU Op-194 from Kamchatka, 6 mm (preserved length). E, jaw (SEM). F, jaws, details (SEM). G, anterior part of the radula (SEM). H, posterior part of the radula (SEM). Scale bars: E, 200 μm; F, 50 μm; G, H, 20 μm. Photos: A–D, Tatiana Korshunova, E–H, Alexander Martynov.

revitalize Ainu culture based on descendants with partial Ainu ancestry have been carried out recently in Kamchatka without governmental support and official recognition (e.g., Tanaka, 2017). In Japan, formerly forcedly-assimilated Ainu now have governmental support for their language and culture with official recognition (Tsunemoto, 2019).

External morphology. Body moderately wide. Foot and tail broad. Oral tentacles moderate. Rhinophores similar in size to oral tentacles, smooth to slightly wrinkled. Dorsal cerata elongate, thick, arranged in a moderate number of continuous rows. Five pre-anal unbranched ceratal rows. Anal opening acleioproctic.

Colour (*live*). Background colour yellowish white. Digestive gland diverticula in cerata brownish to light orange. Ceratal tips with opaque white spot, sometimes with very small white spots. Rhinophores semi-transparent and covered with a dense white pigment at the top (fig. 6A).

Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of distinct denticles (fig. 6D, E).

Radula. Radula formula 18 × 0.1.0. Central tooth elongated with a strongly protracted, pointed non-compressed cusp (fig. 6F, G). Central tooth bears up to 7 lateral denticles. Cusp clearly delineated from the adjacent first lateral denticles.

Reproductive system. Diaulic. Hermaphroditic duct leads to a relatively short, slightly bent, swollen ampulla. Vas deferens short, without a distinct prostate. Supplementary gland long, inserts into the vas deferens a short distance from the elongated penial sheath. Penis conical, unarmed. Oviduct connects through the insemination

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duct into the female gland complex. Receptaculum seminis in distal position, on a short stalk, elongate-oval (fig. 19C).

Ecology. Only found on soft bottom with stones at 14 m depth.

Distribution. Matua Island, Middle Kuril Islands.

Remarks. According to the molecular phylogenetic analysis *Cuthonella ainu* sp. nov. is closely related to *C. benedykti* sp. nov. (figs 1, 2). The maximum intragroup distance in *C. ainu* sp. nov. is 0.15%. The lowest CO1 intergroup distance of 2.65% is found between *C. ainu* sp. nov. and *C. benedykti* sp. nov. (table 1). Morphological analysis reveals differences in radular patterns between *C. benedykti* sp. nov. and *C. ainu* sp. nov. (figs 6F, G and 7G, H). Externally, *C. ainu* sp. nov. differs from *C. benedykti* sp. nov. by its orange-brownish colouration and spot-shaped rather than ring-shaped patterns of the white pigment on the ceratal apices. For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella benedykti* sp. nov.**

(Figs 1, 2, 7, 19D, 21)

ZooBank: http://urn:lsid:zoobank.org:act:D4CDE4F2-05F3-46E4-8C6B-B233722AAB25

Type material. Holotype. ZMMU Op-194, 1 spec., *L* = 6 mm length (preserved), Pacific Ocean, Kamchatka, Starichkov Island, 6–12 m, stones, collected by T.A. Korshunova and A.V. Martynov, 19.08.2008.

Etymology. The name is in honour of a polymath scientist of Polish origin, Benedykt Dybowski (1833–1930), who made substantial achievements especially in zoology and the anthropology of Russian Siberia and the Far East. Benedykt Dybowski belonged to the Polish intelligentsia, and he was arrested after the Polish rebellion against the Russian Empire (1863, "January Uprising") and sentenced to death, later changed to exile in Siberia, where he started his research (Wszolek et al., 1990). He also served as the only physician at the time (starting in 1879) for the large region of Kamchatka, the type locality of this new species. Among other achievements, Dybowski contributed to Kamchatka's Ainu dictionary.

External morphology. Body moderately wide. Foot and tail broad. Oral tentacles moderate. Rhinophores blunt and similar in size to oral tentacles, smooth to slightly wrinkled. Dorsal cerata elongate, thick, arranged in continuous rows. Five pre-anal unbranched ceratal rows. Anal opening acleioproctic.

Colour (*live*). Background colour yellowish white. Digestive gland diverticula in cerata brownish with a darker reddish to brown hue. Ceratal tips with opaque white ring or spot, sometimes with additional yellow ring, and small white spots. Rhinophores light yellowish with white pigment on the top (fig. 7A–D).

Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of distinct denticles (fig. 7E, F).

Radula. Radula formula 36 × 0.1.0 (specimen 6 mm in length). Central tooth elongated with a strongly protracted, pointed non-compressed cusp (fig. 7G, H). Central tooth bears up to 5 lateral denticles. Cusp clearly delineated from the adjacent first lateral denticles.

Reproductive system. Diaulic. Hermaphroditic duct leads to a relatively short, swollen ampulla. Vas deferens wide and moderate in length, without a distinct prostate. Supplementary gland relatively short, inserts into the vas deferens a short distance from the elongated penial sheath. Penis conical, unarmed. Oviduct connects through the insemination duct into the female gland complex. Receptaculum seminis in distal position, on a short stalk, oval (fig. 19D).

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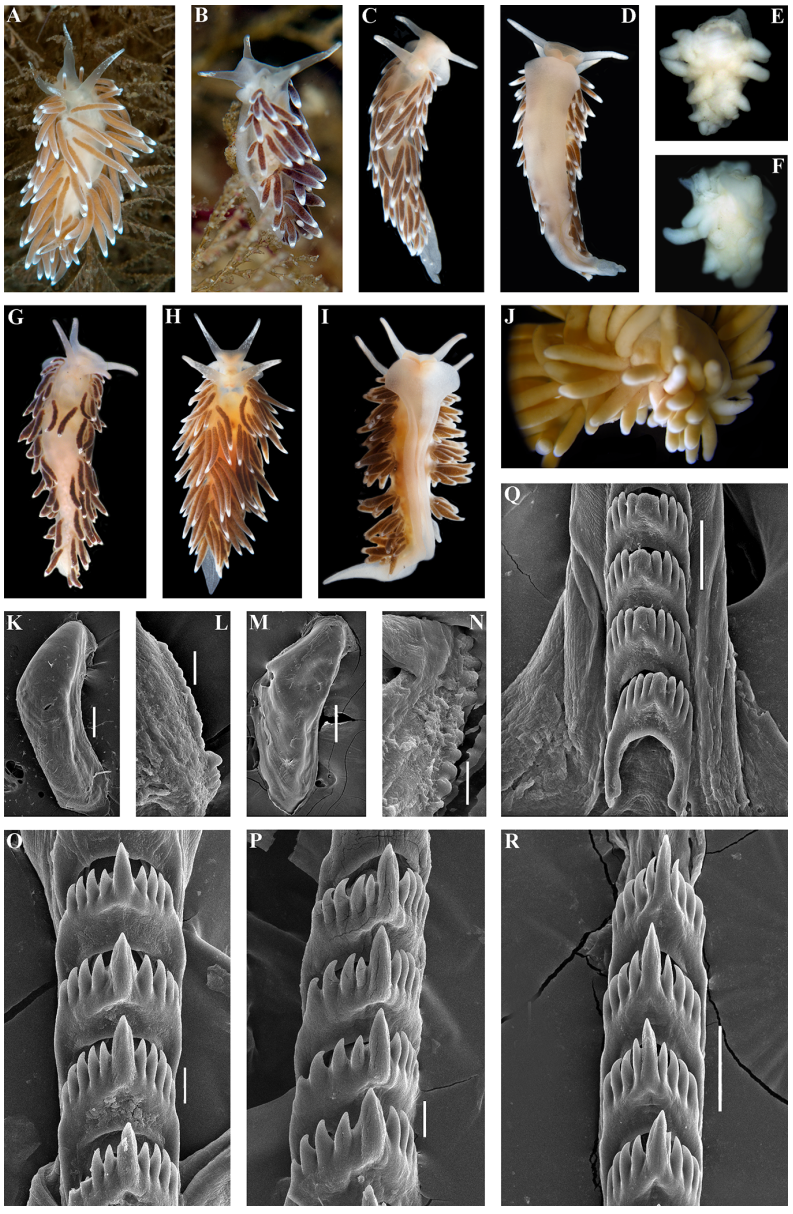

FIGURE 8 *Cuthonella concinna concinna* (Alder & Hancock, 1843). A, living specimen GNM Gastropoda 8866, Sweden, 9.5 mm (preserved length), dorsal view. B, living specimen from UK, 3.5 mm (preserved length), laterodorsal view. C, D, living specimen from Finnmark, Norway, 12.5 mm (live specimen), dorsal and ventral views respectively. E, F, lectotype of "*Cuthona distans*", ZMO D 25946, Finnmark, Norway, 3 mm (preserved length), dorsal and ventral views respectively. G, living specimen from the Barents Sea, Russia, 9 mm (preserved length), dorsal view. H, I, living specimen from the White Sea (previously identified as "*C. marisalbi*"), Russia, ZMMU Op-523, 8 mm (preserved length), dorsal and ventral views respectively. J, same, lateral view of fixed specimen. K, jaw, GNM 8866, Sweden (SEM). L, same, details. M, jaw, Finnmark, Norway (SEM). N, same, details. O, anterior part of the radula, Sweden (SEM). P, posterior part of the radula, Sweden (SEM). Q, anterior part of the radula, Norway (SEM). R, posterior part of the radula, Norway (SEM). Scale bars: K, M, 200 μm; L, N, O, P, 20 μm; Q, R, 50 μm; Photos: A, Klas Malmberg, B, Bernard Picton, C–I, Tatiana Korshunova, J–R, Alexander Martynov.

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Ecology. Lives on stones at depths of *c.* 6–12 m.

Distribution. Kamchatka, Pacific side.

Remarks. According to the molecular phylogenetic analysis *Cuthonella benedykti* sp. nov. forms a separate clade sister to *C. ainu* sp. nov. (figs 1, 2). The maximum intragroup distance in *C. benedykti* sp. nov. is 0.16%. The minimum CO1 intergroup distance of 2.65% is found between *C. benedykti* sp. nov. and *C. ainu* sp. nov. (Table 1). Morphological analysis reveals considerable differences in the denticulation of the central teeth between *C. benedykti* sp. nov. and its sister *C. ainu* sp. nov. as well as more distantly related, *C. georgstelleri* sp. nov., *C. hiemalis, C. osyoro,* and *C. soboli* (figs 6, 7, 11, 12, 14, 17). Externally, *C. benedykti* sp. nov. (fig. 7A–D) differs from *C. ainu* sp. nov. (fig. 6A) by a more brownish colouration with a dark reddish hue, and more distinct ring-shaped white pigment on the ceratal apices. For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella cocoachroma* (Williams & Gosliner, 1979)**

Cuthona cocoachroma Williams & Gosliner, 1979: 204–211, figs. 3–6.

Remarks. Cuthonella cocoachroma has been described in detail by Williams & Gosliner (1979), which will not be repeated here except to say that it differs from the sympatric *C. concinna bellatula* in having rhinophores which are twice as long as the oral tentacles, having fewer pre-anal ceratal rows (3–4 vs 5–6) and fewer ceratal rows altogether (9–10 vs 10–12), and lacking scattered white or bluish spots on its cerata. In the present material commonly up to 4 pre-anal rows in *C. concinna bellatula*, that make external differences from *C. cocoachroma* as more subtle. According to figure 5D in Williams & Gosliner (1979), *C. cocoachroma* possess a supplementary gland which is inserted into the penial base instead of the vas deferens. This feature needs to be particularly commented on, because all the other 15 species of the genus *Cuthonella* invariably possess a supplementary gland inserted into the vas deferens and not into the penial sheath or penial base. The reproductive system of *C. cocoachroma* (not available for the present study) needs to be re-examined in this respect, considering that according to the molecular data it belongs to the genus *Cuthonella* (fig. 1). The thecate hydroid *Thuiaria* sp. was reported as a food object for *C. cocoachroma* (Goddard, 1985). The maximum intragroup distance in *C. cocoachroma* is 1.52%. Interestingly, the minimum CO1 intergroup distance of 9.74% is found between *C. cocoachroma* and the allopatric *C. punicea* (table 1) rather than between the sympatric *C. cocoachroma* and *C. concinna bellatula* subsp. nov. which are externally nearly identical. For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella concinna concinna* (Alder & Hancock, 1843)**

(Figs 1–3, 8, 19E, 21)

Eolis concinna Alder & Hancock, 1843: 234; Alder & Hancock, 1845–1855: 50, fam. 3, pl. 24, plus unnumbered pages.

Cuthona concinna – Brown, 1980: 249–250, fig. 5H; 6D, H.

Cuthona distans Odhner, 1922: 28–29, figs 11, 12, syn. nov.

Cratenopsis concinna – Nordsieck, 1972: 81.

Trinchesia concinna – Pruvot-Fol, 1954: 385.

Cuthonella marisalbi Roginskaya, 1963: 258–264, figs 1–7; Martynov & Korshunova, 2011: 200 –201, figs.

Cuthonella concinna – Martynov, 1992: 23; Martynov, 2006: 290; Martynov & Korshunova, 2011: 198 –200, figs.

Type material. Natural History Museum, London, one specimen collected by Joshua Alder at Cullercoats (original type locality) and indicated as "type" (NHM, 2020).

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Other material. ZMMU Op-41, 2 spec., *L* = 9 mm and 5 mm length (preserved), Barents Sea, Dalnie Zelentsy, intertidal, collected by T. A. Korshunova, 08.2006. KM 452, *L* = 3 mm length (preserved), Barents Sea, Dalnie Zelentsy, 0.2–0.5 m depth, collected by T.A. Korshunova and A.V. Martynov, 05.08.2005. KM 453, *L* = 8 mm length (preserved), Barents Sea, Dalnie Zelentsy, 0.2–0.5 m depth, collected by T.A. Korshunova and A.V. Martynov, 01.08.2005. ZMMU Op-523, two spec., *L* = 7 mm and 8 mm length (preserved), White Sea, Rugozerskaya Bay, intertidal, collected T.A. Korshunova and A.V. Martynov, 15.06.2009. GNM Gastropoda 8866, *L* = 9.5 mm length (preserved), Skagerrak, Sweden, 5–10 m depth, collected by Klas Malmberg. KM 616, *L* = 3.5 mm length (preserved), the North Atlantic, Northern Ireland, Strangford Lough, UK, 10–20 m depth, collected B. Picton, 23.05.2015. ZMO D 25946 (lectotype of *"Cuthona" distans*), *L* = 3 mm length (preserved), Finnmark, Vadsø, collected G.O. Sars. KM 767, 1 spec., *L* = 12.5 mm (live), Finnmark, Kirkenes vicinity, intertidal, collected by T.A. Korshunova and A.V. Martynov, 29.04.2019. NTNU-VM 76078, 1 spec., Finnmark, Altafjorden, 70.156664°N 23.285329°E, intertidal, collected by T.A. Korshunova, A.V Martynov, and K. Hårsaker, 08.05.2019. NTNU-VM 76079, 1 spec., Finnmark, Altafjorden, 70.156664°N 23.285329°E, intertidal, collected by T.A. Korshunova, A.V Martynov, and K. Hårsaker, 08.05.2019. NTNU-VM 75959, 1 spec., Finnmark, Bugøynes, 69.972744°N 29.627895°E, intertidal, collected by T.A. Korshunova and A.V. Martynov, 29.04.2019. NTNU-VM 76009, 1 spec., Finnmark, Porsanger, 70.245495°N 24.999314°E, intertidal, collected by T.A. Korshunova, A.V Martynov, and K. Hårsaker, 03.05.2019. NTNU-VM 76010, 1 spec., Finnmark, Porsanger, 70.245495°N 24.999314°E, intertidal, collected by T.A. Korshunova, A.V Martynov, and K. Hårsaker, 03.05.2019. NTNU-VM 75991, 1. spec., Finnmark, Berlevåg, 70.85021°N 29.151252°E, intertidal, collected by T.A. Korshunova, A.V Martynov, and K. Hårsaker, 01.05.2019. NTNU-VM 76044, 1 spec., Finnmark, Kamøyvær, 71.049696°N 25.91252°E, intertidal, collected by T. Bakken, C. Skauge, 05.05.2019. NTNU-VM 76045, 2 spec., Finnmark, Kamøyvær, 71.049696°N 25.91252°E, intertidal, collected by T. Bakken, C. Skauge, 05.05.2019. NTNU-VM 75960, 1 spec., Finnmark, Bugøynes, 69.972744°N 29.627895°E, intertidal, collected by T.A. Korshunova and A.V. Martynov, 29.04.2019. NTNU-VM 75981, 1. spec., Finnmark, Berlevåg, 70.850088°N 29.154291°E, intertidal, collected by T. Bakken, T.A. Korshunova, A.V. Martynov, and K. Hårsaker, 30.04.2019. NTNU-VM 75992, 1. Spec., Finnmark, Berlevåg, 70.85021°N 29.151252°E, intertidal, collected by T.A. Korshunova, A.V Martynov, and K. Hårsaker, 01.05.2019. NTNU-VM 75994, 4. Spec., Finnmark, Berlevåg, 70.85021°N 29.151252°E, intertidal, collected by T.A. Korshunova, A.V Martynov, and K. Hårsaker, 01.05.2019.

External morphology. Body moderately wide.

Foot and tail broad. Rounded foot corners present. Oral tentacles moderate. Rhinophores similar in size, or slightly longer than oral tentacles, smooth to slightly wrinkled. Dorsal cerata elongate, arranged in continuous rows. Up to 6 pre-anal unbranched ceratal rows. Anal opening acleioproctic.

Colour (*live*). Background colour yellowish white. Digestive gland diverticula in cerata brown to purplish-brown. Ceratal tips with opaque white subapical band or spot, sometimes with a bluish hue and smaller white spots. Rhinophores and oral tentacles semi-transparent with commonly white pigment on the tips (fig. 8A–D, G–I).

Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of distinct denticles (fig. 8K–N).

Radula. Radula formula 30 × 0.1.0 (specimen 8 mm in length), 29 × 0.1.0 (specimen 9.5 mm

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in length), 19 × 0.1.0 (specimen 3 mm in length), 26 × 0.1.0 (specimens 8 mm in length). Central tooth elongated with a strongly protracted cusp (fig. 8O–R). Central tooth bears up to 10 lateral denticles (more commonly, up to 4–5). Cusp clearly delineated from the adjacent first lateral denticles.

Reproductive system. Diaulic. Hermaphroditic duct leads to a relatively short or folded swollen ampulla. Vas deferens relatively long, without a distinct prostate. Supplementary gland usually relatively long, sometimes shorter, inserts into the vas deferens at a relatively short distance from the elongated penial sheath. Penis conical, unarmed. Oviduct connects through the insemination duct into female gland complex. Receptaculum seminis in a more proximal position than in most other *Cuthonella* species, and on a short stalk, without a distinct reservoir (fig. 19E).

Ecology. Lives on stones and rocks. Intertidal to 30 m depth.

Distribution. Boreal European waters of the NE Atlantic (France, British Isles, Netherlands, Denmark, Sweden, Norway to the Barents Sea and the White Sea in Russia) and the Atlantic coast of the USA and Canada.

Remarks. In the present study we obtained morphological and molecular data from specimens of *C. concinna concinna* from the British Isles (the type locality of this subspecies) and thereby confirm that it is conspecific with our other specimens from different localities across the North Atlantic. Present molecular phylogenetic analysis (figs 1, 2) hereby confirms that *C. concinna concinna* has an amphiatlantic distribution, but North Pacific populations belong to the separate subspecies *C. concinna bellatula* subsp. nov. (see details below). The range of *C. concinna concinna* is confirmed here from the White Sea to the Northeast Atlantic coast, including occurrences in Eastern Canada, the Netherlands, Norway, Russia, Sweden, the UK, and the Eastern USA.

In this study we also obtained recently collected specimens (fig. 8C, D) from the type locality of the enigmatic Norwegian species *Cuthona distans* Odhner, 1922 in the northernmost mainland Norwegian county of Finnmark. We also studied the type specimen of *C. distans* from the Oslo Natural History Museum in Norway (ZMO D 25946, designated here as the lectotype) (fig. 8E, F). According to the morphological study of the type material of *C. distans*, it has a supplementary gland that inserts into the vas deferens relatively close to the penis, similar to that of *C. concinna concinna*. Molecular analysis shows that new specimens from Finnmark belong to *C. concinna concinna* (figs 1–3). Morphological data from the original description of *C. distans* (Odhner, 1922) and our study of the type material also confirm that *C. distans* syn. nov. is a junior synonym of *C. concinna concinna*. In the northern localities such as the Barents Sea and the Finnmark region, *C. concinna concinna* is one of the most common shallow-water species of nudibranchs. Several thecate hydroid species of the families Campanulariidae and Sertulariidae were reported as food objects for *C. concinna concinna*: *Diphasia fallax* (Johnston, 1847), *Dynamena pumila* (Linnaeus, 1758), *Sertularia* spp. (Roginskaya, 1987; Martynov & Korshunova, 2011), *Hartlaubella gelatinosa* (Pallas, 1766), *Laomedea flexuosa* Alder, 1857, *Obelia longissima* (Pallas, 1766), *Sertularia argentea* Linnaeus, 1758, *Sertularia cupressina* Linnaeus, 1758 (Alder & Hancock, 1845–1855; Swennen, 1961; Brown, 1980; Thompson & Brown, 1984; Picton & Morrow, 1994). A report of the feeding on the athecate *Tubularia indivisa* Linnaeus, 1758 (Hamond, 1972) needs a verification.

The maximum intragroup distance in *C. concinna concinna* is 0.91%. The minimum COI interspecies distance of 9.28% is found between *C. concinna concinna* and *C. vasentsovichi*

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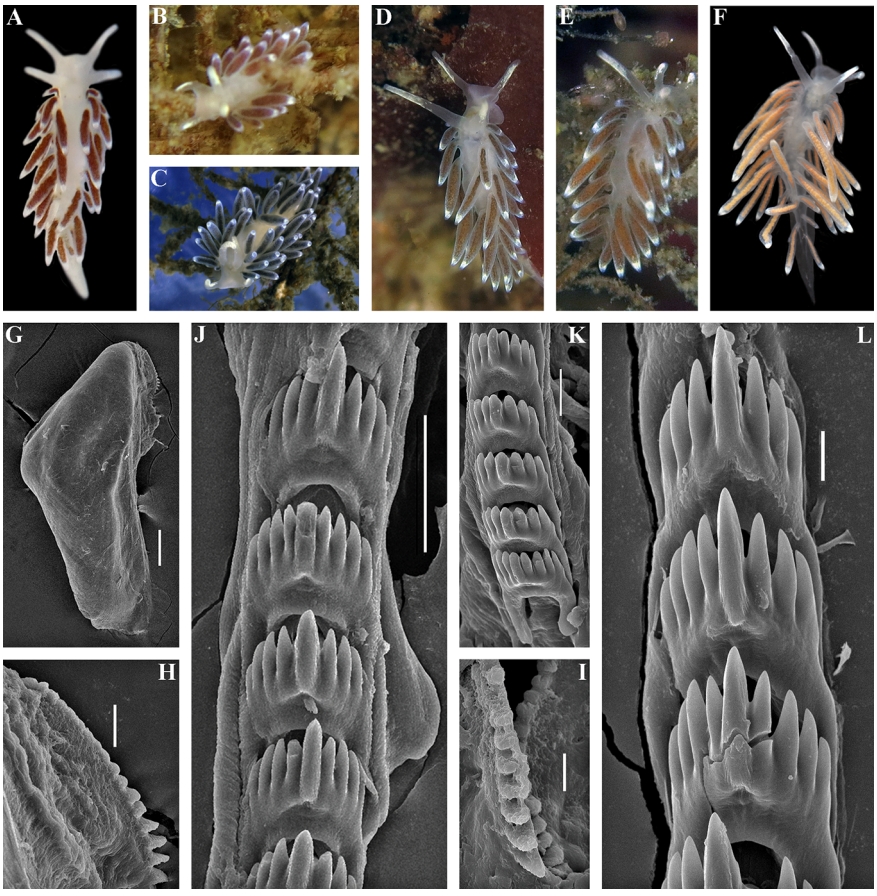

FIGURE 9 *Cuthonella concinna bellatula* subsp. nov. A, living holotype ZMMU Op-729 from the NE Pacific, Port Orchard, USA, 6 mm (live length), dorsal view. B, living holotype in natural conditions. C, living paratype ZMMU Op-728 in natural conditions on a hydroid of the family Sertulariidae, Port Orchard, USA, 8 mm (live length), dorsolateral view. D, E, two living paratypes ZMMU Op-742, 5–6 mm (live length), dorsal view in natural conditions, including hydroid of the family Sertulariidae (E). F, living paratype ZMMU Op-740, Port Orchard, USA, 7 mm (live length), dorsal view. G, jaw, paratype ZMMU Op-728 (SEM). H, same, details. J, anterior and middle parts of radula of paratype ZMMU Op-728 (SEM). K, same, anterior part of the radula (SEM). I, jaw, details of the paratype ZMMU Op-740 (SEM). L, posterior part of the radula paratype ZMMU Op-740 (SEM). Scale bars: G, 100 μm; H, K, 20 μm; I, L,10 μm; J, 50 μm; Photos: A–F, Karin Fletcher, G–L, Alexander Martynov.

sp. nov. (Table 1). Morphologically, the nominative subspecies differs from *C. concinna bellatula* subsp. nov. by its larger maximum body size (20 mm compared to 15 mm), and a larger number of lateral denticles of the central teeth of the radula. We also checked several specimens of *C. concinna* s.l. from different locations over large geographic distances, but were unable to confirm the presence of a narrow distal "bursa" (in addition to the receptaculum) reported for this species by Williams & Gosliner (1979). The reason the receptaculum in *C. concinna* s.l. (figs 19E, F) appears to be placed in a more proximal position than in the majority of *Cuthonella* species (figs 19, 20) is possibly because a channel from the receptaculum to the female opening is partially concealed within female gland mass. For a morphological comparison with other *Cuthonella* species, see table 2.

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***Cuthonella concinna bellatula* subsp. nov.**

(Figs 1–3, 9, 19F, 21)

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Cuthonella concinna s.l. auct., e.g. O'Donoghue, 1922: 162–163; Millen, 1983: 384; Behrens, 1980: 98; Korshunova et al., 2018a: 317, non Alder & Hancock, 1843

Type material. Holotype. ZMMU Op-729, *L* = 6 mm length (live), NE Pacific, Rich Passage, West of Pt. Glover, *c.* 12 m depth, collected by Karin Fletcher, 13.07.2013.

Paratypes. ZMMU Op-728, one spec., *L* = 8 mm length (live), NE Pacific, Rich Passage, Port Orchard, 10.7 m, collected by Karin Fletcher, 18.04.2012. ZMMU Op-740, one spec., *L* = 7 mm length (live), NE Pacific, Rich Passage, West of Pt. Glover, *c.* 10 m depth, collected by Karin Fletcher, 02.02.2019. ZMMU Op-742, two spec., *L* = 5–6 mm length (live), NE Pacific, Rich Passage, West of Pt. Glover, *c.* 10 m depth, collected by Karin Fletcher, 30.04.2014.

Etymology. From Latin *bellatula* ("small beautiful") referring to the morphological similarity, but smaller size, compared to the nominative subspecies *C. concinna concinna,* for which the name "concinna" has a similar meaning in Latin, "beautiful, well-proportionated".

External morphology. Body moderately narrow. Foot and tail moderate. Rounded foot corners present. Oral tentacles moderate. Rhinophores similar in size, or slightly longer than oral tentacles, smooth to slightly wrinkled. Dorsal cerata elongate, arranged in continuous rows. Potentially up to 6, but in present material commonly up to 4 pre-anal unbranched ceratal rows. Anal opening acleioproctic.

Colour (*live*). Background colour white to yellowish white. Digestive gland diverticula pinkish, brownish-orange, reddish, grayish-purple to blackish. Cerata can have a bluish sheen and a few scattered white or bluish spots. Ceratal tips with opaque white spots or bands. Rhinophores and oral tentacles semi-transparent with white pigment on the tips (fig. 9A–F).

Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of distinct denticles (fig. 9G, H, I).

Radula. Radula formula about 17 × 0.1.0 (specimen 8 mm in length), Central tooth elongate with protracted, pointed non-compressed cusp (fig. 9J, K, L). Central tooth bears 3–5 lateral denticles. Cusp clearly delineated from the adjacent first lateral denticles.

Reproductive system. Diaulic. Hermaphroditic duct leads to a short, swollen ampulla. Vas deferens short, without a distinct prostate. Supplementary gland short, inserts into the vas deferens a relatively long distance from the elongated penial sheath. Penis conical, unarmed. Oviduct connects through the insemination duct into the female gland complex. Receptaculum seminis in a more proximal position than in most other *Cuthonella* species, and on a short stalk, with only a weakly defined reservoir (fig. 19F).

Ecology. Lives on stones and rocks at depths of *c.* 10–15 m, primarily found between March-September on its prey, the hydroids of the family Sertulariidae.

Distribution. Temperate NE Pacific waters from Alaska to Sonoma County, California.

Remarks. Morphologically *C. concinna bellatula* subsp. nov. differs from the nominative subspecies by its smaller maximum body size (15 mm compared to 20 mm), more varied ceratal colour (in *C. concinna bellatula* subsp. nov. the ceratal colour ranges from pinkish to brownish-orange, reddish, grayish-purple to blackish, whereas in *C. concinna concinna* the colour is a rather uniform brownish to dark brown) and fewer number of lateral denticles on the central teeth of the radula (in *C. concinna*

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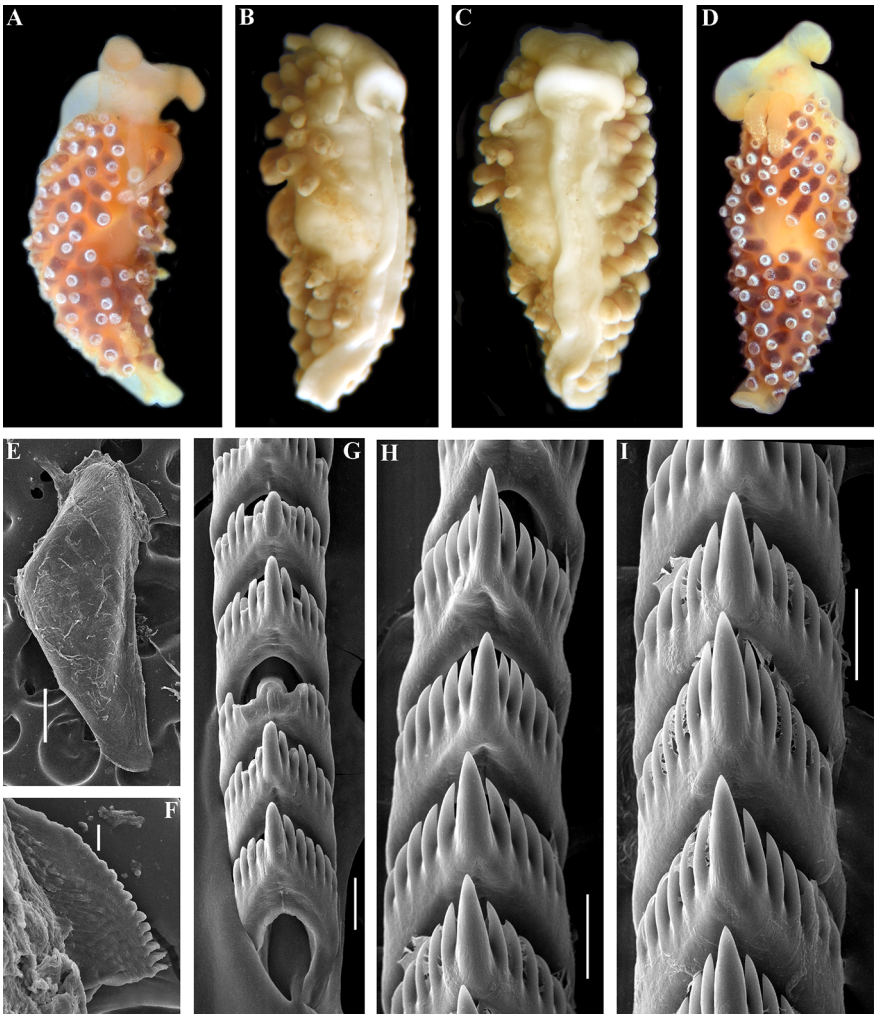

FIGURE 10 *Cuthonella denbei* sp. nov. A, living holotype ZMMU Op-730, 6 mm (preserved length), Matua Island, dorsal view. B, preserved holotype, lateral view. C, preserved holotype, ventral view. D, living paratype Op-741, 7 mm (preserved length), Matua Island, dorsal view. E, jaw, paratype ZMMU Op-673 (SEM). F, jaw, same, details. G, anterior part of the radula of the paratype ZMMU Op-673 (SEM). H, I, middle and posterior part of the radula of the paratype ZMMU Op-673 respectively (SEM). Scale bars: E, 200 μm; F, 20 μm; G–I, 30 μm; Photos: A, B, Nadezhda Sanamyan, C–I, Alexander Martynov.

bellatula subsp. nov. the number of lateral denticles is commonly no more than 5, whereas in the nominative subspecies the number of denticles can reach up to 10).

Cuthonella concinna bellatula and *C. cocoachroma* are also likely to be mistaken for each other. These two species are so similar externally that two of the five specimens collected at the same time in Sonoma County, California (CASIZ 181307a and CASIZ 181307d), plus another specimen collected from the same site on a different date (CASIZ 179469), all putatively considered to be *C. cocoachroma* when they were collected, turned out to be *C. concinna* (named *C. concinna bellatula* in this paper). These results were not discussed in details within the study which originally sequenced the specimens (Cella et al., 2016)

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but until then the southernmost limit of the range of *C. concinna bellatula* was Vancouver Island, British Columbia, Canada. A record of *Cuthonella concinna* s.l. from the Commander Islands (Martynov, 1997) may also include a different species and needs further investigation. Several hydroid species were previously reported as food objects for NE Pacific *C. concinna* s.l.: *Bougainvillia glorietta* Torrey, 1904, *Obelia commissuralis* McCrady, 1859 (currently also mentioned as *Obelia dichotoma* (Linnaeus, 1758)), *Coryne eximia* Allman, 1859 (Waters, 1966), and *Sertularia* sp. (Behrens & Hermosillo, 2005). These reports need verification. In the present study we found *C. concinna bellatula* subsp. nov. on hydroids of the family Sertulariidae.

The maximum intragroup distance in *C. concinna bellatula* subsp. nov. is 1.67%. At the same time, the minimum intergroup distance between *C. concinna concinna* and *C. concinna bellatula* subsp. nov. is 1.07%. A considerable intragroup genetic divergence suggests that the present North Pacific populations of *C. concinna bellatula* subsp. nov. may conceal potentially more taxonomic diversity and may also have experienced a genetic introgression with Atlantic *C. concinna concinna* occasionally introduced to the Pacific coast. While making a decision on the taxonomic status of "*C. concinna*" from the NE Pacific we encountered a difficult situation because of the lack of a clear and universal definition of a "species" concept. "*Cuthonella concinna*" from the NE Pacific is case of a "species" (or a part of a group of species) which has likely only relatively recently started to diverge into a separate species, where specimens already show some morphological and molecular differences from *C. concinna concinna*, but these differences are not distinct enough for a full species status.

At the same time, a clear and significant geographic gap was revealed in the case of *C. concinna bellatula* subsp. nov. from the NE Pacific compared to the location of the nominative subspecies. In our opinion, the best decision in this case was the separation of such forms as subspecies, which meets the requirements of both the ICZN and general taxonomic practice when subspecies status commonly implies a considerable geographic separation. It is possible that with a really large dataset this decision can be clarified, but given the amount of currently available data we prefer to consider it a subspecies. The maximum intragroup distance in *C. concinna bellatula* is 1.67%. The minimum COI intergroup distance of 9.74% is found between *C. concinna bellatula* subsp. nov. and *C. vasentsovichi* sp. nov. (table 1). For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella denbei* sp. nov.**

(Figs 1, 2, 10, 20A, 21)

ZooBank: http://urn:lsid:zoobank.org:act:9DD902C3-B8CA-4941-9712-11E77977DB77

Type material. Holotype. ZMMU Op-730, *L* = 6 mm length (preserved), Pacific Ocean, Middle Kuril Islands, Matua Island, Klyuv Cape, intertidal, collected by N.P. Sanamyan, 06.08.2017.

Paratypes. ZMMU Op-674, 1 spec., *L* = 4.5 mm length (preserved), Pacific Ocean, Middle Kuril Islands, Matua Island, Klyuv Cape, intertidal, collected by N.P. Sanamyan, 22.08.2016. ZMMU Op-673, 1 spec., *L* = 4 mm length (preserved), Pacific Ocean, Middle Kuril Islands, Matua Island, Klyuv Cape, 16 m depth, on brown algae *Thalassiophyllum clathrus*, collected by N.P. Sanamyan, 23.08.2016. ZMMU Op-741, 1 spec., *L* = 7 mm length (preserved), Pacific Ocean, Middle Kuril Islands, Matua Island, Klyuv Cape, intertidal, collected by N.P. Sanamyan, 06.08.2017.

Etymology. Named in honour of the Japanese merchant clerk Denbei (Dembei) –

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伝兵衛（でんべえ）(*c.*1670–1714) from Osaka who represented the first well-documented case of the appearance of a Japanese native in Russia. Denbei arrived in Russia due to the shipwrecking of a Japanese vessel on the Kamchatka coast, followed by a long drift through the Kuril Islands chain, the type locality of the present species. Afterwards, Denbei had an audience with the Russian tsar Peter the Great in 1702. This became an historic event since Denbei promoted the first official connections between Japan and Russia, and also established the first school of Japanese language in Russia (e.g., Ikuta, 2008).

External morphology. Body moderately narrow. Foot and tail broad. Oral tentacles moderate. Rhinophores similar in size to oral tentacles, smooth to slightly wrinkled. Dorsal cerata elongate, thick, arranged in continuous rows. Up to 6 pre-anal unbranched ceratal rows. Anal opening acleioproctic.

Colour (*live*). Background colour yellowish to more intense yellow-pinkish. Digestive gland diverticula within cerata brownish to dark-reddish. Ceratal tips with distinct ring-shaped opaque white pigment, sometimes with few scattered white spots. Rhinophores light yellowish with a sparse white pigment at the top (fig. 10A, B).

Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of distinct denticles (fig. 10E, F).

Radula. Radula formula 19 × 0.1.0 (specimen 4 mm in length). Central tooth elongated with a strongly protracted, pointed non-compressed cusp (fig. 10G–I). Central tooth bears up to 7 lateral denticles. Cusp clearly delineated from the adjacent first lateral denticles.

Reproductive system. Diaulic. Hermaphroditic duct leads to a relatively short, swollen ampulla. Vas deferens moderately long, without a distinct prostate. Supplementary gland relatively short, inserts into the vas deferens a considerable distance from the elongated penial sheath. Penis conical, unarmed. Oviduct connects through the insemination duct into the female gland complex. Receptaculum seminis in a distal position, on a short stalk, pear-shaped (fig. 20A).

Ecology. Lives on soft bottoms with stones. Intertidal to 16 m depth.

Distribution. Matua Island, Middle Kuril Islands.

Remarks. The maximum intragroup distance in *C. denbei* sp. nov. is 0.30%. The minimum CO1 intergroup distance of 9.30% is found between *C. denbei* sp. nov. and *C. concinna concinna* (table 1). Morphological analysis reveals considerable differences in the denticulation of the central teeth between *C. denbei* sp. nov. and related species *C. benedykti, C. georgstelleri* sp. nov., *C. hiemalis* sp. nov., *C. osyoro,* and *C. soboli* (figs 7, 11, 12, 14, 17). For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella elenae* Martynov, 2000**

Cuthonella elenae Martynov, 2000: 5–9, Figs 1–3; Martynov, 2006b: 290.

Remarks. Cuthonella elenae from the Chukchi Sea has been described in detail in Martynov (2000), which will not be repeated here. This species has all the diagnostic characters of the genus *Cuthonella*, including a supplementary gland inserted into the vas deferens, which unambiguously places this species in the genus *Cuthonella,* even in the absence of molecular data. At the same time, this species evidently shows several unique features, including small lobes around the penial opening, a very broad penial sheath, a relatively short supplementary gland, and flattened oral tentacles.

These characters clearly delineate this species from any other *Cuthonella* species, including the newly-described ones in

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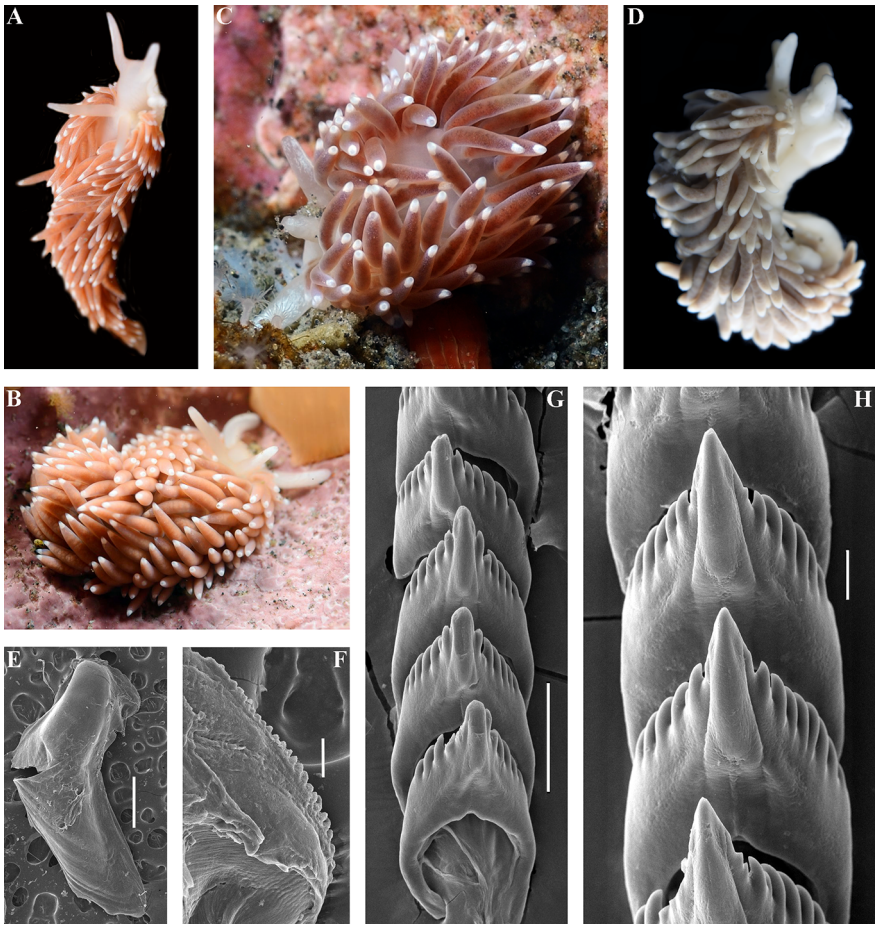

FIGURE 11 *Cuthonella georgstelleri* sp. nov. A, B, living holotype ZMMU Op-670, Matua Island, 14 mm (preserved length), dorsal and dorsolateral views respectively. C, Living paratype ZMMU Op-731, Matua Island, 10 mm (preserved length), dorsal view. D, Preserved paratype ZMMU Op-731, lateral view. E, jaw, holotype (SEM). F, jaw, same, details. G, anterior part of the radula of the holotype (SEM). H, posterior part of the radula of the holotype (SEM). Scale bars: E, 500 μm; F, 50 μm; G, 100 μm; H, 30 μm; Photos: A–C, Nadezhda Sanamyan, D–H, Alexander Martynov.

this study. By the presence of the many-branched digestive gland, this species shares a common plesiomorphic condition with the type species, *C. abyssicola* s.l. There are no additional specimens collected since the original description, and molecular phylogenetic data are not available for this species. For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella georgstelleri* sp. nov.**
(Figs 1, 2, 11, 20B, 21)

ZooBank: http://urn:lsid:zoobank.org:act:FF40FDD4-CF8D-4758-899A-6D2A548E686B

Type material. Holotype. ZMMU Op-670, 1 spec., *L* = 14 mm length (preserved), Pacific Ocean, Middle Kuril Islands, Matua Island, Klyuv Cape, 16 m depth, collected by N.P. Sanamyan, 28.08.2016.

Paratypes. ZMMU Op-672, 1 specimen, *L* = 12 mm length (preserved), same locality, date and collector as holotype. ZMMU Op-731, 1 spec., *L* = 10 mm length (preserved), Pacific

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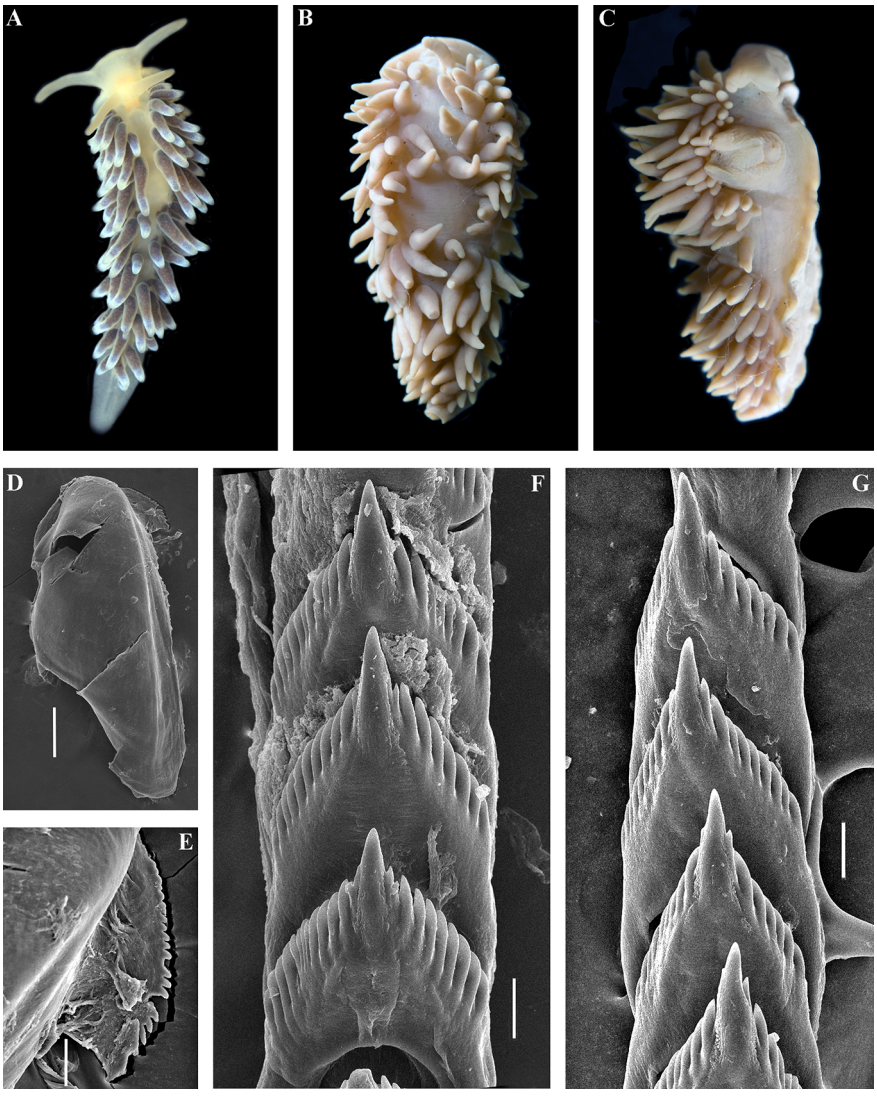

FIGURE 12 *Cuthonella hiemalis* (Roginskaya, 1987). A, living specimen from the type locality, White Sea, dorsal view, *c.* 5 mm (preserved length). B, C. preserved syntype collected and identified by I.S. Roginskaya, ZMMU Op-732, White Sea, 14 mm (preserved length), dorsal and lateral views respectively. D, jaw, ZMMU Op-732 (SEM). E, jaw, same, details. F, anterior part of the radula, ZMMU Op-732 (SEM). G, posterior part of the radula, same (SEM). Scale bars: D, 200 μm; E, 50 μm; F, G, 20 μm; Photos: A, courtesy of Anna Zhadan, B–G, Alexander Martynov.

Ocean, Middle Kuril Islands, Matua Island, Klyuv Cape, 14 m depth, collected by N.P. Sanamyan, 20.08.2017.

Etymology. The name is in honour of the prominent 18th-century scientist Georg Wilhelm Steller (1709–1746) of German origin who served in the Russian Empire and made substantial efforts to study the North Pacific region, and particularly the Kuril and Commander Islands, but met a very unfortunate fate. Georg Steller was the only professional scientist who saw and personally described the now extinct Steller's sea cow (*Hydrodamalis gigas*). Georg Steller is also

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considered the first European who stepped onto the land of Alaska (Stejneger, 1936). In 1742, Georg Steller was falsely accused of organizing a rebellion against the Russian Government in Kamchatka and was forced to return to mainland Russia, but on the way to Moscow he died in the Siberian area of Tyumen. The majority of the descriptions of his collected materials and prepared notes (in his diaries) was published after his death.

External morphology. Body moderately wide. Foot and tail broad. Oral tentacles moderate. Rhinophores similar in size to oral tentacles, smooth to slightly wrinkled. Dorsal papillae elongate, thick, arranged in continuous rows. Up to 8 pre-anal unbranched or partially branched ceratal rows. Anal opening cleioproctic.

Colour (*live*). Background colour whitish. Digestive gland diverticula light orange-brownish and salmon-brownish to dark, intensive brownish reddish. Ceratal tips with extended opaque white band or spot, sometimes with few white small spots. Rhinophores whitish to light yellowish with slight disperse white pigment (fig. 11A–C).

Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of denticles (fig. 11E, F).

Radula. Radula formula 30 × 0.1.0 (specimen 14 mm in length). Central tooth elongated with a strongly protracted, pointed non-compressed cusp (fig. 11 G, H). Central tooth bears up to 10 lateral denticles. Cusp clearly delineated from the adjacent first lateral denticles.

Reproductive system. Diaulic. Hermaphroditic duct leads to a relatively short, swollen ampulla. Vas deferens moderate in length, without a distinct prostate. Supplementary gland long, inserts into the vas deferens at a considerable length from the elongated penial sheath. Penis conical, unarmed. Oviduct connects through the insemination duct into the female gland complex. Receptaculum seminis distal, on a long stalk, compressed (fig. 20B).

Ecology. Lives on soft bottoms with stones at depths of 14–16 m.

Distribution. Matua Island, Middle Kuril Islands.

Remarks. The maximum intragroup distance in *C. georgstelleri* sp. nov. is 0.30%. The minimum COI intergroup distance of 7.75% is found between *C. georgstelleri* sp. nov. and *C. benedykti* sp. nov. (table 1). Phylogenetically, *C. georgstelleri* sp. nov. is close to *C. soboli, C. osyoro, C. ainu* sp. nov., and *C. benedykti* sp. nov. Morphological analysis reveals considerable differences in the denticulation of the central teeth between *C. georgstelleri* and the related species *C. ainu* sp. nov., *C. hiemalis, C. osyoro* and *C. soboli* (figs 6, 12, 14, 17). For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella hiemalis* (Roginskaya, 1987)**

(Figs 1, 2, 12, 20C, 21)

Cuthona hiemalis Roginskaya, 1987: 197–199; Fig. 118 was supposed to illustrate this species in the original description, but it was omitted in the publication due to an editorial error.

Cuthonella hiemalis (Roginskaya, 1987) – Martynov, 1992: 23; Martynov, 2006b: 290; Martynov & Korshunova, 2011: 195–197, figs.

Type material. The previously indicated (Martynov, 2006b) syntypes series (including labelled, but not published by Roginskaya (1987) "holotype") is not traceable. A syntype was discovered, accompanied by a label written by I.S. Roginskaya. The syntype was collected over the same period of time in the same locality with the previously mentioned type series: ZMMU Op-732, *L* = 14 mm (preserved), White Sea, Rugozerskaya Bay, intertidal, collected by I.S. Roginskaya, 7.02.1962.

Other materials. ZMMU Op-186, egg-mass and juveniles (preserved), White Sea,

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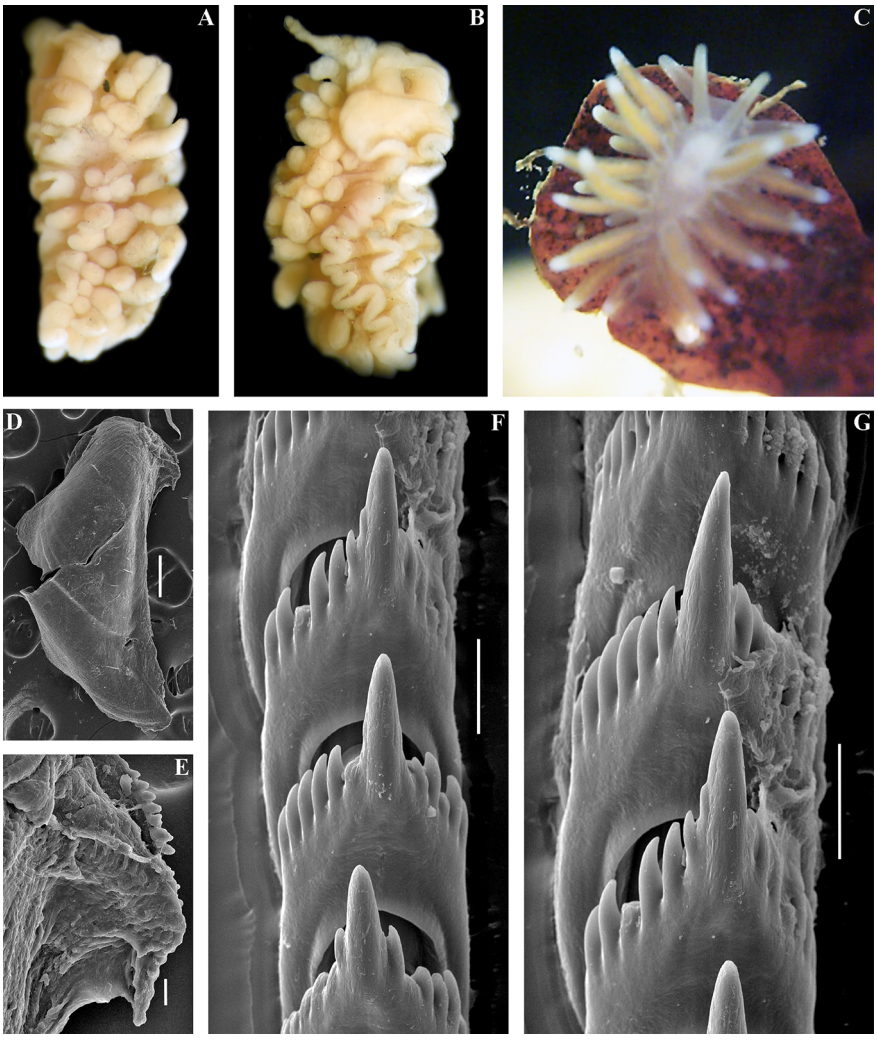

FIGURE 13 *Cuthonella orientosiberica* sp. nov. A, B, preserved holotype ZMMU Op-184, the East Siberian Sea, 3.5 mm (preserved length), dorsal and ventral views respectively. C, photograph of a living specimen (juvenile, not collected), the East Siberian Sea, *c.* 2–3 mm. D, jaw, paratype, ZMMU Op-185, the East Siberian Sea (SEM). E, jaw, same, details. F, anterior part of the radula, ZMMU Op-185 (SEM). G, posterior part of the radula, same. Scale bars: D, 200 μm; E, 20 μm; F, G, 30 μm; Photos: A, B, Alexander Martynov, C, courtesy of Sergei Gagaev, D, G, Alexander Martynov.

Rugozerskaya Bay, intertidal, collected by T.A. Korshunova, and A.V. Martynov, 14.06.2009. ZMMU Op-666, 5 spec., *L* = c. 5 mm each (preserved), White Sea, Rugozerskaya Bay, collected by A.E. Zhadan, 2009–2010.

External morphology. Body moderately wide. Foot and tail broad. Oral tentacles moderate. Rhinophores similar in size or slightly shorter than oral tentacles, smooth to slightly wrinkled. Dorsal cerata elongate, thick, arranged in continuous rows. Up to 7 pre-anal unbranched ceratal rows. Anal opening acleioproctic.

Colour (*live*). Background colour yellowish, sometimes with dispersed orange pigment. Digestive gland diverticula in cerata from dark beige to dark brown. Ceratal tips with peculiar opaque bluish to whitish subapical band or spot, without opaque white pigment.

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Rhinophores yellowish without distinct white pigment at the top (fig. 12A).

Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of distinct denticles (fig. 12D, E).

Radula. Radula formula 23 × 0.1.0 (specimen 14 mm in length). Central tooth elongated with a strongly protracted, pointed non-compressed cusp (fig. 12F, G). Central tooth bears up to 12 lateral denticles. Cusp clearly delineated from the adjacent first lateral denticles.

Reproductive system. Diaulic. Hermaphroditic duct leads to a relatively long, folded, non-swollen ampulla. Vas deferens long, without a distinct prostate. Supplementary gland long, inserts into the vas deferens a considerable distance from the elongated penial sheath. Penis conical, unarmed. Oviduct connects through the insemination duct into the female gland complex. Receptaculum seminis in a distal position, on a long massive stalk, oval (fig. 20C).

Ecology. Lives on stones and rocks. Intertidal to 5 m depth. Larvae exhibit direct development without a planktonic stage.

Distribution. Currently known only from the White Sea, possibly it also occurs in the Barents Sea.

Remarks. According to the molecular phylogenetic analysis, *Cuthonella hiemalis* forms a separate clade sister to the clade containing *C. soboli*, *C. osyoro*, *C. benedykti* sp. nov., *C. georgstelleri* sp. nov., and *C. ainu* sp. nov. (figs 1, 2). The maximum intragroup distance in *C. hiemalis* is 0.31%. The minimum CO1 intergroup distance of 8.37% is found between *C. hiemalis* and *C. osyoro* (table 1).

Morphological analysis reveals considerable differences in the denticulation of the central teeth between *C. hiemalis* and the related species *C. benedykti* sp. nov., *C. denbei* sp. nov., *C. georgstelleri* sp. nov., *C. osyoro,* and *C. soboli* Martynov, 1992 (figs 7, 10, 11, 14, 17). Reproduction occurs in the wintertime. *Cuthonella hiemalis* feeds on the athecate hydroids *Clava multicornis* (Forsskål, 1775), *Sarsia lovenii* (M. Sars, 1846), and on the thecate *Dynamena pumila* (Linnaeus, 1758) (Roginskaya, 1987). For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella orientosiberica* sp. nov.**

(Figs 1, 2, 13, 20D, 21)

ZooBank: http://urn:lsid:zoobank.org:act:-106FE0CB-1D90-4EDC-B649-BB4AE07932C7

Type material. Holotype. ZMMU Op-184, *L* = 3.5 mm length (preserved), East Siberian Sea, 70° 09.90′ N, 161° 16.18′ E, depth 9 m, collected by A.Y. Voronkov, 06.09.2004.

Paratypes. ZMMU Op-733, *L* = 4 mm length (preserved), East Siberian Sea, 70° 09.90′ N, 161° 16.18′ E, depth 9 m, collected by A.Y. Voronkov, 06.09.2004. ZMMU Op-185, *L* = 4 mm length, East Siberian Sea, 69° 10.50′ N, 169° 52.87′ E, depth 15 m, collected by A.Y. Voronkov, 07.09.2004.

Etymology. The name refers to the type locality. Oriento-, Lat. "belonging to the east" and the Siberian Sea.

External morphology. Body moderately wide. Foot and tail broad. Oral tentacles moderate. Rhinophores similar in size to oral tentacles, smooth to slightly wrinkled. Dorsal cerata elongate, thick, arranged in continuous rows. Up to 6 pre-anal unbranched ceratal rows. Anal opening acleioproctic.

Colour (*live*). Background colour yellowish white. Digestive gland diverticula light brownish to yellowish in juveniles and brownish to dark brown in adults. Ceratal tips whitish. Rhinophores light yellowish with white pigment at the top.

Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of denticles (fig. 13D, E).

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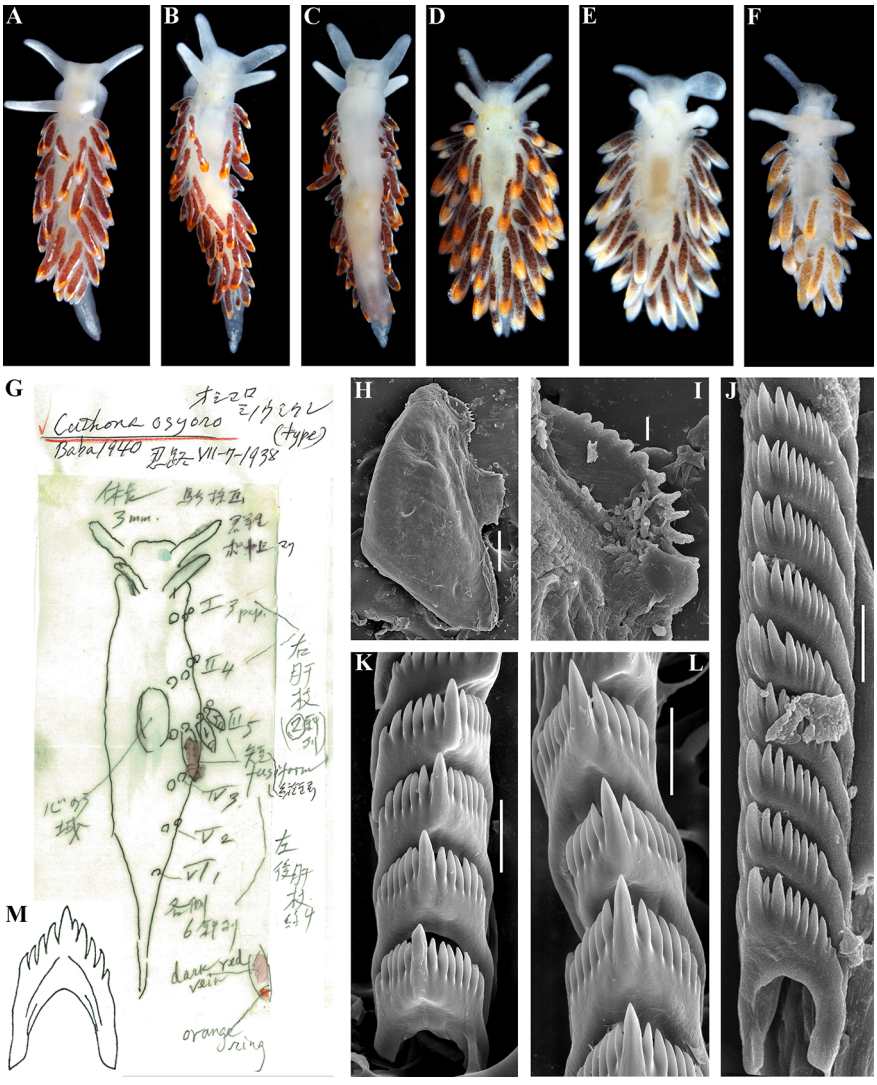

FIGURE 14 *Cuthonella osyoro* (Baba, 1940). A, living neotype ZMMU Op-743, the Sea of Japan, 4 mm (live length), dorsal view. B, C, living specimen ZMMU Op-613, the Sea of Japan, 9 mm (live length), dorsal and ventral views respectively. D, living specimen ZMMU Op-607, the Sea of Japan, 4 mm (preserved length), dorsal view. E, living specimen ZMMU Op-524, the Sea of Japan, 3 mm (preserved length), dorsal view. F, living specimen ZMMU Op-606, the Sea of Japan, 3 mm (preserved length), dorsal view. G, original drawings of external view by Kikutaro Baba, essentially similar to those used for the original description of *"Cuthona" osyoro* Baba, 1940. H, jaw, ZMMU Op-607 (SEM). I, same, details. J, anterior and middle parts of the radula, ZMMU Op-607 (SEM). K. anterior part of the radula, ZMMU Op-604 (SEM). L, posterior part of the radula, ZMMU Op-604 (SEM). M, original drawings of radular teeth of *"Cuthona" osyoro* by Kikutaro Baba. Scale bars: G, 100 μm; H, J, K, 10 μm; I, 20 μm; Photos: A–F, Tatiana Korshunova, G, M, drawings by Kikutaro Baba courtesy of Yoshiaki Hirano, So Ishida and Sho Kashio, H–L, Alexander Martynov.

Radula. Radula formula 28 × 0.1.0 (specimen 4 mm in length). Central tooth elongated with a strongly protracted, pointed non-compressed cusp (fig. 13F, G). Central tooth bears up to 9 lateral denticles. Cusp clearly delineated from the adjacent first lateral denticles.

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Reproductive system. Diaulic. Hermaphroditic duct leads to a relatively long, folded, swollen ampulla. Vas deferens moderately long, without a distinct prostate. Supplementary gland long, inserts into the vas deferens a considerable distance from the elongated penial sheath. Penis conical, unarmed. Oviduct connects through the insemination duct into the female gland complex. Receptaculum seminis in a distal position, on a short stalk, oval (fig. 20D).

Ecology. Lives on stones and rocks at depths of *c.* 9–15 m.

Distribution. Arctic Seas – East Siberian Sea, Laptev Sea, possibly also Chukchi Sea.

Remarks. According to the morphological data, *Cuthonella orientosiberica* sp. nov. is similar to *C. hiemalis* (Roginskaya, 1987) and *C. soboli* Martynov, 1992. However, there are differences in the denticulation of the central teeth between *C. orientosiberica* sp. nov. and the species *C. hiemalis* and *C. soboli* (figs 12, 17). The available material was not suitable for molecular study, despite several attempts to extract DNA. For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella osyoro* (Baba, 1940)**

(Figs 1, 2, 14, 20E, 21)

Cuthona osyoro Baba, 1940: 108, fig. 8

Cuthonella osyoro (Baba, 1940) – Martynov, 2006b: 290; Martynov, Korshunova, 2011, partim, only the fig. on page 198.

Type material. Holotype, lost. Neotype ZMMU Op-743, *L* = 4 mm length (live), the Sea of Japan, Spokoinaya Bay, 3–5 m depth, brown algae, stones, collected by T.A. Korshunova and A.V. Martynov, 25.09.2014.

Other material. ZMMU Op-734, *L* = *c.* 15 mm length (preserved, *c.* 25 mm live), the Sea of Japan, Vostok Bay, 0.2–0.4 m, stones, collected by A.V. Martynov, 18.02.1990. ZMMU Op-606, 1 spec., *L* = 3 mm length (preserved), the Sea of Japan, Spaseniya Bay, 0.3–0.7 m, stones, collected by T.A. Korshunova and A.V. Martynov, 16.09.2014. ZMMU Op-607, 1 spec., *L* = 4 mm length (preserved), the Sea of Japan, Spaseniya Bay, 0.3–0.7 m, stones, collected by T.A. Korshunova and A.V. Martynov, 16.09.2014. ZMMU Op-524, 1 spec., *L* = 3 mm length (preserved), the Sea of Japan, Gornostay Bay, 0.5–0.7 m, stones, collected by T.A. Korshunova and A.V. Martynov, 18.09.2014. ZMMU Op-604, 1 spec., *L* = 4 mm length (live), the Sea of Japan, Spokoinaya Bay, 3–5 m, brown algae, stones, collected by T.A. Korshunova and A.V. Martynov, 25.09.2014. ZMMU Op-613, 1 spec., *L* = 9 mm length (live), the Sea of Japan, Spokoinaya Bay, 3–5 m, brown algae, stones, collected by T.A. Korshunova and A.V. Martynov, 25.09.2014.

External morphology. Body moderately wide. Foot and tail broad. Oral tentacles moderate. Rhinophores similar in size to oral tentacles, smooth to slightly wrinkled. Dorsal papillae elongate, thick, arranged in continuous rows. Up to 6 pre-anal unbranched ceratal rows. Anal opening acleioproctic.

Colour (*live*). Background colour translucent whitish, sometimes slightly yellowish. Digestive gland diverticula brownish to dark red or violet. Ceratal tips with variously expressed red or orange band or spot. On cerata white streaks or dots may be present. Rhinophores semi-transparent, sometimes with white pigment at the top (fig. 14A–G).

Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of distinct denticles (fig. 14H, I).

Radula. Radula formula 26 × 0.1.0 (specimen 9 mm in length), 24 × 0.1.0 (specimen 8 mm in length). Central tooth elongated with a strongly protracted, pointed non-compressed cusp (fig. 14 J–M). Central tooth bears up to 11 lateral denticles. Cusp clearly delineated from the adjacent first lateral denticles.

Reproductive system. Diaulic. Hermaphroditic duct leads to a relatively short,

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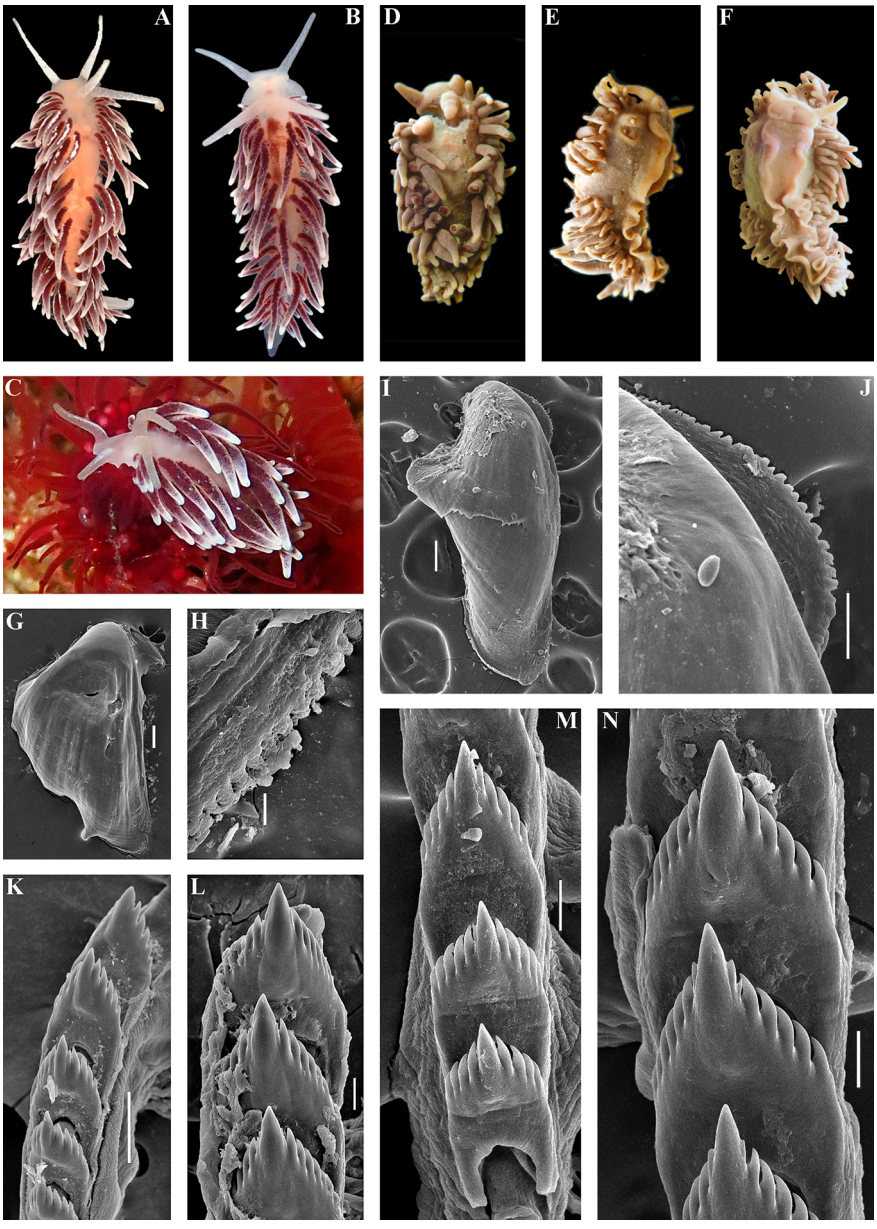

FIGURE 15 *Cuthonella punicea* (Millen, 1986). A, living specimen, British Columbia, Plumper Islands, 21 mm (live length), dorsal view. B, living specimen, British Columbia, Plumper Islands, 13 mm (live length), dorsal view. C, living specimen on the hydroid *Zyzzyzus rubusidaeus*, food object (specimen was not collected). D–F, topotype specimen collected and identified by Sandra Millen, British Columbia, Plumper Islands, ZMMU Op-735, 7 mm (preserved length), dorsal, lateral and ventral views respectively. G, jaw, from specimen 15 mm (SEM). H, jaw, details, same. I, jaw, ZMMU Op-735 (SEM). J, jaw, details, same. K, anterior part of the radula from specimen 15 mm (SEM). L, posterior part of the radula, same (SEM). M, anterior part of the radula, ZMMU Op-735 (SEM). N, posterior part of the radula, same. Scale bars: G, I, 100 μm; H, 10 μm; J, K, 50 μm; L–N, 20 μm; Photos: A, B, Karin Fletcher, C, Neil McDaniel, D–N, Alexander Martynov.

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swollen, convoluted ampulla. Vas deferens moderately long, without a distinct prostate. Supplementary gland long, inserts into the vas deferens a considerable distance from the elongated penial sheath. Penis conical, unarmed. Oviduct connects through the insemination duct into the female gland complex. Receptaculum seminis in a distal position, on a short stalk, rather rounded (fig. 20E).

Ecology. Lives on stones and rocks. Intertidal to 20 m depth.

Distribution. The Northern part of the Sea of Japan, Hokkaido, possibly also the Southern Kuril Islands.

Remarks. According to the molecular phylogenetic analysis, *Cuthonella osyoro* forms a sister clade with *C. soboli* and is also a member of a larger clade which includes *C. hiemalis*, *C. benedykti* sp. nov., *C. georgstelleri* sp. nov., and *C. ainu* sp. nov. (figs. 1, 2). The maximum intragroup distance in *C. osyoro* is 1.15%. The minimum COI intergroup distance of 2.89% is found between *C. osyoro* and *C. soboli* (table 1). *Cuthonella osyoro* differs externally from the closely related species *C. soboli* (fig. 17) in always having red or orange spots or rings on the ceratal tips. This variable-sized reddish or orange spot at the ceratal tips is present in all specimens of *C. osyoro* that we have observed, even in small juveniles, which was confirmed in the present study (fig. 14E, F). However, prior to this study *C. osyoro* specimens were sometimes mistaken for *C. soboli* because the pale orange ceratal spot on juvenile *C. osyoro* specimens that were sequenced (fig. 14D, for example) was inadvertently overlooked (Korshunova et al., 2017b, 2018a).

In the original description, Baba (1940) described a juvenile specimen from Hokkaido which is identifiable by the presence of red markings on the ceratal apices and patterns of the radula. In the present study, we specially visited the archive of Baba's material in Osaka and have presented a copy of the original painting by Baba (fig. 14G, M) to confirm the identity of this species. In the summertime in the intertidal and upper subtidal zones of the Sea of Japan juveniles of *C. osyoro* are quite common, and therefore Baba (1940) described a juvenile of exactly this species from a neighbouring location at the Hokkaido coast of the Sea of Japan. In order to avoid confusion between two sympatric sister species *C. soboli* and *C. osyoro*, neotype is selected here for *C. osyoro* (fig. 14A). The neotype is essentially similar in colouration and size to the first description of *C. osyoro* and was collected in the Sea of Japan across from the type locality in Hokkaido. The food objects of *C. osyoro* possibly include athecate hydroids. For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella punicea* (Millen, 1986)**

(Figs 1, 2, 15, 20F, 21)

Cuthona punicea Millen, 1986: 1356–1358, figs 1–7.

Cuthonella punicea (Millen, 1986) – Martynov, 1992: 23.

Non "*Tenellia*" *pustulata* sensu Cella et al., 2016 (= *Zelentia nepunicea*, see discussion in Korshunova et al., 2017a, 2018b; misidentification of *Zelentia nepunicea* with *Cuthonella punicea* in Cella et al., 2016).

Type material. Holotype. CASIZ 060327, NE Pacific, Canada, British Columbia, Plumper Islands, 50° 36′ N, 126° 49′ W, 13 m depth, rocks, collected by S.V. Millen, 06.05.1985.

Topotypes. ZMMU Op-735, 3 specimens, $L = 7$ mm, 7.2 mm, and 4 mm length (preserved), NE Pacific, Canada, British Columbia, Plumper Islands, 50° 36′ N, 126° 49′ W, 20–22 m, rocks, collected by S.V. Millen, 07.05.1983. KM 765, 1 specimen, $L = 21$ mm, NE Pacific, Canada, British Columbia, Plumper Islands, 8.2–17.7 m, collected by Karin Fletcher, 12.04.2019. KM 766, $L = 15$ mm, NE Pacific, Canada, British Columbia, Plumper Islands, 8.2–17.7 m, collected by Karin Fletcher, 12.04.2019.

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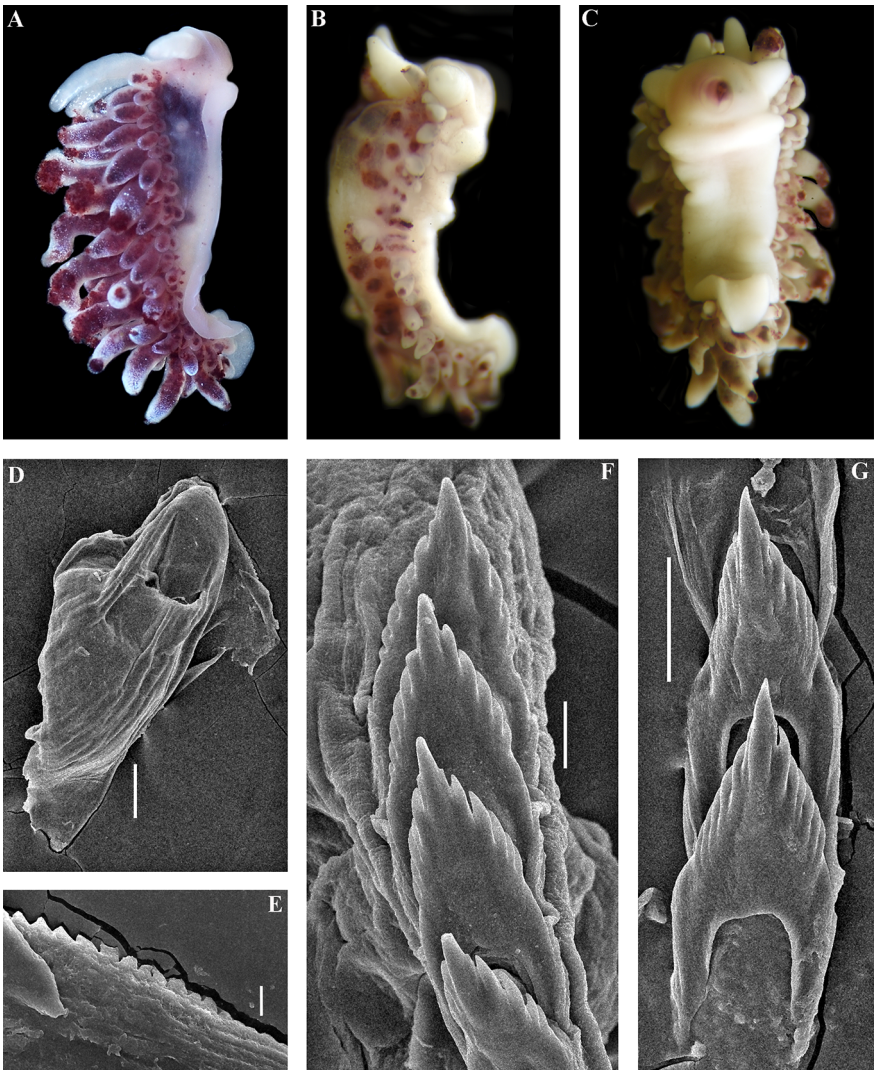

FIGURE 16 *Cuthonella sandrae* sp. nov. A, living holotype, Matua Island, ZMMU Op-671, 4 mm (preserved length), lateral view. B, C, same, preserved holotype, lateral and ventral views respectively. D, jaw, holotype (SEM). E, jaw, details, same. F, anterior part of the radula, holotype (SEM). G, posterior part of the radula, same. Scale bars: D, 100 μm; E, 10 μm; F, 20 μm; G, 50 μm; Photos: A, Nadezhda Sanamyan, B–G, Alexander Martynov.

External morphology. Body wider in front than behind. Foot and tail broad. Oral tentacles moderate. Rhinophores smooth and similar in size or slightly longer than the oral tentacles. Dorsal papillae elongate, arranged in continuous rows. Up to 8 pre-anal partially branched ceratal rows. Anal opening cleioproctic.

Colour (*live*). Background colour pinkish-yellowish white to pale peach. Digestive gland diverticula from purple to dark wine-red,(pomegranate colour). Cerata with white spots or streaks on surface. Cerata with dispersed white tips. Rhinophores and oral tentacles semi-transparent to light yellowish and often frosted with varying amounts of white pigment for almost the entire length, or the pigment can form a line (fig. 15A–C).

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Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of distinct denticles (fig. 15G–J).

Radula. Radula formula 12 × 0.1.0 (specimen 7 mm in length), c. 18 × 0.1.0 (spec. 15 mm in length). Central tooth elongated with a strongly protracted, pointed non-compressed cusp (fig. 15K–N). Central tooth bears up to 7 lateral denticles. Cusp clearly delineated from the adjacent first lateral denticles.

Reproductive system. Diaulic. Hermaphroditic duct leads to relatively short, straight, swollen ampulla. Vas deferens long, without a distinct prostate. Supplementary gland long, inserts into the vas deferens a considerable distance from the elongated penial sheath. Penis conical, narrow, unarmed. Oviduct connects through the insemination duct into the female gland complex. Tubular receptaculum seminis in a distal position, without a distinct reservoir (fig. 20F).

Ecology. Lives on soft bottoms with stones at depths of 8–33 m, on or near its hydroid prey, the large athecate species *Zyzzyzus rubusidaeus* Brinckmann-Voss & Calder, 2013 (Millen, 1986; Brinckmann-Voss & Calder, 2013). Eggs hatch after 14–15 days as planktotrophic veligers.

Distribution. Northeast Pacific, so far only known from the Plumper Island group located on the northern end of Vancouver Island, British Columbia.

Remarks. In the present study, molecular data from recently collected *Cuthonella punicea* from the exact type locality of the Plumper Islands (Canada, British Columbia) is presented for the first time (figs 1, 2, 21). According to that molecular phylogenetic data, the species originally described by Millen (1986) as "*Cuthona*" belongs to the same subclade with the type species of *Cuthonella*, *C. abyssicola*, and to a larger clade with all other *Cuthonella* (figs 1, 2). We also examined topotypes originally collected by Sandra Millen in 1983 (fig. 15D–F, I, J, M, N), and confirm their essential similarity with the recent specimens collected from the type locality (fig. 15A–C).

The profound morphological differences between this cuthonellid, *Cuthonella punicea,* and the trinchesiid *Zelentia nepunicea* have previously been highlighted (see Korshunova et al., 2017a, 2018b). Those differences combined with the examination of original topotypes and fresh material for molecular analysis in this study provide irrefutable evidence that the synonymy of those two species proposed by Cella et al. (2016) is not valid.

A cuthonellid from the NW Pacific (Matua Island), *Cuthonella sandrae* sp. nov., with a similar purple colour is a sister species to *C. punicea* (figs 1, 2), but differs significantly according to genetic distances, molecular phylogenetic analysis, external patterns of the digestive gland branches and the shape of the radular teeth (figs 15, 16).

Cuthonella punicea forms the clade sister to the clade containing *Cuthonella sandrae* sp. nov. and *C. abyssicola kryos* subsp. nov. (fig. 1). The maximum intragroup distance in *C. punicea* is 0.76%. The minimum COI intergroup distance of 6.85% is found between *C. punicea* and *C. sandrae* sp. nov (table 1). For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella sandrae* sp. nov.**

(Figs 1, 2, 16, 21)

ZooBank: http://urn:lsid:zoobank.org:act:-F04A4DCF-8A29-45BA-88B7-9749DA6E4C72

Type material. Holotype. ZMMU Op-671, 1 spec., *L* = 4 mm length (preserved), Pacific Ocean, Middle Kuril Islands, Matua Island, Klyuv Cape, 14 m depth, collected by N.P. Sanamyan, 20.08.2017.

Etymology. Named in honour of Sandra Violet Millen, a prominent nudibranch researcher of North Pacific nudibranch

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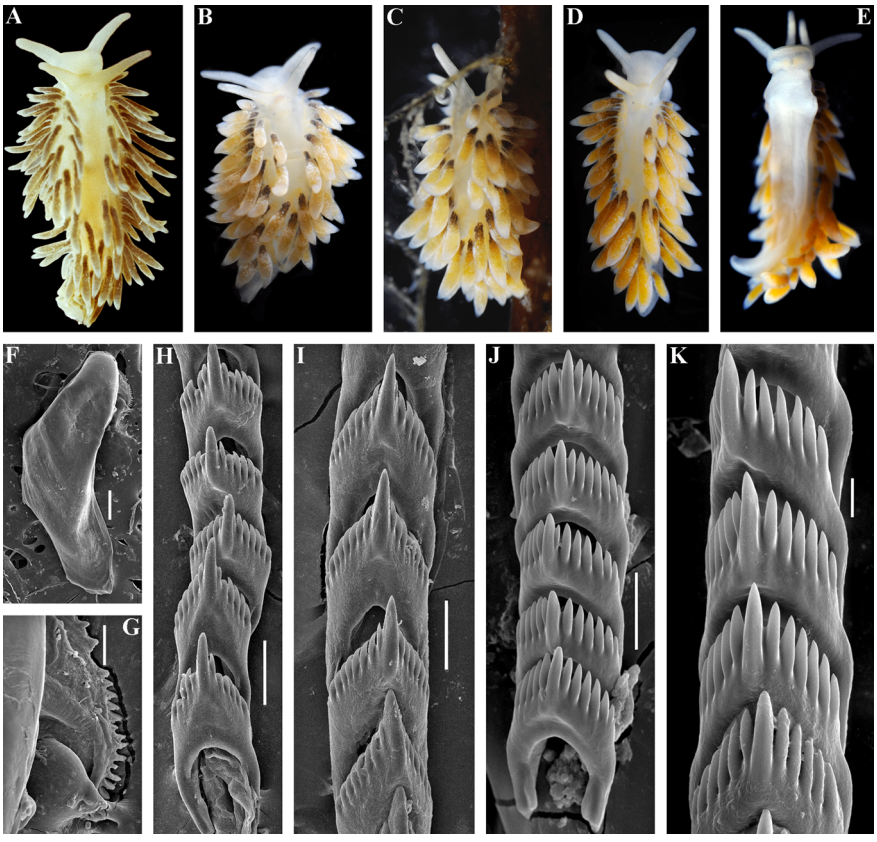

FIGURE 17 *Cuthonella soboli* Martynov, 1992. A, living holotype ZMMU Op-736 (adult), the Sea of Japan, Sobol Bay, *c.* 30 mm (live length) dorsal view. B, living specimen ZMMU Op-605, the Sea of Japan, Spokoinaya Bay, 8 mm, semi-juvenile (live length), dorsal view. C, same specimen on substrate. D, E, second living specimen, from the same location and lot, dorsal and ventral views respectively. F, jaw, ZMMU Op-737 (SEM). G, jaw, details, same. H, anterior part of radula, ZMMU Op-737. I, posterior part of the radula, same. J, anterior part of radula, ZMMU Op-605 (SEM). K, posterior part of radula, same. Scale bars: F, 200 μm; G, H, 50 μm; I, J, 30 μm; K, 10 μm; Photos: A, F–K, Alexander Martynov, B–E, Tatiana Korshunova.

molluscs. Most remarkably, in the present study we discovered a new species from the Kuril Islands which is a sister species to *Cuthonella punicea* (Millen, 1986) previously described by Sandra Millen from British Columbia, and which is similar to the new species in its reddish-purple colouration (fig. 15A–C) but with substantial genetic and radular differences.

External morphology. Body moderately wide. Foot and tail broad. Oral tentacles moderate. Rhinophores similar in size to oral tentacles, smooth to slightly wrinkled. Dorsal papillae elongate, thick, arranged in continuous rows. Up to *c.* 7 pre-anal branched ceratal rows. Anal opening cleioproctic.

Colour (*live*). Background colour semi-transparent white with purple-bluish areas. Digestive gland diverticula in the cerata violet-purple. Ceratal tips with dispersed white pigment and bluish hue. Rhinophores semi-transparent with sparse white pigment at the top (fig. 16A).

Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of distinct denticles (fig. 16D, E).

Radula. Radula formula 12 × 0.1.0 (specimen 4 mm in length). Central tooth elongated

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with a strongly protracted, pointed non-compressed cusp (fig. 16F, G). Central tooth bears up to 8 lateral denticles. Cusp relatively unclearly delineated from the adjacent first lateral denticles.

Reproductive system is underdeveloped in the holotype and not suitable for a detailed study.

Ecology. Lives on soft bottoms with stones at 14 m depth.

Distribution. Matua Island, Middle Kuril Islands.

Remarks. According to the molecular phylogenetic analysis, *Cuthonella sandrae* sp. nov. is closest to *C. punicea* (Millen, 1986) and *C. abyssicola kryos* (figs 1, 2). The minimum COI intergroup distance of 6.85% is found between *C. sandrae* sp. nov. and *C. punicea* (Table 1). Morphological analysis and molecular analysis reveal considerable differences between *C. sandrae* sp. nov. and any other species of the genus *Cuthonella*, including the externally similar *C. punicea* (fig. 15). Particularly in *C. sandrae* sp. nov. a continuous series of small branches of the digestive gland forms between the anterior and posterior parts of the digestive gland even at a relatively small size. In contrast, *C. punicea* has a rather linear, only weakly branched digestive gland which does not form a continuous row in between the anterior and posterior parts of the digestive gland even at a considerably larger size. The radular patterns between *C. punicea* and *C. sandrae* sp. nov. are also considerably different (figs 15M, N and 16F, G). For a morphological comparison with other *Cuthonella* species, see table 2.

Cuthonella soboli Martynov, 1992

(Figs 1, 2, 17, 20G, 21)

Cuthonella soboli Martynov, 1992: 18–23, figs 1–3; Martynov, 2006b: 290; Martynov, 2015b: 80; Martynov & Korshunova, 2011: 197–198, fig. on page 197, excluding the figure on page 198 (*C. osyoro*).

Type material. Holotype. ZMMU Op-736, *L* = *c.* 30 mm (live), The Sea of Japan, Sobol Bay, intertidal, stones, 03.03.1992. *Paratype.* ZMMU Op-737, *L* = 15 mm length (preserved), The Sea of Japan, Sobol Bay, 0.2–0.7 m depth, stones, collected by A.V. Martynov, 05.02.1992.

Other material: ZMMU Op-605, 2 spec., *L* = 8 mm length (live), The Sea of Japan, Spokoinaya Bay, 3–5 m depth, brown algae, stones, collected by T.A. Korshunova and A.V. Martynov, 25.09.2014.

External morphology Body moderately wide. Foot and tail broad. Oral tentacles moderate. Rhinophores similar in size, or slightly longer than oral tentacles, smooth to slightly wrinkled. Dorsal cerata elongate, thick, arranged in continuous rows. Up to 6 pre-anal ceratal rows. Anal opening acleioproctic.

Colour (*live*). Background colour yellowish white. Digestive gland diverticula in cerata from light brownish and sandy to tobacco- and dark-brown. Basal parts of cerata commonly darker. White spots or streaks on the ceratal external surface. Ceratal tips colourless or with dispersed white pigment. Rhinophores semi-transparent to light yellowish and orange ochre with indistinct to dispersed white pigment on the top (fig. 17A–E).

Jaws. Jaws broad, yellowish in colour. Masticatory processes of jaws covered with a single row of distinct denticles (fig. 17F, G).

Radula. Radula formula 28 × 0.1.0 (specimen 15 mm in length), 24 × 0.1.0 (specimen 8 mm in length). Central tooth elongated with a strongly protracted, pointed non-compressed cusp (fig. 17H–K). Central tooth bears up to 10 lateral denticles. Cusp clearly delineated from the adjacent first lateral denticles.

Reproductive system. Diaulic. Hermaphroditic duct leads to a moderately long, swollen ampulla. Vas deferens

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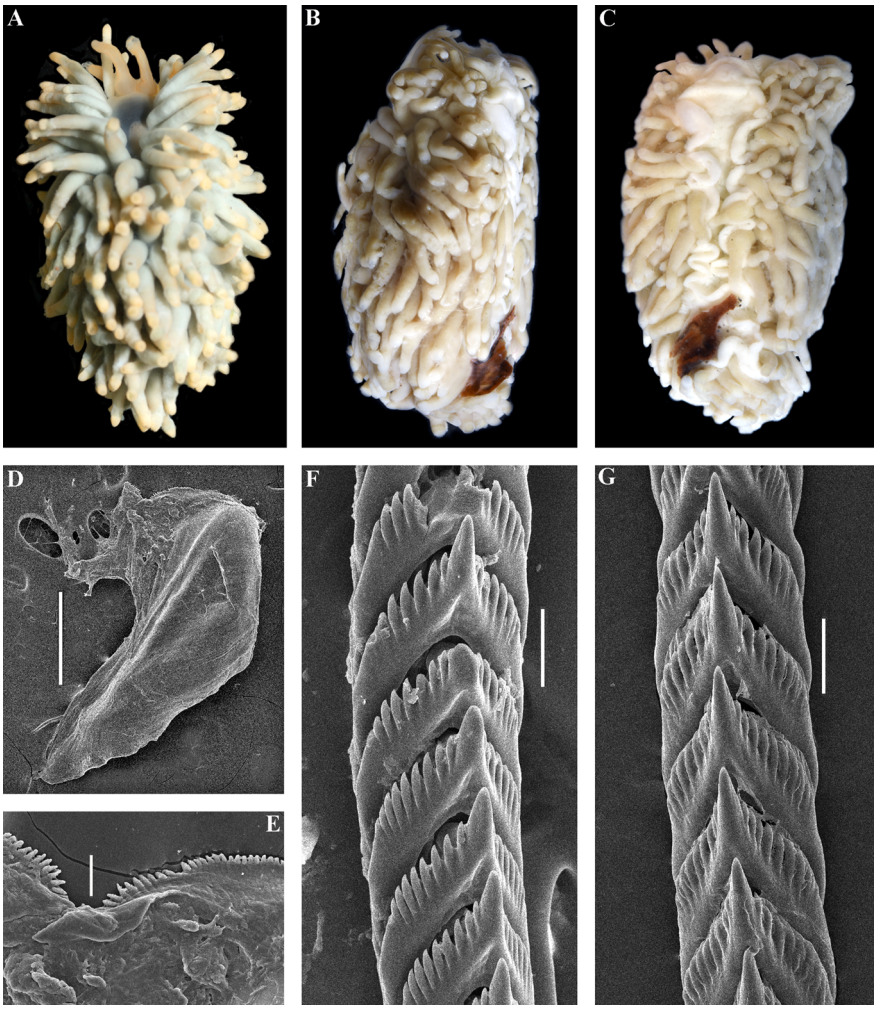

FIGURE 18 *Cuthonella vasentsovichi* sp. nov. A, living holotype ZMMU Op-738, Matua Island, 21 mm (preserved length), dorsal view. B, C, preserved holotype, lateral and ventral views respectively. D, jaw, paratype ZMMU Op-739, Matua Island (SEM). E, jaw, details, same. F, anterior part of the radula, paratype (SEM). G, posterior part of the radula, same. Scale bars: D, 500 μm; E, F, G, 50 μm; Photos: A, Nadezhda Sanamyan, B– G, Alexander Martynov.

moderately long, without a distinct prostate. Supplementary gland long, inserts into the vas deferens a considerable distance from the elongated penial sheath. Penis conical, unarmed. Oviduct connects through the insemination duct into the female gland complex. Receptaculum seminis in a distal position, on a moderately long stalk, pear-shaped (fig. 20G).

Ecology. Stones, rocks. Intertidal to c. 10 m depth. Veligers exhibit direct development or a shortened planktonic stage.

Distribution. The northern part of the Sea of Japan, possibly also the Southern Kuril Islands and Hokkaido.

Remarks. According to the molecular phylogenetic analysis, *Cuthonella soboli* Martynov, 1992 forms a separate clade sister

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to the *C. osyoro* clade (figs 1, 2). The minimum COI intergroup distance of 2.89% is found between *C. soboli* and *C. osyoro* (Table 1). Externally *C. soboli* differs from the closely related species *C. osyoro* by the absence of any reddish or orange spots on the cerata (fig. 17). Morphological analysis reveals considerable differences in the denticulation of the central teeth between *C. hiemalis, C. osyoro, C. soboli,* and the type species of the genus *Cuthonella*, *C. abyssicola* s.l. (figs 4, 5, 12, 14, 17). Reproduction occurs in the wintertime. The food objects of *C. soboli* possibly include athecate hydroids (Martynov & Korshunova, 2011). For a morphological comparison with other *Cuthonella* species, see table 2.

***Cuthonella vasentsovichi* sp. nov.**

(Figs 1, 2, 18, 20H, 21)

ZooBank: http://urn:lsid:zoobank.org:act:B49EBF1D-8E9F-4743-9F13-86003D7FA9C

Type material. Holotype. ZMMU Op-738, *L* = 21 mm length (preserved), Pacific Ocean, Middle Kuril Islands, Matua Island, Klyuv Cape, 14 m, collected by N.P. Sanamyan, 20.08.2017.

Paratype. ZMMU Op-739, *L* = 15 mm length (preserved), Pacific Ocean, Middle Kuril Islands, Matua Island, Klyuv Cape, 14 m, collected by N.P. Sanamyan, 20.08.2017.

Etymology. Named in honour of Vladislav Konstantinovich Vasentsovich (1898–1961). He was a Division Commander in the Soviet Far East before WWII and was repressed during Stalin's Great Purge, imprisoned for 15 years and freed only a few years before his death (Milbakh, 2003). Vladislav Vasentsovich is a relative of one of the authors of this article (AM). The name was also chosen because the Kuril Islands (type locality of the new species) belongs to the Russian Far East region and for the additional cultural intersection with Benedykt Dybowski, who like Vladislav Vasentsovich, was of a Polish origin and was also repressed earlier in the tsar's Russian Empire.

External morphology. Body wide. Foot and tail broad. Oral tentacles moderate. Rhinophores similar in size to oral tentacles, smooth to slightly wrinkled. Dorsal papillae numerous, elongate, thick, arranged in continuous rows. Up to 10 (or more) pre-anal branched and unbranched ceratal rows. Anal opening cleioproctic.

Colour (*live*). Background colour greyish. Digestive gland diverticula in cerata greyish to light greenish. Ceratal tips yellowish. Rhinophores dark yellowish, without distinct white pigment at the top (fig. 18A).

Jaws. Jaws moderately broad, yellowish in colour. Masticatory processes of jaws covered with a single row of denticles (fig. 18D, E).

Radula. Radula formula 40 × 0.1.0 (specimen 15 mm in length). Central tooth elongated with a strongly protracted, pointed non-compressed cusp (fig. 18F, G). Central tooth bears up to 9 lateral denticles. Cusp clearly delineated from the adjacent first lateral denticles.

Reproductive system. Diaulic. Hermaphroditic duct leads to a relatively short, partially swollen, convoluted ampulla. Vas deferens moderate in length, without a distinct prostate. Supplementary gland relatively short, inserts into the vas deferens a considerable distance from the elongated penial sheath. Penis conical, unarmed. Oviduct connects through the insemination duct into the female gland complex. Receptaculum seminis in a distal position, on a short stalk, oval (fig. 20H).

at 14 m depth.

Distribution. Matua Island, Middle Kuril Islands.

Remarks. The maximum intragroup distance in *C. vasentsovichi* is 0.15%. The minimum COI intergroup distance of 9.28% is found between *C. vasentsovichi* sp. nov. sp. nov. and *C. concinna concinna* (table 1).

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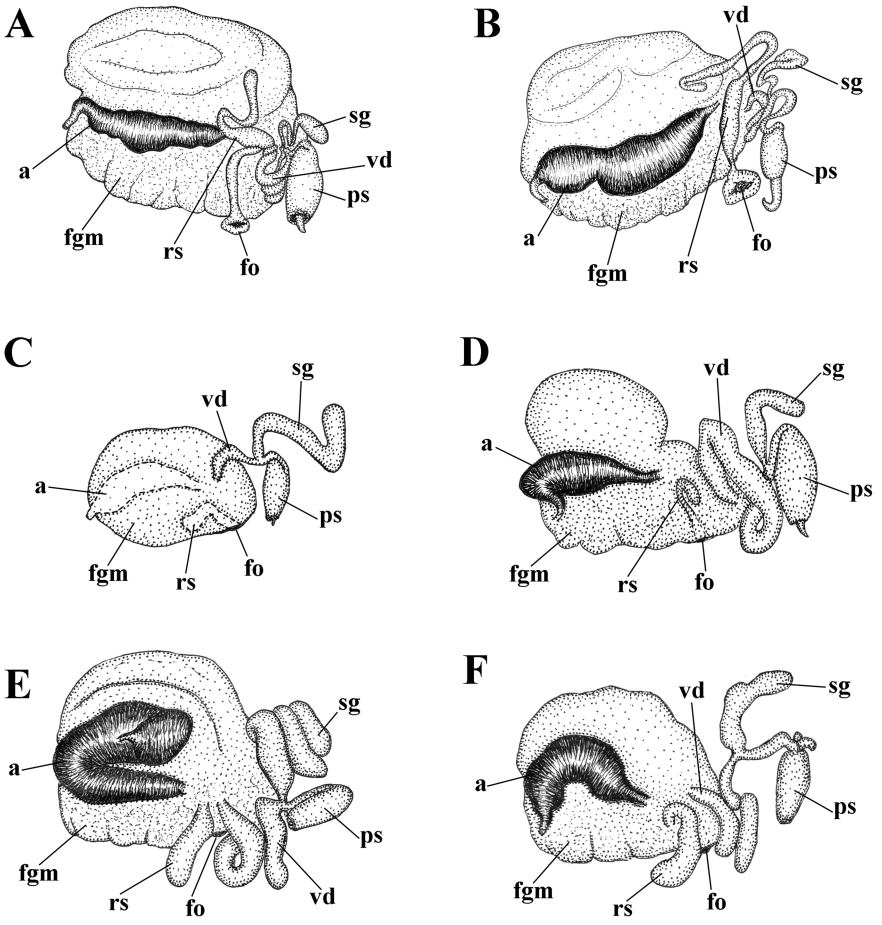

FIGURE 19 Reproductive systems of the genus *Cuthonella.* A, *Cuthonella abyssicola abyssicola;* B, *Cuthonella abyssicola kryos* subsp. nov.; C, *Cuthonella ainu* sp. nov.; D, *Cuthonella benedykti* sp. nov.; E, *Cuthonella concinna concinna;* F, *Cuthonella concinna bellatula* subsp. nov. Abbreviations: a, ampulla; fgm, female gland mass; fo, female opening; ps, penial sheath; rs, receptaculum seminis; sg, supplementary gland; vd, vas deferens.

By a combination of morphological characters *Cuthonella vasentsovichi* sp. nov. readily differs from any previously described *Cuthonella* species. Morphological analysis also reveals considerable differences in the denticulation of the central teeth between *C. vasentsovichi* sp. nov. (fig. 18) and any related species, e.g., *C. ainu* sp. nov., *C. denbei* sp.nov., *C. hiemalis,* and others from this clade (figs 6, 7, 10–12, 14, 17). Externally *C. vasentsovichi* sp. nov. differs from all known species of the genus *Cuthonella* by a peculiar "shaggy" appearance of numerous, densely placed cerata (fig. 18A). The large number of ceratal rows makes *C. vasentsovichi* sp. nov. partially resemble *Cuthonella abyssicola* s.l. (figs 4, 5), but *C. vasentsovichi* differs in having a broader body with greyish to greenish colouration instead of reddish or light pinkish, and by the morphology of its radula and reproductive system. Such multilevel differences between the new species and the type species are remarkable and align well with the recently proposed scheme of multilevel organismal diversity (Korshunova et al., 2019b). For a morphological comparison with other *Cuthonella* species, see table 2.

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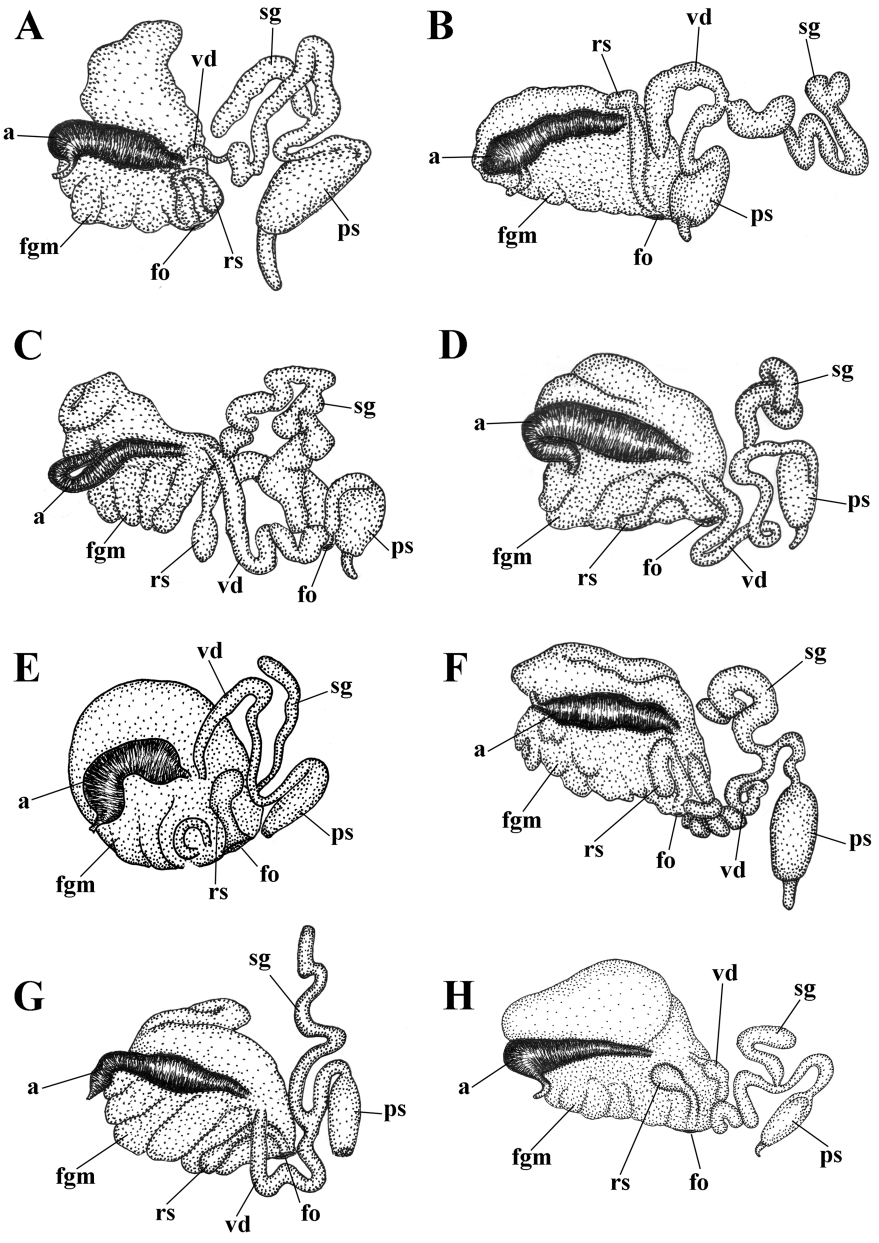

FIGURE 20 Reproductive systems of the genus *Cuthonella.* A, *Cuthonella denbei* sp. nov.; B, *Cuthonella georgstelleri* sp. nov.; C, *Cuthonella hiemalis;* D, *Cuthonella orientosiberica* sp. nov.; E, *Cuthonella osyoro;* F, *Cuthonella punicea;* G, *Cuthonella soboli;* H, *Cuthonella vasentsovichi* sp. nov. Abbreviations: a, ampulla; fgm, female gland mass; fo, female opening; ps, penial sheath; rs, receptaculum seminis; sg, supplementary gland; vd, vas deferens.

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TABLE 2 Morphological comparison of the species of the genus *Cuthonella*

Species	Body length (max)	Cerata colouration	Number of anterior branches of digestive gland (max) and its pattern	Radula formula (max)	Central teeth	Ampulla	Patterns of supplementary gland, vas deferens and penis	Receptaculum seminis	Distribution
***C. abyssicola abyssicola* Bergh,** 1884	30 mm (preserved)	Possibly reddish to pinkish, tips without distinct spots or bands of opaque white pigment	17, branched	21 × 0.1.0	Up to 14 lateral denticles, which are rarely clustered. Cusp is rather clearly delineated from the adjacent lateral denticles which do not reach top of the teeth	Long, moderately swollen, convoluted	Long, inserts into a long vas deferens at a considerable distance from penial sheath. Penis conical, strong, unarmed	On a very long stalk, tubular, widened in middle part with a small oval reservoir	North Atlantic and Sub-arctic, commonly at shelf and bathyal depths (up to 1000 m)
***C. abyssicola kryos* subsp. nov.**	25 mm (preserved)	Light pinkish to whitish, tips with dispersed white	17, branched	27 × 0.1.0	Central teeth have up to *c.* 36 lateral denticles, often clustered and increasingly irregular towards the cusps. Cusp is not clearly delineated from the adjacent lateral denticles which may reach top of the cusp	Long, moderately swollen, convoluted	Long, inserts into a long vas deferens at a considerable distance from penial sheath. Penis conical, strong, unarmed	On a very long stalk, tubular, widened basally, with a small pear-shaped reservoir	High latitude Arctic, shallow waters

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Species	Body length (max)	Cerata colouration	Number of anterior branches of digestive gland (max) and its pattern	Radula formula (max)	Central teeth	Ampulla	Patterns of supplementary gland, vas deferens and penis	Rece-ptaculum seminis	Distribution
***C. ainu* sp. nov.**	4 mm (preserved)	Brownish to light orange, ceratal tips with opaque white spot	5, unbranched	18 × 0.1.0	Up to 7 distinct lateral denticles, cusp well delineated	Relatively short, slightly bent, swollen	Long, inserts into a short vas deferens at a short distance from penial sheath. Penis conical, unarmed	On a short stalk, elongate-oval	Middle Kuril Islands, shallow waters
***C. benedykti* sp. nov.**	6 mm (preserved)	Brownish with darker reddish to brown hue, ceratal tips with opaque white ring, sometimes with additional yellow ring	5, unbranched	36 × 0.1.0	Up to 5 distinct lateral denticles, cusp well delineated	Relatively short, swollen	Relatively short, inserts into a moderately long vas deferens at a short distance from penial sheath. Penis conical, unarmed	On a short stalk, oval	Kamchatka, shallow waters

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TABLE 2 Morphological comparison of the species of the genus Cuthonella (*Cont.*)

Species	Body length (max)	Cerata colouration	Number of anterior branches of digestive gland (max) and its pattern	Radula formula (max)	Central teeth	Ampulla	Patterns of supplementary gland, vas deferens and penis	Rece-ptaculum seminis	Distribution
C. cocoachroma **(Williams & Gosliner, 1979)**	15 mm (live)	Dark brown, deep reddish-brown to dark chocolate brown, tips with opaque white spot	4, unbranched	39 × 0.1.0	Up to 5 distinct lateral denticles, cusp well delineated	Long, moderately swollen, convoluted	Short, reportedly inserts into the penis (Williams & Gosliner, 1979), but without further confirmation. Unarmed penis was reported as possessed a broadened base, which could potentially conceal the distalmost part of the vas deferens	On short stalk, rounded	NE Pacific, California, shallow waters
C. concinna concinna **(Alder & Hancock, 1843)**	20 mm (live)	Brown to purplish-brown, tips with opaque white subapical band or spot with a bluish hue	6, unbranched	30 × 0.1.0	Up to 10 distinct lateral denticles, cusp not well delineated	Relatively short or folded, swollen	Relatively long or shorter, inserts into a relatively long vas deferens at a relatively short distance from penial sheath. Penis conical, unarmed	On a short stalk, without distinct reservoir, in a more proximal position	North Atlantic (both sides), shallow waters

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Species	Body length (max)	Cerata colouration	Number of anterior branches of digestive gland (max) and its pattern	Radula formula (max)	Central teeth	Ampulla	Patterns of supplementary gland, vas deferens and penis	Rece-ptaculum seminis	Distribution
***C. concinna bellatula* subsp. nov.**	15 mm (live)	Pinkish, brownish-orange, reddish, grayish-purple to blackish, often with few scattered white or bluish spots, tips with opaque white spots or band	4, unbranched	17 × 0.1.0	Up to 5 distinct lateral denticles, cusp well delineated	Relatively short, bent, swollen	Short, inserts into a short vas deferens at a relatively long distance from penial sheath. Penis conical, unarmed	On a short stalk, with only weakly distinct reservoir, in a more proximal position	NE Pacific from Alaska to California, shallow waters
***C. denbei* sp. nov.**	7 mm (preserved)	Brownish to dark-reddish, tips with ring-shaped opaque white pigment	6, unbranched	19 × 0.1.0	Up to 7 distinct lateral denticles, cusp well delineated	Relatively short, swollen	Relatively short, inserts into a moderately long vas deferens at a long distance from penial sheath. Penis conical, unarmed	On a short stalk, pear-shaped	Middle Kuril Islands, shallow waters
***C. elenae* Martynov, 2000**	45 mm (preserved)	Unknown	15, branched and unbranched	26 × 0.1.0	Up to 7 distinct lateral denticles, cusp not well delineated	Consists of few short reservoirs	Short, inserts into a very long vas deferens at a considerable distance from penial sheath. Penis very wide, unarmed, but with several triangular papillae around opening	On a very long stalk, small, drop-shaped	Chukchi Sea off Wrangel Island region, shallow waters

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TABLE 2 Morphological comparison of the species of the genus Cuthonella (*Cont.*)

Species	Body length (max)	Cerata colouration	Number of anterior branches of digestive gland (max) and its pattern	Radula formula (max)	Central teeth	Ampulla	Patterns of supplementary gland, vas deferens and penis	Rece-ptaculum seminis	Distribution
***C. georgstelleri* sp. nov.**	14 mm (preserved)	Light orange-brownish and salmon-brownish to dark, intensive brownish reddish, tips with extended opaque white band or spot	8, unbranched plus few branched	30 × 0.1.0	Up to 10 distinct lateral denticles, cusp well delineated	Relatively short, swollen	Long, inserts into a moderately long vas deferens at a considerable distance from penial sheath. Penis conical, unarmed	On a long stalk, compressed	Middle Kuril Islands, shallow waters
***C. hiemalis* (Roginskaya, 1987)**	26 mm (live)	From dark beige to dark brown, tips with peculiar opaque bluish subapical band or spot, without opaque white pigment	7, unbranched	23 × 0.1.0	Up to 12 distinct lateral denticles, cusp well delineated	Relatively long, folded, non-swollen	Long, inserts into long vas deferens at a considerable distance from penial sheath. Penis conical, unarmed	On a long massive stalk, oval	White Sea, shallow waters
***C. orientosiberica* sp. nov.**	4 mm (preserved)	Light brownish to yellowish in juveniles and brownish to dark brown in adults, tips whitish	6, unbranched	28 × 0.1.0	Up to 9 distinct lateral denticles, cusp well delineated	Relatively long, slightly folded, swollen	Long, inserts into a moderately long vas deferens at a considerable distance from penial sheath. Penis conical, unarmed	On a short stalk, oval	East Siberian Sea, Laptev Sea, shallow waters

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Species	Body length (max)	Cerata colouration	Number of anterior branches of digestive gland (max) and its pattern	Radula formula (max)	Central teeth	Ampulla	Patterns of supplementary gland, vas deferens and penis	Rece-ptaculum seminis	Distribution
C. osyoro **(Baba, 1940)**	23 mm (live)	Brownish to dark red or violet, tips with variously expressed red or orange band or spot, on ceratal surface white streaks or dots may be present	6, unbranched	26 × 0.1.0	Up to 11 distinct lateral denticles, cusp well delineated	Moderately short, bent, swollen	Long, inserts into a moderately long vas deferens at a considerable distance from penial sheath. Penis conical, unarmed	On short stalk, rounded	The Sea of Japan and neighbouring waters, shallow waters
C. punicea **(Millen, 1986)**	24 mm (live)	From purple to dark wine-red, with white spots or streaks, tips with dispersed white	8, branched and unbranched	20 × 0.1.0	Up to 7 distinct lateral denticles, cusp clearly delineated from the adjacent first lateral denticles	Relatively long, swollen	Long, inserts into a long vas deferens at a considerable distance from penial sheath Penis long, narrow, unarmed	On a moderately long stalk, elongate	NE Pacific, so far known only from British Columbia, shallow waters
C. sandrae **sp. nov.**	4 mm (preserved)	Violet-purple, tips with dispersed white and bluish hue	7, branched	12 × 0.1.0	Up to 8 distinct lateral denticles, cusp relatively unclear delineated from the adjacent first lateral denticles.	Unknown	Unknown	Unknown	Middle Kuril Islands, shallow waters

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TABLE 2 Morphological comparison of the species of the genus Cuthonella (*Cont.*)

Species	Body length (max)	Cerata colouration	Number of anterior branches of digestive gland (max) and its pattern	Radula formula (max)	Central teeth	Ampulla	Patterns of supplementary gland, vas deferens and penis	Rece-ptaculum seminis	Distribution
C. soboli **Martynov, 1992**	30 mm (live)	From light brownish and sandy to tobacco- and dark-brown, basal part commonly darker, white spots or streaks on ceratal external surface, tips colourless or with dispersed white pigment	6, unbranched, (in some specimens a few can be branched)	29 x 0.1.0	Up to 10 distinct lateral denticles, cusp well delineated	Moderately long, slightly bent, swollen	Long, inserts into a moderately long vas deferens at a considerable distance from penial sheath. Penis conical, unarmed	On a moderately long stalk, pear-shaped	The Sea of Japan and neighbouring waters, shallow waters
C. vasentsovichi **sp. nov.**	21 mm (preserved)	Greyish to light greenish, tips yellowish	10(+), branched and unbranched	40 × 0.1.0	Up to 9 distinct lateral teeth, cusp well delineated	Relatively short, partially swollen	Relatively short, inserts into a moderately long vas deferens at a considerable distance from penial sheath. Penis conical, unarmed	On a short stalk, oval	Middle Kuril Islands, shallow waters

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Discussion

Cold-water biodiversity hotspot: the Cuthonella case

In the past five years, our knowledge of the nudibranch fauna of the Arctic Sea and the Northwest Pacific Ocean has advanced substantially (e.g., Martynov et al., 2015a, b, 2020b; Korshunova et al., 2016a, b, 2017a, c, 2018a, b). Prior to that, *Cuthonella* species from these areas, such *C. hiemalis* and *C. soboli,* were shown to have direct development, i.e. without a planktonic stage (Roginskaya, 1987; Martynov, 1992). Although we have no data for the developmental patterns of our newly described species from the NW Pacific, five of them belong to the same clade as *C. hiemalis* and *C. soboli* according to our molecular data (figs 1, 2). Therefore, it is plausible to suggest that these species may also have direct or a shortened planktonic development as they inhabit essentially the same cold-water environment. Direct development implies limited dispersal capabilities, and hence more opportunities to form separate species. For other marine invertebrates, an increasing rate of speciation has been linked to direct development (e.g., Hurtado et al., 2017).

Thorson (1950), in his study of the reproductive and larval ecology of marine bottom invertebrates, concluded that direct or other non-feeding development is the dominate reproductive mode in polar waters. Therefore, a higher proportion of direct-development nudibranch species might be found in cold-water and polar regions. Although "Thorson rule" has been contested, recent broad-scale analyses confirm its validity in several groups (e.g. Fassio et al., 2019). Alternately, planktonic development has been noted for *C. concinna* s.l., *C. cocoachroma* and *C. punicea* (Thompson & Brown, 1984; Goddard, 1992; Millen, 1986), however these three species occur in relatively temperate conditions of the North Atlantic and the NE Pacific respectively, compared to the very cold NW Pacific (including the Kuril Islands), where negative sea water temperatures can occur in the wintertime. The Kuril Islands group, including Matua Island, are a chain of active volcanic islands (e.g., Blokh et al., 2018). They are located on the edge of the continental shelf and are in the confluence of the southward flowing Oyashio current and the Western Subarctic gyre (Qiu, 2001). Matua is a small island, only about 11 × 6.5 km, essentially just the top of a volcano.

Five new species (*C. ainu* sp. nov., *C. denbei* sp. nov., *C. georgstelleri* sp. nov., *C. sandrae* sp. nov. and *C. vasentsovichi* sp. nov., see descriptions above, figs 1, 2, 6, 10, 11, 16, 18, 21) were discovered in the shallow waters of this island, plus the new species *C. benedykti* sp. nov was discovered from a neighbouring Kamchatka locality (figs 7, 21). This peculiar geologic composition and the geographic position between the warm Japanese waters with abundant fauna, the Arctic sea, and the oceanic currents, supports a high abundance of marine life and active speciation.

We therefore suggest that the cold-water biodiversity hotspot exemplified by the cuthonellids is a result of the special biogeographic conditions coupled with direct development among some species. Because several *Cuthonella* species occur sympatrically in a restricted area, we suggest that they could have originated by a direct-development-driven evolution in isolated narrow areas in relatively remote parts of the middle Kuril Islands and adjacent regions. In contrast, for the North Atlantic subspecies from temperate waters such as *C. concinna concinna*, planktonic development has been documented (Roginskaya, 1987; Martynov & Korshunova, 2011). This suggests a case of allopatric speciation between the North

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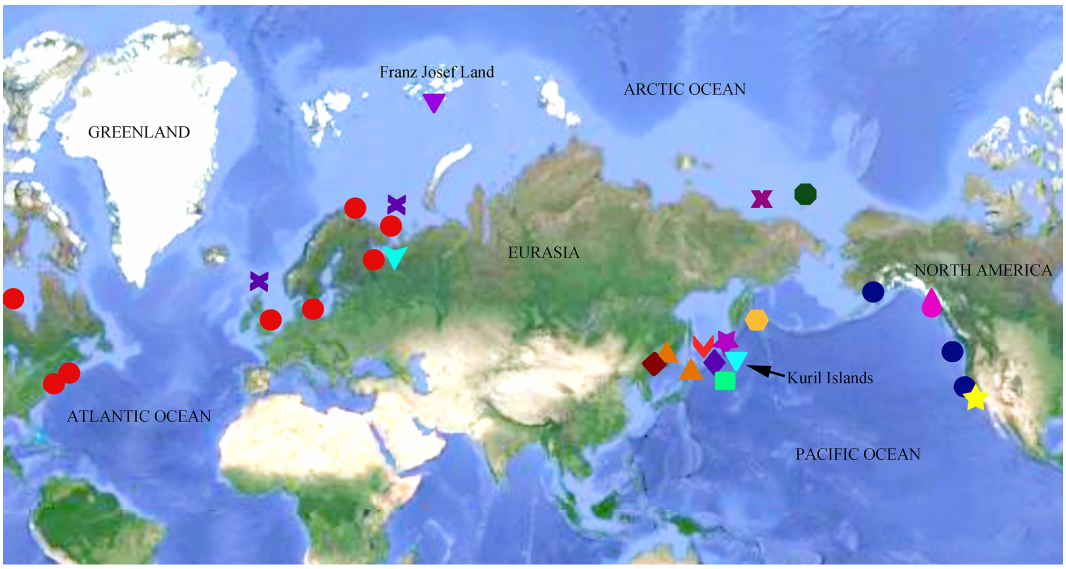

FIGURE 21 World map showing the distribution of *Cuthonella* species. Coloured symbols are indicated on the figure.

Atlantic *C. concinna concinna* and its sister NE Pacific subspecies *C. concinna bellatula* subsp. nov. Allopatric speciation has previously been well documented from various species of nudibranchs (e.g., Korshunova et al., 2018b, 2020a). The reasons why the biodiversity hotspot for cuthonellids in the Middle Kuril Islands has not been recognised before can be explained by both insufficient sampling and a deficit of taxonomic reviews for this region.

Taxonomy of Cuthonella: a morphological prediction and molecular confirmation

The genus *Cuthonella* Bergh, 1884 was until quite recently only considered valid by a few authors (e.g., Odhner in Franc, 1968; Miller, 1977), especially after the genus *Cuthonella* was synonymized with the genus *Cuthona* (Millen, 1986). After 1986, *Cuthonella* was replaced by *Cuthona* Alder & Hancock, 1855 in descriptive papers and guide books (e.g., Behrens & Hermosillo, 2005). However, in 1992 it was shown that the genus *Cuthonella* differs considerably from the genus *Cuthona* and from any other genera of the traditional tergipedids according to the morphology of the reproductive system and so it was considered a valid taxon (Martynov, 1992, 2002, 2006b; Martynov & Korshunova, 2011) (fig. 22A).

Only since the work of Martynov (1992) was a diagnosis for the genus provided which characterized the genus (fig. 22A). The genus

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Cuthonella was expanded to encompass not only the deep-sea type species, but also shallow-water species such as *C. concinna* s.l., *C. hiemalis*, *C. punicea* and *C. soboli*. Recently, the validity of the genus *Cuthonella* was supported by molecular phylogenetic studies (Korshunova et al., 2017b, 2018a; Martynov et al., 2020a), albeit with few species involved. In the present study, we confirm the validity and monophyly of the genus *Cuthonella* by involving a considerably broader species diversity of the genus (figs 1, 2, 21). This is the largest expansion of the number of species of the genus *Cuthonella* since 1992 and one of the largest recent expansions of described diversity among northern nudibranchs.

Here we present novel molecular data for a species that is morphologically similar to *C. abyssicola*, the type species of the genus *Cuthonella*. It is separated here as *C. abyssicola kryos* subspec. nov. This subspecies clusters together with other species included in this study, forming a well-supported monophyletic group (fig. 1). In total, we obtained and analysed molecular data for 13 of the 15 currently recognised species of the genus. For all species of *Cuthonella*, except for *C. cocoachroma* (which was unavailable for our morphological study), we confirmed that the supplementary gland in the male part of the reproductive system is inserted into the vas deferens instead of the penis. Hence, this is a well-supported morphological synapomorphy for the genus *Cuthonella*. For *C. cocoachroma*, Williams & Gosliner (1979) reported that the supplementary gland inserts into the penis instead of the vas deferens. Since the insertion of the supplementary gland into the vas deferens is a very stable morphological character among species in the genus *Cuthonella* according to our data, there are at least two possibilities for *C. cocoachroma*. The first is that in this species, a supplementary gland inserting into the penis has evolved in parallel to the families Cuthonidae and Cuthonellidae. The second is that the supplementary gland in *C. cocoachroma* in reality inserts into the vas deferens, but closer to the penis, and this was missed by Williams & Gosliner (1979). Except for this detail, the genus *Cuthonella* appears to be very consistent internally among all examined species, with the presence of an unarmed penis and protruding radulae cusps in most of the species.

External morphological features vary considerably within the species of the genus *Cuthonella*. The type species, *Cuthonella abyssicola* s.l., and some species such as *C. sandrae* sp. nov. and *C. punicea,* possess branched anterior ceratal rows and may have a cleioproctic anus. Instead, other species, such as *C. ainu* sp. nov.*, C. benedykti* sp. nov.*, C. hiemalis*, *C. concinna* s.l., *C. soboli*, and *C. osyoro*, possess unbranched anterior ceratal rows and an acleioproctic anus. The correlation of these features with molecular phylogenetic data is quite a mosaic (figs 1, 2, 4 –9, 14, 17), so at this stage we have not separated more genera, but retained just the one the genus *Cuthonella* within the family Cuthonellidae, though with more data more genera will most likely be necessary. Therefore, we do not synonymise the previously established subgenus *Fiocuthona* with the type species *C. concinna* s.l. (Martynov, 1992) or further differentiating the taxonomic structure of the family Cuthonellidae pending more data from other species.

In total, the species diversity within the genus *Cuthonella* has now increased over threefold, from five valid species (Martynov, 1992) plus two which are verified here as synonyms, *C. marisalbi* (Roginskaya, 1963) and *C. distans* (Odhner, 1922), to the current 15 species and two subspecies (figs 1, 2, 21), thus confirming the phylogenetic pattern of the almost 30-year-old prediction based on morphology (Martynov, 1992).

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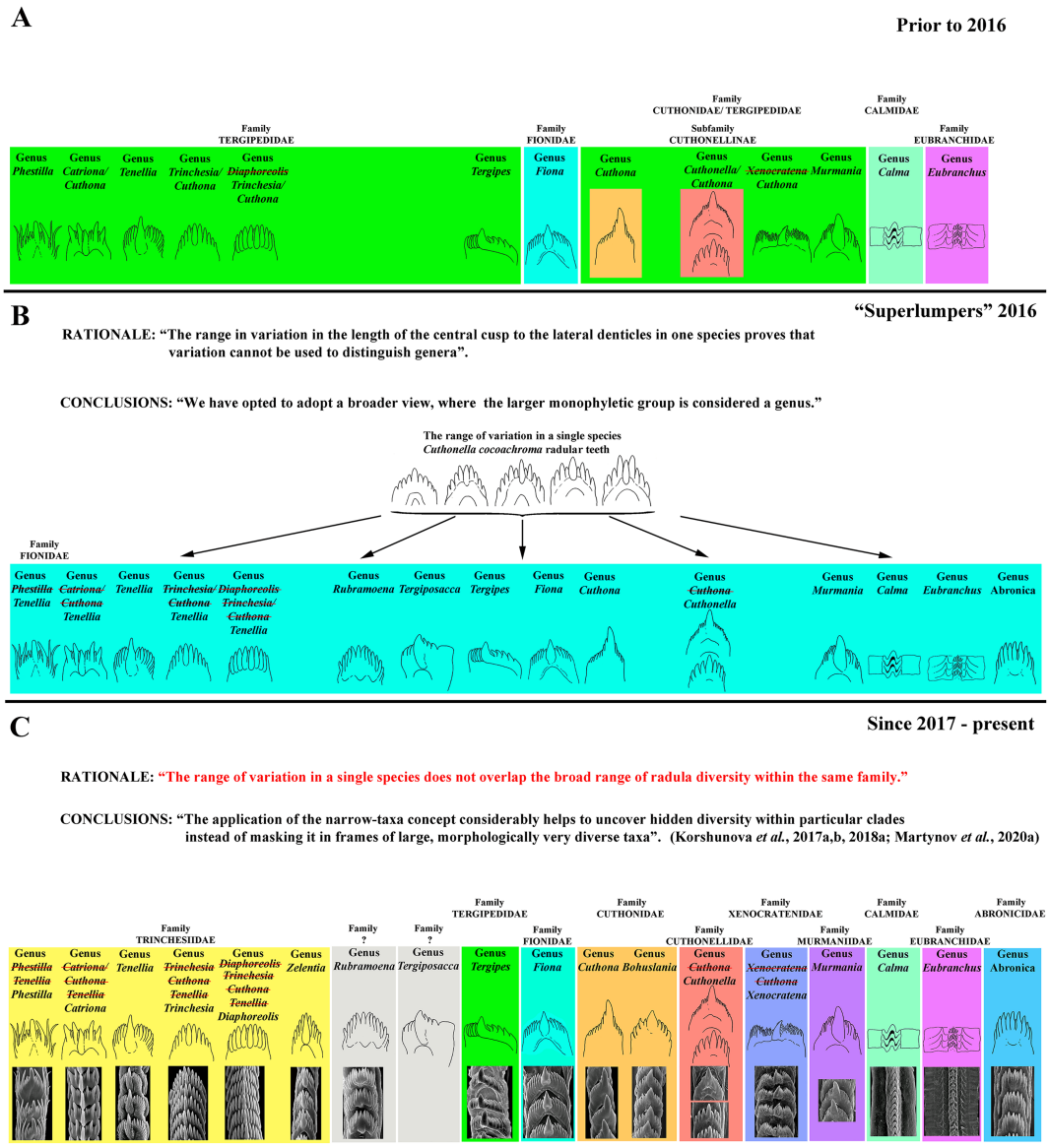

FIGURE 22 Discussion of the radula characters and fine-scale diagnostics in the taxonomy of the former "tergipedid" families. A. Taxonomic composition of the tergipedid aeolidacean nudibranchs before 2016. B. A 'superlumping' aggregation of the "family Fionidae *sensu latissimo*" (Cella et al., 2016; Epstein et al., 2019) lacking morphological apomorphies. C. Modern fine-scale tergipedid taxonomy that integrates molecular data and provides morphological apomorphies for several separate families and genera (Korshunova et al., 2017a, b; 2018a,b, 2019a, b; Mehrotra et al., 2020). The crossed-out taxon names signify a change in the genus status, the normally displayed names signify valid taxa at every consequential level of the history of the taxonomy of this group. All drawing schemes and SEM images are original.

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Fine-scale differentiation of the family Cuthonellidae

One practical question should be particularly addressed in respect to the revision of the genus *Cuthonella*. Marcus (1958) noted that the degree of protrusion of the central cusp of the radular teeth can vary within the same species among the traditional "tergipedid" group. Recently, Korshunova et al. (2017a) demonstrated that various genera or groups of genera, particularly within the family Trinchesiidae, have their own peculiar patterns of radular teeth, not just because of the degree of the relative height of the central cusp and lateral teeth, but also because of patterns that integrate several specific traits.

For example, the genera *Trinchesia* s.str. and *Diaphoreolis* have arch-shaped teeth with the central cusp similar in length to the central teeth. The genus *Catriona,* as another example, has a central cusp, not just lower than the lateral denticles but strongly retracted, making the general shape of the teeth a distinctive trait (fig. 22). The genus *Phestilla* also has a special combination of long needle-like teeth and a lower central cusp covered with smaller denticles (fig. 22). None of these trinchesiid radular patterns show similarity to those of the family Cuthonellidae and the genus *Cuthonella* (fig. 22B). The genus *Tenellia* s.str. (the family Trinchesiidae, fig. 22C) has a peculiar tooth shape, displaying only little variation, contrary to the statement in Epstein et al. (2019).

According to the molecular phylogenetic data, the family Cuthonellidae forms a well-supported clade, which is only distantly related to the Trinchesiidae (Korshunova et al., 2017b, 2018a; Martynov et al., 2019, 2020a). When more of the diversity within the essentially tropical Trinchesiidae and cold-water Cuthonellidae will be investigated, with successively finer differentiated characters and an increasing number of monophyletic subclades, it will be necessary to establish more genera. The old notion that if genera have some putative overlap of morphological patterns (Mayr, 1969; Gosliner & Griffiths, 1981) they should be merged into a single large genus, without morphological apomorphies (fig. 22B), is counterproductive to phylogenetic investigation.

Obviously, with such an approach an integrative taxonomy involving morphology and molecular analysis will be contradictory. We have already clearly demonstrated this fact for the "superlumping" concept of the "family Fionidae" s.l. (fig. 22), which has no reliable morphological apomorphies (see discussion in Korshunova et al., 2017a). Only narrower, more finely defined taxa of genus- and family groups can be used to integrate morphological and molecular data (Korshunova et al., 2017b, 2020a, b, c) (fig. 22C).

These integrative arguments were not understood and were contradicted recently and labelled "cumbersome" and based on "dubious, minor characters" by Epstein et al. (2019). Notably, it was a reverse reiteration of the argument from our previous study (Martynov, 1992) regarding the genus *Cuthona*: "if (one) does not intend to create a cumbersome, unnatural genus *Cuthona*, it is necessary to apply a less lumping approach than what has been applied by most of the recent authors" (translated from Russian; Martynov, 1992: 23). Further molecular analysis (see discussions in Korshunova et al., 2017a, 2018a, b, c; Martynov et al., 2020a) confirmed the conclusions of that almost 30-year-old study. The "*Cuthona sensu lato*" was revealed as a large polyphyletic assemblage and *Cuthona* s.str. was then limited to only a few morphologically similar species. Importantly, the genus *Cuthonella* was shown to be neither closely related to *Cuthona* nor *Trinchesia*. When defining the characters of the "family Fionidae sensu latissmo" Cella et al. (2016) (fig. 22B) used characters that are not present in the type genus *Fiona*, like a

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penial gland, and hence the real Fionidae s.str. has a reproductive system as well as patterns of external morphology that are drastically different from any other "Fionoidea". In table 3 of our 2017 study (Korshunova et al., 2017a) we mentioned the relative height of the central cusp and formally described the differences in the shape of the teeth along with several other characters, and thus did not build a classification solely on a single character. Moreover, Eubranchidae have a triserial radula, Calmidae have radula with fused teeth, and both conditions are very different from the uniserial radula of *Cuthonella* (fig. 22C). Furthermore, Epstein et al. (2019) based their arguments on an older drawing based on light microscopy studies in Williams & Gosliner (1979, fig. 5) without any additional SEM study.

To present modern comparative morphological data, in this study we made a thorough SEM investigation of a majority of the species of the genus *Cuthonella* (figs 4–18). We specially show that in some species of *Cuthonella*, e.g., *C. concinna* s.l., *C. denbei* sp. nov., and *C. osyoro*, the relative height of the central cusp and lateral denticles can vary to some degree between the anterior and posterior teeth (figs 8O–R, 10G –I, 14J–L), but they never attain any similarity in the general radular pattern to any of the trinchesiid genera (fig. 22).

Furthermore, in this study we made a novel review of data for all species of the genus *Cuthonella*, including seven new ones (figs 1–21), and none of the species possess radular teeth that have a similar pattern to any trinchesiid genera (Korshunova et al., 2017a) (fig. 22C). Therefore, the conclusion that the shape of the radular teeth cannot be used as taxonomic characters in Fionoidea (fig. 22B) is incorrect, and to the contrary, these characters are very useful for taxonomy in an integrative context. It is important to highlight that it is pointless to make a classification using only radular characters and to argue that if radulae among some taxa demonstrate some similarities or similar variabilities these taxa must automatically be synonymized.

Instead, every taxon at the family- and genus-level demonstrates a complicated multilevel mosaic of morphological characters (including potentially a big disparity between characters of different organ systems) and molecular features. Any diagnosis that professes to encompass a complex evolutionary history in a classification must be based on such multilevel differences, and not on simplistic binary alternatives such as "presence" or "absence", "lower" or "higher" or on an overestimated "variability".

Recently, the obvious problems of the 'superlumping' approach were revealed within the large aeolidacean group in which a very complex molecular pattern was shown to be aligned with an extremely mosaic distribution of morphological characters (Korshunova et al., 2017b, 2019a, b; Martynov et al., 2020a). In conclusion, to have a 'superlumping' name for such a group, one has to go much further than to unite many disparate taxa into a single "family Fionidae" but to unite all order-level diversity of the Aeolidacea into a single family, Aeolidiidae. This would lead to a morphologically non finely diagnosable group, with only the most general potential apomorphy (possession of a cnidosac at the extremity of each ceras) which corresponded to the taxonomic level of order/suborder, and not to the family level, because a majority of aeolidaceans from any family possess a cnidosac.

However, even such a potential general apomorphy would be problematic since several non-related genera lack cnidosacs, e.g., *Phestilla* Bergh, 1874 in the family Trinchesiidae or *Phyllodesmium* Ehrenberg, 1831 in the family Myrrhinidae. In contrast, when separating many finely defined

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families and genera, including Abronicidae, Calmidae, Cuthonellidae, Cuthonidae, Eubranchidae, Fionidae s.str., Tergipedidae, Trinchesiidae, Xenocratenidae, Murmaniidae, and potentially several others (fig. 22C), it facilitates making complex morphological diagnoses and a list of morphological apomorphies that is maximally consistent. Importantly, it is also concordant with the molecular data. Every narrowly defined family and genus has its own set of finely scaled characters, that, if taken separately, may be incorrectly considered "overlapping" ones.

The pitfalls of the 'superlumping' approach can immediately influence practical taxonomy. For example, the maximally broad approach that evoked the single huge "family Fionidae" (which then "overlaps" by almost all possible morphological apomorphies with all other aeolid families, see Korshunova et al., 2017a, 2019a) led to the result (Cella et al., 2016) of failing to distinguish two externally similar taxa with drastically different internal morphologies: *Cuthonella punicea* (Millen, 1986) and *Zelentia nepunicea* Korshunova et al., 2018.

Thus, the maximally broad approach (e.g., Williams & Gosliner, 1979; Epstein et al., 2019) not only "does not permit other users of the classification (largely other comparative biologists) to identify taxa readily from living examples", but clearly misleads nudibranch taxonomists per se. Alternately, the fine-scale approach of numerous narrowly-defined families and genera easily avoids such pitfalls: *Cuthonella punicea* belongs to the family Cuthonellidae, whereas *Zelentia nepunicea* belongs to the family Trinchesiidae. Both families have a minimally overlapping particular set of morphological characters (which of course are not absolutely "stable" because of the continuing evolutionary process) and show significant molecular divergence, and thus are only distantly related to each other (Korshunova et al., 2017a, b, 2018a, b, 2019b).

Most recently, our fine-scale approach was supported by an independent study of the tropical trinchesiid genus *Phestilla* (Mehrotra et al., 2020). The review presented here of the genus *Cuthonella* and the family Cuthonellidae is therefore of high relevance for demonstrating the benefits of this approach, since this is a properly narrow family and genus, whose validity has been confirmed first by using morphological data (Martynov, 1992; Martynov & Korshunova, 2011) then recently by the application of molecular data in Korshunova et al. (2018a) and finally by the addition of seven new species and two new subspecies detailed in this study.

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Appendix

TABLE A1 Primers

Name	5′→3′	References	Program
LCO 1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al., 1994	95° C 60 s, 35× (95° C 15 s, 45° C 15 s, 72° C 30s), 72° C 7 min
HCO 2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al., 1994	
16S arL	CGCCTGTTTAACAAAAACAT	Palumbi et al., 2002	95° C 3 min, 40× (94° C 15 s, 52° C 15 s, 72° C 30s), 72° C 7 min
16S R	CCGRTYTGAACTCAGCTCACG	Puslednik & Serb, 2008	
H3 AF	ATGGCTCGTACCAAGCAGACGG	Colgan et al., 1998	95° C 3 min, 40× (94° C 15 s, 52° C 15 s, 72° C 30s), 72° C 7 min
H3 AR	ATATCCTTGGGCATGATGGTGAC	Colgan et al., 1998	
28S C1	ACCCGCTGAATTTAAGCAT	Dayrat et al., 2001	95° C 3 min, 40× (94° C 15 s, 50° C 15 s, 72° C 30s), 72° C 7 min

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TABLE A2 List of samples, localities, and voucher references.

Species name	Voucher	Locality	COI	16S	H3	28S
Calma glaucoides (Alder & Hancock, 1854)	ZMMU:Op-603	Norway	MG323544	MG323550	MG323565	-
Calma glaucoides (Alder & Hancock, 1854)	CPIC00562	-	JQ699567	JQ699477	JQ699388	-
Cuthonella abyssicola kryos subsp. nov.	ZMMU:Op-727	Russia: Franz Josef Land	**MW150847**	**MW158728**	**MW158323**	**MW158713**
Cuthonella ainu sp. nov.	ZMMU:Op-618	Russia: Matua	**MW150866**	**MW158746**	**MW158334**	**MW158725**
Cuthonella benedykti sp. nov.	ZMMU:Op-194	Russia: Kamchatka	**MW150867**	**MW158747**	**MW158322**	**MW158726**
Cuthonella benedykti sp. nov.	WS3452	Russia: Kamchatka	KY129023	KY128814	KY128608	-
Cuthonella benedykti sp. nov.	WS3450	Russia: Kamchatka	KY129019	KY128810	KY128594	-
Cuthonella cocoachroma (Williams & Gosliner, 1979)	CAS179471	USA: California	KY128925	KY128720	KY128513	-
Cuthonella cocoachroma (Williams & Gosliner, 1979)	CAS185193	USA: California	KY128931	KY128726	KY128519	-
Cuthonella cocoachroma (Williams & Gosliner, 1979)	CAS181307b	USA: California	KY128927	KY128722	KY128515	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	KM767	Norway: Finnmark	**MW150854**	-	-	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	GNM8866	Sweden	MG323543	MG323549	MG323564	MG323555
Cuthonella concinna concinna (Alder & Hancock, 1843)	KM452	Russia: Barents Sea	**MW150851**	**MW158732**	**MW158327**	**MW158715**
Cuthonella concinna concinna (Alder & Hancock, 1843)	KM453	Russia: Barents Sea	**MW150852**	**MW158733**	**MW158328**	**MW158716**
Cuthonella concinna concinna (Alder & Hancock, 1843)	WS3444	Russia: Barents Sea	KY129013	KY128817	KY128611	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	WS3445	Russia: Barents Sea	KY129014	KY128805	KY128612	-

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TABLE A2 List of samples, localities, and voucher references. (*Cont.*)

Species name	Voucher	Locality	COI	16S	H3	28S
Cuthonella concinna concinna (Alder & Hancock, 1843)	ZMMU:Op-523	Russia: White Sea	MF523377	MF523459	MF523302	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	WS3449	Russia: White Sea	KY129018	KY128808	KY128603	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	WS3443	Russia: White Sea	KY129012	KY128804	KY128600	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	WS3447	Russia: White Sea	KY129016	KY128807	KY128602	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	KM616	UK	**MW150853**	**MW158734**	-	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	09PROBE-00278	Canada: Churchill	KF644266	-	-	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	CAS182701	USA: New Hampshire	KY128933	KY128728	KY128521	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	CAS182702	USA: Maine	KY128934	KY128729	KY128522	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	CAS183926	USA: Maine	KY128935	KY128730	KY128523	-
Cuthonella concinna concinna (Alder & Hancock, 1843)	CAS183932	USA: Maine	KY128936	KY128731	KY128524	-
Cuthonella concinna bellatula subsp. nov.	CAS181522b	USA: Alaska	KY128932	KY128727	KY128520	-
Cuthonella concinna bellatula subsp. nov.	CAS179469	USA: California	KY128924	KY128719	KY128512	-
Cuthonella concinna bellatula subsp. nov.	CAS181307a	USA: California	KY128926	KY128721	KY128514	-
Cuthonella concinna bellatula subsp. nov.	CAS181307d	USA: California	KY128929	KY128724	KY128517	-
Cuthonella concinna bellatula subsp. nov.	ZMMU:Op-728	USA: Washington	**MW150848**	**MW158729**	-	**MW158714**
Cuthonella concinna bellatula subsp. nov.	ZMMU:Op-729	USA: Washington	**MW150849**	**MW158730**	-	-
Cuthonella concinna bellatula subsp. nov.	ZMMU:Op-740	USA: Washington	**MW150850**	**MW158731**	-	-

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Species name	Voucher	Locality	COI	16S	H3	28S
Cuthonella denbei sp. nov.	ZMMU:Op-673	Russia: Matua	**MW150868**	**MW158748**	**MW158331**	**MW158727**
Cuthonella denbei sp. nov.	ZMMU:Op-674	Russia: Matua	**MW150869**	**MW158749**	**MW158332**	-
Cuthonella denbei sp. nov.	ZMMU:Op-730	Russia: Matua	**MW150870**	**MW158750**	-	-
Cuthonella georgstelleri sp. nov.	ZMMU:Op-672	Russia: Matua	**MW150860**	**MW158740**	**MW158329**	**MW158721**
Cuthonella georgstelleri sp. nov.	ZMMU:Op-670	Russia: Matua	**MW150861**	**MW158741**	**MW158330**	**MW158722**
Cuthonella georgstelleri sp. nov.	ZMMU:Op-731	Russia: Matua	**MW150862**	**MW158742**	-	-
Cuthonella hiemalis (Roginskaya, 1987)	ZMMU:Op-186	Russia: White Sea	MG323545	MG323551	-	MG323556
Cuthonella hiemalis (Roginskaya, 1987)	WS3439	Russia: White Sea	KY129008	KY128800	KY128596	-
Cuthonella hiemalis (Roginskaya, 1987)	WS3440	Russia: White Sea	KY129009	KY128801	KY128597	-
Cuthonella hiemalis (Roginskaya, 1987)	WS3441	Russia: White Sea	KY129010	KY128802	KY128598	-
Cuthonella hiemalis (Roginskaya, 1987)	WS3438	Russia: White Sea	KY129007	KY128799	KY128595	-
Cuthonella hiemalis (Roginskaya, 1987)	WS3442	Russia: White Sea	KY129011	KY128803	KY128599	-
Cuthonella osyoro (Baba, 1940)	ZMMU:Op-524	Russia: Sea of Japan	MF523378	MF523457	MF523303	MF523523
Cuthonella osyoro (Baba, 1940)	ZMMU:Op-604	Russia: Sea of Japan	MG323546	MG323552	MG323566	MG323557
Cuthonella osyoro (Baba, 1940)	ZMMU:Op-606	Russia: Sea of Japan	**MW150855**	**MW158735**	**MW158325**	**MW158717**
Cuthonella osyoro (Baba, 1940)	ZMMU:Op-607	Russia: Sea of Japan	**MW150856**	**MW158736**	**MW158326**	**MW158718**
Cuthonella osyoro (Baba, 1940)	WS3453	Russia: Sea of Japan	KY129024	KY128815	-	-
Cuthonella osyoro (Baba, 1940)	WS3451	Russia: Sea of Japan	KY129021	KY128812	KY128606	-
Cuthonella punicea (Millen, 1986)	KM765	Canada: British Columbia	**MW150857**	**MW158737**	-	-
Cuthonella punicea (Millen, 1986)	KM766	Canada: British Columbia	**MW150858**	**MW158738**	**MW158337**	**MW158719**
Cuthonella sandrae sp. nov.	ZMMU:Op-671	Russia: Matua	**MW150863**	**MW158743**	**MW158333**	**MW158723**
Cuthonella soboli Martynov, 1992	ZMMU:Op-605	Russia: Sea of Japan	**MW150859**	**MW158739**	**MW158324**	**MW158720**
Cuthonella vasentsovichi sp. nov.	ZMMU:Op-739	Russia: Matua	**MW150865**	**MW158745**	**MW158336**	**MW158724**
Cuthonella vasentsovichi sp. nov.	ZMMU:Op-738	Russia: Matua	**MW150864**	**MW158744**	**MW158335**	-
Murmania antiqua Martynov, 2006	ZMMU:Op-399	Russia	MF523390	MF523394	MF523315	MF523470
Xenocratena suecica Odhner, 1940	GNM9816	Sweden	MN850079	MN850072	MN850055	MN850062
Xenocratena suecica Odhner, 1940	GNM9770-1	Norway	MN850080	MN850073	MN850056	MN850063
Xenocratena suecica Odhner, 1940	GNM9770-2	Norway	MN850081	MN850074	MN850057	MN850064

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